FEAR OF PARASITES: LONE STAR TICKS INCREASE GIVING-UP DENSITIES IN WHITE-TAILED DEER

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ABSTRACT
Nonconsumptive effects of predators on their prey are extensive and diverse, with significant consequences for community structure and ecosystem function. However, despite many theoretical similarities between predator–prey and host–parasite interactions, nonconsumptive effects of parasites on their hosts remain poorly understood. Further, such effects may be of consequence to human and wildlife health, when host–parasite interactions involve hematophagous arthropods that vector infectious diseases. We used giving-up density estimation techniques to measure the response of white-tailed deer (Odocoileus virginianus) to the risk of parasitism by lone star ticks (Amblyomma americanum), an important vector of several infectious diseases in the southeastern United States. We also deployed carnivore scent stations to estimate activity levels of potential deer predators, conducted deer dung count surveys to control for effects of deer abundance, and controlled for topographic aspect, a primary determinant of vegetative biomass and community composition. We found a significant, positive correlation between giving-up densities in deer and the densities of A. americanum, but no effect of canid predators, deer abundance, or topographic aspect. Our results are consistent with the few other empirical examples that demonstrate nonconsumptive effects of parasites on their hosts. Considering that host–parasite interactions have enormous potential to influence the prevalence of vector-borne diseases that affect human health, incorporating indirect effects of parasites on their hosts into infectious disease ecology may be necessary to effectively mitigate disease risk.

Keywords: Amblyomma americanum, white-tailed deer, giving-up density, Ozark ecosystem, host–parasite ecology, infectious disease ecology, ecology of fear

INTRODUCTION
Ecologists have increasingly recognized the importance of indirect effects in structuring ecological communities over the last two decades (Werner and Anholt, 1996). Among

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these indirect effects, nonlethal effects of predators on prey species (e.g., increased vigilance, altered habitat use), has become the subject of a rich body of literature, often referred to as the “ecology of fear” (Brown et al., 1999). Several studies now indicate that nonconsumptive effects of predators on communities can sometimes actually outweigh the direct effects of predation (Werner and Peacor, 2003; Pressier et al., 2005). However, few empirical or theoretical efforts have bridged the gap between nonlethal effects of predators on their prey and potentially parallel effects of parasites on their hosts despite the ubiquity of parasitism as one of the most common life-history strategies (Raffel et al., 2008; Rohr et al., 2009). Here, we define nonconsumptive effects of parasites on their hosts as any potential effects due to parasites other than the direct consumption of a host’s resources. One hypothesis for the lack of attention paid to potential nonconsumptive effects of parasites on their hosts is that antiparasite responses are often considered weaker than antipredator responses, since the consequences of parasitism are less often immediately fatal (Dobson and Hudson, 1986). However, parasitic infections can impose severe consequences on the survival and reproduction of hosts, and likely occur more frequently than predation events (Raffel et al., 2008). Therefore, the potential for parasites to strongly influence host fitness, and thereby alter community interactions of parasites on host movements and behavior, deserves further study for their potential impacts on larger scale processes (Mouritsen and Poulin, 2005).

In particular, interactions among wildlife hosts, arthropod vectors, and the pathogens they transmit are the subject of enhanced interest in community ecology because of the potential to forecast and mitigate human risk of exposure to vector-borne diseases (Ostfeld et al., 2008). Many studies now demonstrate that changes in host abundance and diversity can significantly impact human risk and incidence of vector-borne diseases (Ezenwa et al., 2006; Chaves et al., 2008; Suzan et al., 2009). However, in the study of community interactions affecting vector-borne disease dynamics, scant consideration is paid to the potential for nonconsumptive effects of vectors on host distributions. We postulate that such interactions may have profound consequences for human risk of exposure to vector-borne diseases, when parasites of wildlife hosts are also potential vectors of infectious diseases to humans. Altered movements and habitat use of wildlife hosts in response to the threat of parasitism could create shifting mosaics of vector-borne disease risk, confounding efforts to study and control infectious disease dynamics and resultant human exposure risk.

