Biophysical and host-associated factors influencing the fine-scale spatial distribution of questing hard ticks (Acari: Ixodidae) in the Long Island Central Pine Barrens

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Abstract

Hard ticks (Acari: Ixodidae) are important vectors of disease and represent a growing threat to public health in the United States. The risk of encountering ticks and tick-borne diseases (TBDs) in natural systems requires an understanding of tick questing patterns in relation to tick-host behavior, microclimate conditions, and vegetative structure. While previous studies frequently analyze the geographic distribution and abundance of ticks at regional and landscape-level scales, few studies have focused on finer resolutions that could better inform tick encounter risk and implementation of management techniques. This study addresses this gap by modelling tick-host temporal occurrence (TO) and biophysical factors affecting tick questing to understand the spatial distribution of ticks on a fine scale (1m resolution). A 20-ha forest management unit of the pine barrens ecosystem at the Brookhaven National Laboratory was selected for the study. Five 3-m x 15-m plots were set up and sampled for vegetative and microclimate factors, tick-host TO, and tick abundance over three weeks in July 2025. At each plot, a camera trap recorded host TO for 14 days, and vegetative variables were measured once prior to rotational microclimate measurements and tick dragging. The data was analyzed with generalized linear mixed models,

and the most parsimonious model was selected with Akaike's information criterion. The results will help inform land managers on how questing ticks are distributed within habitats at a biologically relevant scale, improving targeted applications of tick management methods, like acaricides or prescribed fire. This study contributes to the mission of Brookhaven National Laboratory by furthering our knowledge of tick ecology to ultimately reduce public risk exposure to ticks and TBDs. From this work, we have cultivated our skills in designing integrative ecological sampling methodologies, managed geospatial data in ArcGIS Pro, processed camera trap data, and improved our ability to write and present professionally.

1. Introduction

Hard ticks (Acari: Ixodidae) are important vectors of pathogens that cause disease in people and animals. In the United States, the rise in tick-borne disease cases, such as Lyme disease, presents a significant and growing public health challenge (Rosenberg, 2018). Encountering ticks and subsequent pathogen transmission depends on multiple factors that shape tick distribution, questing behavior, and survival. Ticks typically acquire pathogens by ingesting them during blood meals from infected vertebrate hosts (Sonenshine and Roe, 2014). To find hosts, ticks engage in host-seeking behaviors, where they either actively "hunt" or "quest" by climbing vegetation, extending their front legs, and waiting to latch onto passing hosts. On a broad scale, tick survival and host encounters are shaped by climate. Ticks require environments with high relative humidity; they are vulnerable to desiccation due to their high surface area to volume ratio (Berger et al., 2014). Additionally, as tick life cycles take two years to complete, ticks must survive overwintering, which adds a temperature limitation to their range. Historically, this has limited tick abundance in northern latitudes. However, as climate change has produced high annual temperatures and different climatic patterns, ticks are now less constrained by the climate in regions like the Northeastern United States (Eisen et al., 2023). This has resulted in more encounters with questing ticks and consequently higher rates of tick-borne diseases (Stafford et al., 2018).

On a finer scale, Host-seeking behaviors are shaped by microclimatic conditions, such as temperature and relative humidity as well as vegetative structure that provides climatic refugia and suitable questing sites (Barnard, 1991; Curtis et al., 2020; Thomas et al., 2020). Additionally, temporal patterns of host presence can affect questing behavior (Ferroglio et al., 2024; Vada et al., 2024). Understanding tick host-seeking patterns in relation to tick host behavior, microclimatic conditions, and vegetative structure could inform the likelihood of tick and tick-borne disease encounter risk in natural areas where ticks are prevalent (Hofmeester et al., 2017).

The distribution of ticks and risk of tick-borne diseases are frequently analyzed at broad geographic scales in the U.S. Generally, climatic and environmental variables are used to model and predict tick population abundance (Sharma et al., 2024), disease prevalence (Diuk-Wasser et al., 2021; Shaw et al., 2024), and range expansions (Springer et al., 2015). Other studies have focused on host community dynamics, particularly the role of white-tailed deer (*Odocoileus virginianus* Zimmermann), which due to ticks' preference for them as a host in adult life stages facilitate tick population abundance and infection prevalence (Roome et al., 2017; Rochlin et al., 2025). Additionally, research has been conducted on understanding the differences in climate preferences for individual tick species, as the mosaic of species has shifted in many areas of the U.S and the colonizing *A. americanum* has greater environmental hardiness then *I. scapularis(Springer et al., 2015; Eisen et al., 2021).*

In regions identified with high tick populations or disease prevalence, broad-scale environmental and host management strategies are applied to manage ticks, including prescribed fire, vegetation management, acaricide treatments, host-targeted treatment devices, and host population management (Stafford et al., 2017; Eisen and Stafford, 2021; Gallagher et al., 2022). For example, invasive plant species like Japanese Barberry provide moist, shady refugia for ticks. Management efforts have thus been undertaken to remove vegetation with these characteristics to reduce suitable habitat for ticks (Thomas et al., 2020).