A host–parasite system that lends itself to exploring the role for parasites in the ecology of fear, with potential consequences for vector-borne disease risk, exists in the Ozark Ecosystem of the central United States. The lone star tick (Amblyomma americanum) is the most abundant ixodid tick in this ecosystem (Bacon et al., 2003), and white-tailed deer (Odocoileus virginianus) serve as both the preeminent host for all three life stages of A. americanum (Childs and Paddock, 2003) as well as the primary zoonotic reservoir for pathogens transmitted to humans by this tick species (Paddock and Yabsley, 2007). Additionally, A. americanum is the putative vector of several wildlife pathogens that may be agents of disease in deer, such as “white-tailed deer agent”, a nearly ubiquitous Anaplasma infection found in deer from this region (Arens et al., 2003). Natural preda-
tors of white-tailed deer in this landscape are few due to historical extirpations of large predator species by humans (Woodroffe, 2000). The remaining potential nonhuman predators are primarily mesocarnivores, including bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and both red (*Vulpes vulpes*) and grey foxes (*Urocyon cinereoargenteus*), some of which may pose a threat of predation to adult deer under some circumstances (e.g., Gese and Grothe, 1995), but primarily are predators of fawns (Beasom, 1974; Stout, 1982; Nelson and Woolf, 1987).

Efforts to quantify nonconsumptive effects of predators on their prey often rely upon estimation of giving-up densities (GUDs). Derived from optimal foraging theory (MacArthur and Pianka, 1966; Charnov, 1976), the use of GUDs to quantify predation risk depends upon the prediction that a consumer should leave a depletable resource patch when the benefits of harvesting resources no longer outweigh the metabolic, predation, and missed opportunity costs (Brown, 1988). Thus, if habitats possess similar resource levels, animals should spend more time foraging in safer habitats, and when offered a depletable food resource, they should “give up” more food in riskier environments (Brown, 1988; Kotler et al., 1993). While these predictions have been historically applied to the study of predation risk, we hypothesize that they may also be applicable to determining how hosts respond to the threat of parasitism. Here, we sought to test the hypothesis that white-tailed deer respond to the risk of tick parasitism, a potentially important selective force in forested landscapes of the eastern United States. Specifically, we used GUD estimation techniques to determine the risk perceived by deer among sites that varied considerably in densities of *A. americanum*. We also measured the activity levels of potential deer predators, and the abundance of deer themselves, to account for the potential contributions of each factor to GUDs of deer at our study sites. We predicted that deer would respond to the threat of tick parasitism, and modify their habitat use accordingly.

**MATERIALS AND METHODS**

**STUDY SITE**

This research was conducted June–August 2004 at the Tyson Research Center in Eureka (Saint Louis County), Missouri. Tyson Research Center is an 809 ha biological field station located on the northeastern end of the Ozark Highlands Plateau, 25 miles southwest of Saint Louis (38°31′N, 90°33′W). This region is dominated by oak–hickory forests on steep ridges and an herbaceous understory (Yang et al., 2008).

**STUDY DESIGN**

We selected three replicate ridges with slopes facing in each of the four cardinal directions for a total of 12 study sites at the Tyson Research Center. The direction a slope faces, or its “topographic aspect,” is one of the most important determinants of abiotic conditions, vegetative structure, and community composition in the Ozark Ecosystem (Ware et al., 1992). Generally, north- and east-facing slopes receive less direct sunlight,
and thus have moister soils with greater vegetative biomass, while south- and west-facing slopes tend to be drier and less heavily vegetated. Accordingly, we grouped the six south- and west-facing slopes, and the six north- and east-facing slopes, separately for statistical analyses (although treating all four separately did not qualitatively alter results).

**SURVEYS**

At each of these 12 study sites, we placed three GUD stations separated by ~50 m. GUD stations consisted of a ~15 L bucket, covered with wire mesh fencing (10 × 10 cm), weighed down with rocks and buried into the hillside. Each bucket was filled with 1200 grams of corn and an equal amount of inedible substrate (2.5 cm diameter pieces of PVC pipe) by volume. This substrate provided a depletable food patch with diminishing returns, fulfilling the requirement that foraging effort per unit time increases with time spent at a GUD station (Kotler et al., 1994). GUD stations were established in mid-June, and corn was replenished every other day for six weeks to allow deer to acclimate to the presence of these stations. From August 3 until August 20, 2004, GUD stations were monitored intensively every other day by measuring the amount of corn remaining at all 12 study sites to determine GUDs of white-tailed deer. For each study site, the amount of corn remaining was averaged across the three GUD stations for the 3-week time period, and log-transformed to linearize the data for statistical analyses.

The density of ticks at each study site was estimated by drag-sampling with a 1 m² white cloth dragged over three 100-m transects on each slope (Schulze et al., 1997). Ticks were removed with forceps every 20 m and placed in glass vials containing 70% ethanol for subsequent identification under a dissecting microscope. Tick surveys were conducted during the August 3–20 study period, coinciding with the peak in abundance for the larval life stage of *A. americanum* in Missouri (Kollars et al., 2000). The number of larval *A. americanum* collected at each study site was divided by the total area drag-sampled (300 m²) to obtain a relative density estimate. The drag-sampling method is highly accurate for estimating densities of the juvenile life-stages of *A. americanum* (Schulze et al., 1997).

Deer dung cluster surveys (White and Eberhardt, 1980) were conducted using the same three 100-m transects at each study site during August 3–20. Briefly, an investigator walked along each transect, counting any deer dung clusters (consisting of three or more pellets) visible within two meters of either side of each transect. The number of dung clusters observed was summed for the three transects at each site and square-root transformed (+0.5) to normalize the data for statistical analyses.

The activity of carnivores at each study site was estimated using carnivore scent stations, whereby 2.25 m² plastic sheets, weighed down at the corners by rocks, were covered in fine sand (Sargeant et al., 2003). In the center of each station a wood post was driven through the plastic sheet into the ground. The posts were then covered in petroleum jelly and baited with a fried chicken egg, and canine urine was placed on vegetation surrounding the station. The sand was maintained to form a smooth surface, such that visiting carnivores could be identified to species by the imprints of their tracks in the
sand (Elbroch, 2003). Carnivore scents stations were established mid-June and re-baited weekly to acclimatize carnivores to their presence. Weekly monitoring continued during the August 3–20 study period, with all visits by carnivores identified to species except for the two species of fox, which could not be distinguished. The numbers of visits by all carnivores were summed for the three week period and square-root transformed (+0.5) to normalize the data for statistical analyses.

**STATISTICAL ANALYSES**
We used Multivariate Analysis of Variance (MANOVA) to examine relationships between aspect (a categorical variable) and the density of larval *A. americanum*, deer density, and predator activity. We then used Analysis of Variance (ANOVA) to examine univariate relationships between aspect and these variables. Simple linear regressions were used to analyze relationships between continuous independent and dependent variables, including the relationship between the densities of larval *A. americanum* and giving-up densities in deer. Finally, we used Analysis of Covariance (ANCOVA) to examine the effects of aspect, and various continuously-measured covariates, including density of larval *A. americanum*, deer density, and predator activity, as well as any potential interactions among them, on the GUDs of deer.

**RESULTS**
Densities of larval life stage *A. americanum* varied considerably among the 12 study sites (range = 0.10–2.86 larvae/m², mean = 1.47 larvae/m²), indicating we successfully captured a strong gradient in risk of exposure to tick parasitism. Deer densities also varied considerably (range = 1–10 dung clusters per site, mean = 4.08). Carnivore scent stations were visited by raccoons (*Procyon lotor*), coyotes (*Canis latrans*), and either red (*Vulpes vulpes*) or grey foxes (*Urocyon cinereoargenteus*). For the purposes of estimating activity of potential deer predators, we used the total number of Canidae tracks (coyotes and foxes) only. Canid activity was also variable across sites (range = 0–4 visits, mean = 1.33).

A MANOVA indicated no significant, interactive effects of aspect on the density of deer, density of larvae, or activity of canids ($F_{(3,8)} = 3.089, p = 0.090$). Using ANOVA to test for direct correlations between aspect and the density of deer, the density of larvae, canid activity and the GUDs of deer, we did not find a significant effect of aspect on the density of deer ($F_{(1,10)} = 0.807, p = 0.390$), the density of larvae ($F_{(1,10)} = 2.720, p = 0.130$), or canid activity ($F_{(1,10)} = 2.553, p = 0.141$). The effect of aspect on the GUDs of deer also was not significant ($F_{(1,10)} = 0.898, p = 0.366$).

A significant, positive relationship was found between the density of *A. americanum* larvae and the GUDs of deer at our study sites (Linear Regression: $R^2 = 0.536, p = 0.007$; Fig. 1). There was no relationship between the density of deer and the density of larval *A. americanum* ($R^2 = 0.018, p = 0.674$), nor was there an effect of the density of deer ($R^2 = 0.013, p = 0.729$) or the activity of carnivores ($R^2 = 0.002, p = 0.886$) on the GUDs of deer.
Using an ANCOVA to control for the potentially interacting effects of aspect and other potentially important biotic covariates (density of larval *A. americanum*, density of deer and carnivore activity levels) on the GUDs of white-tailed deer, we found that aspect (north and east vs. south and west) was not a significant predictor of GUDs for deer (Table 1). Neither was the overall density of deer, as measured by dung cluster surveys. No relationship was found between the activity levels of carnivores and the GUDs of deer. No interaction terms were significant in various iterations of this model, including the most biologically plausible interaction between aspect and larval tick density, which was included in the final ANCOVA model (Table 1). The only significant predictor of deer GUDs in the ANCOVA model was the density of larval life stage *A. americanum*, which were strongly positively correlated with the amount of corn remaining at GUD stations during the study period (Table 1).

**DISCUSSION**

To our knowledge, GUD estimation techniques, which have been effectively used to document “landscapes of fear” in how prey respond to predation risk (e.g., Brown, 1988; Kotler et al., 1991, 1994; Altendorf et al., 2001; Ripple and Beschta, 2004), have not been previously applied to the study of nonconsumptive effects of parasites on their hosts. Thus it is noteworthy that we found a strong, positive correlation between the density of larval *A. americanum* ticks and the GUDs of white-tailed deer. We found neither
an effect of predator activity, nor an effect of topographical aspect, a key determinant of vegetative biomass and community composition, which suggests the observed effect was driven primarily by the response of deer to the threat of tick parasitism. Numerous behavioral mechanisms could account for this outcome in deer, including direct detection of parasite burdens (either visually or tactiley) or increased time allocated to grooming in parasite-rich environments at the expense of foraging efforts. The GUD approach may have been particularly appropriate for estimating the response of hosts to the threat of tick parasitism in our study system, since *A. americanum* will actively pursue hosts, even in the larval life stage (Schulze et al., 1997). Other tick species that passively quest for hosts may not measurably affect GUDs, since the cost to a host of remaining at a GUD station may not increase with time spent in proximity to passively questing parasites.

It is difficult to conclude whether this response is due to the threat of parasitism per se, or the risk of pathogen transmission, since *A. americanum* are also vectors of infectious diseases. Generally, host-seeking larval ticks are considered less likely to transmit pathogens, since they have not yet taken a blood meal from a host and thereby have not had the opportunity to acquire a horizontally transmitted pathogen. However, numerous pathogens are also transovarially transmitted in ticks (i.e., from mother to offspring), including at least one putative zoonotic pathogen associated with *A. americanum*, *Borrelia lonestari* (Stromdahl et al., 2003). Whether any pathogens transmitted by *A. americanum* that cause disease in white-tailed deer are transovarially transmitted remains unknown, though presumably would need to occur at high prevalence to be the causative mechanism behind this phenomenon. It would be informative to repeat our experiment during the peak in abundance of nymph and adult life stage *A. americanum*, which are considerably more likely to be infected with pathogenic organisms (Mixson et al., 2006). However, the impact of tick parasitism alone may bear significant fitness consequences. Anemia due to extensive tick burdens has been shown to severely limit production in livestock systems (Barnard, 1985; Ervin et al., 1987). White-tailed deer in

Table 1
General linear model analysis of covariance associating the giving-up densities of white-tailed deer with abiotic and biotic components of 12 forested study sites at the Tyson Research Center in Saint Louis, Missouri

<table>
<thead>
<tr>
<th>Type III tests of fixed effects</th>
<th>Sum-of-Squares</th>
<th>F-ratio</th>
<th>d.f.</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspect (NE vs. SW)</td>
<td>6.605</td>
<td>3.069</td>
<td>1</td>
<td>0.130</td>
</tr>
<tr>
<td>Covariates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. americanum</em> larvae/m²</td>
<td>23.144</td>
<td>10.754</td>
<td>1</td>
<td>0.017</td>
</tr>
<tr>
<td>Deer dung clusters</td>
<td>1.133</td>
<td>0.526</td>
<td>1</td>
<td>0.495</td>
</tr>
<tr>
<td>Canidae visits</td>
<td>4.687</td>
<td>2.178</td>
<td>1</td>
<td>0.190</td>
</tr>
<tr>
<td>Aspect × <em>A. americanum</em> larvae/m²</td>
<td>6.873</td>
<td>3.194</td>
<td>1</td>
<td>0.124</td>
</tr>
<tr>
<td>Error</td>
<td>12.912</td>
<td></td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>
the Ozark region often suffer substantial tick burdens (Kollars et al., 2000), which can cause injury and even death (Bolte et al., 1970).

It is interesting, although perhaps not surprising, that we found no relationship between the abundance of deer and the density of larval *A. americanum* during the study period. The distribution of larval ticks is expected to reflect the availability of hosts for adult female ticks (primarily deer for *A. americanum*) earlier in the year during the adult peak in abundance (March–April in Missouri; Kollars et al., 2000). Since the larval life stage cannot travel significant distances, the locations at which adult female ticks drop-off hosts to oviposit should determine the locations at which larval ticks emerge from eggs in the fall (Childs and Paddock, 2003). Thus, the densities of larval ticks at our study sites in August should correlate strongly with the density of deer at these same sites in the previous spring. The importance of seasonality in determining the spatial distribution and abundance of ticks is well supported by both mathematical theory (Awerbuch-Friedlander et al., 2005) and empirical examples (Manelli et al., 1994). Many factors may influence seasonal and annual changes in habitat use by white-tailed deer, including shifting foraging opportunities and habitat requirements (Cote et al., 2004). Additionally, our results support the hypothesis that deer may shift habitat use in response to the risk of tick parasitism, an effect that persists when controlling for the abundance of deer.

The apparent lack of an effect of predator activity on deer GUDs is perhaps unsurprising as well, considering that the carnivores present in our study area (e.g., small felids and canids) may be relatively ineffective predators of adult deer, though they are often successful in attacking deer fawns (Beasom, 1974; Stout, 1982; Nelson and Woolf, 1987). However, considering that adult females often conceal fawns in vegetation for extended periods of time while foraging (Nelson and Woolf, 1987), high activity levels of these predators in a given area still may not prevent postpartum does from feeding in these locations if their fawns are concealed elsewhere. Thus, we hypothesize that in the absence of large predators, regulation of deer populations by parasites may increase in importance. Indeed, many studies show increases in the prevalence of pathogens and parasites in prey populations when predators are extirpated (Ostfeld and Holt, 2004). Therefore, increases in the frequency of nonconsumptive effects of parasites on hosts when predators are lost may increase as well.

The avoidance of habitats with high risk of tick parasitism by white-tailed deer could have important implications for the dynamics of zoonotic pathogens transmitted by *A. americanum*. Host behaviors that result in high contact rates with parasites and transmission rates for pathogens have been shown to increase the prevalence of numerous infectious diseases (Altizer et al., 2003). Here, the apparent choice by deer to abandon food resources in habitats with high risk of tick parasitism could potentially dampen tick-borne disease dynamics, if as a result fewer ticks obtain blood meals from these reservoir competent hosts (Paddock and Yabsley, 2007), or if deer are exposed to tick-vectored pathogens at a lesser rate, contributing to reservoir decay (as per Schauber and Ostfeld, 2002). Incorporating these additional complexities into models of pathogen basic reproductive rates (e.g., Hartemink et al., 2008) could help generate more realistic predictions of tick-borne disease dynamics at high tick densities.
It is important to consider alternative explanations for the correlations we document here. An unmeasured environmental variable that correlates with tick abundance and causes deer to give-up more food in areas of high tick density, such as microscale variation in vegetation community composition not captured by our measure of topographic aspect, could account for the documented correlation between the abundance of larval A. americanum and giving-up densities in deer. For example, Adler et al. (1992), document that burdens of larval Ixodes scapularis on rodent hosts increases with density of woody vegetation but decreases with herbaceous vegetation. In the absence of such detailed habitat measurements, or perhaps more ideally an experiment in which tick densities are directly manipulated, it is not possible to conclude with certainty whether the correlation with tick densities reported here is directly the cause of higher giving-up densities in deer.

However, our results are consistent with the few other empirical examples of nonconsumptive effects of parasites on their hosts. Mouritsen and Poulin (2005), report community-level consequences for intertidal macroinvertebrates resulting from changes in behavior of a marine bivalve due to trematode infestation, including increased species diversity and the densities of certain functional groups. Rohr et al. (2009), recently show that Bufo americanus tadpoles exhibit avoidance behavior in the presence of parasitic trematode cercariae, and at magnitudes comparable to the presence of conspecific alarm chemicals released during predation events. Examples involving mosquito oviposition behavior have been reported, such as the study by Lowenberger and Rau (1994), which demonstrated Aedes aegypti is less likely to oviposit in containers occupied by conspecific larvae infected with a parasitic trematode. Empirical examples demonstrating nonconsumptive effects of ticks on their hosts with direct consequences for human risk of exposure to vector-borne diseases, to our knowledge, do not yet exist.

However, such scenarios may be widespread, particularly involving hematophagous arthropods that are generalist vectors of both human and wildlife pathogens. Interestingly, several studies suggest that humans may alter their behavior in response to the threat of parasitism by mosquito vectors (Koenraadt et al., 2006; Carrieri et al., 2008). Similar alterations in behavior by wildlife may substantially influence human risk of exposure to vector-borne diseases if host avoidance of areas with high risk of exposure to parasites results in a shifting of host activities to areas that previously exhibited low densities of vector organisms. Ecological studies conducted over relatively short time frames may only capture transient “snap-shots” of vector-borne disease risk, and control efforts may go wasted on areas that only temporarily exhibited high human exposure risk. Therefore, we recommend increased efforts to incorporate nonconsumptive effects of parasites on hosts into the study of host-parasite ecology, which has previously focused primarily on the direct and indirect effects of hosts on parasites, but has seldom considered the reverse pathway.

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