These approaches, however, often lack precision due to limited understanding of tick ecology at finer spatial scales, resulting in suboptimal implementation and effectiveness (Eisen et al., 2021). While large-scale analyses are essential for understanding regional and temporal trends in tick populations and disease risks, they do not provide the additional context on local tick distribution needed to guide efficient management actions.

Tick spatial distribution at finer spatial scales must be considered at microhabitats no more than a few meters in size. Ticks engage with their environment at small scales due to their size and tradeoffs between seeking hosts and maintaining moisture levels (Marshall et al., 2025). Under natural settings, tick movement is spatially limited to a few meters, where *Amblyomma americanum* (L.) moves 9 m per day on average and *Ixodes scapularis* generally moves less due to its preference for questing behaviors (Curtis et al., 2020; Marshall et al., 2025). Furthermore, it is important to consider that ticks tend to be spatially aggregated, or clustered, within their habitats (Goddard, 1997), which may be attributable to their life cycle or factors influencing host-seeking behaviors. Recent research has begun exploring tick spatial distribution on finer scales, but these works examine and utilize different species, regions, methodologies, predictor variables, and resolutions, making comparisons across studies difficult. Each study faced limitations in spatial resolution, integration of all three factors influencing ticks (including hosts, vegetation, and microclimate), and quantification of predictor variables (Stein et al., 2008; Hofmeester et al., 2017; Van Horn et al., 2018; Iijima et al., 2022; Ferroglio et al., 2024; Vada et al., 2024, 2025; Adams, 2025). For example, Adams (2025) accounts for landscape metrics, microclimatic conditions, vegetative structure, and anthropogenic presence to determine fine-scale tick distribution, but the predictor variables were primarily binary presence-absence, which have limited interpretations and application. Regardless, these studies offer foundational approaches to begin understanding tick spatial distribution at a fine scale.

Given the increasing public health threat posed by tick-borne diseases and the limitations of broad-scale management approaches, there is a need to better understand tick questing ecology on fine spatial scales (Hofmeester et al., 2017; Eisen and Stafford, 2021; Vada et al., 2024). The objective of this study is to determine how tick questing behavior is influenced by the temporal occurrence of hosts, microclimate conditions, and vegetative structure at a fine spatial scale (1m). Integrating these three predictive factors at a fine resolution will provide insights into tick hotspots and help inform more targeted and effective management strategies, such as vegetation management, host control, and pesticide applications, that reduce human exposure to ticks in natural areas.

2. Methods

2.1. Study Area

The study was located within 1,394-ha of forests managed by the U.S. Department of Energy at the Brookhaven National Laboratory (BNL), Upton, NY (BSA, 2024). On-site weather data has been recorded at BNL since 1948 with an approximate annual mean temperature of 11.6°C and mean precipitation of 50.0 inches (BSA, 2024). The elevation on-site ranges from 13 to 36 meters above mean sea level (BSA, 2024). The area of pitch pine (*Pinus rigida* P. Mill.) barrens at BNL constitutes nearly 5% of the state-designated Central Pine Barrens region (BSA, 2024) and accounts for a significantly higher amount of protected natural land than surrounding non-BNL properties (Burger and Gochfeld, 2025). Pine barrens encompass a suite of globally rare, early successional, fire-dependent communities of barrens, woodlands, wetlands, shrublands, and grasslands that provide habitat for multiple species of conservation concern (Bried et al., 2014; Gifford et al., 2010; BSA, 2024; Central Pine Barrens Joint Planning and Policy Commission, 1995). These ecosystems face a myriad of conservation challenges, including a limited modern extent (Jordan et al., 2003); emerging stressors like the northward expansion of the southern pine beetle (*Dendroctonus frontalis* Zimmerman) due to climate change (Huess et al., 2019); and threats of land conversion, fire suppression, and fragmentation (Finton, 1998; Jordan et al., 2003). The BNL-owned study region has a diverse history of land use and disturbance regimes, creating a mosaic of pitch pine communities existing in various stages of succession.

A 20-ha tract of a pitch pine-oak forest was selected for this study. The pitch pine-oak forest, as described in Jordan et al. (2003) and Central Pine Barrens Joint Planning and Policy Commission (1995), is a non-barren, late successional community, dominated by an overstory of pitch pine and *Quercus* spp. (e.g., *Q. coccinea, Q. alba, Q. velutina,* and *Q. rubra*) and an understory of low ericaceous shrubs (e.g., *Gaylussacia baccata, Vaccinium pallidum,* and *V. angustifolium*). The forest is maintained by very infrequent, low-intensity fires (Jordan et al., 2003). While prescribed fire and wildfires occurred historically and actively across BNL forests, the selected study site has not experienced fire in at least 20 years. Because of the potential edge effects from fire disturbances on tick abundance (Gleim et al., 2014), we note that the study area was located 80m from burned pine barrens. The advent of severe southern pine beetle infestations within the study site has removed a large majority of living pitch pines, leaving irregular early successional openings of pitch pine snags and an otherwise *Quercus*-dominant overstory. There are a number of tick hosts within the study region, including white-tailed deer; mesomammals such as groundhogs, squirrels, rabbits, raccoons, foxes, and opossums; and small mammals like mice and voles/shrews. Wildlife on-site, particularly white-tailed deer, are monitored and managed regularly by BNL staff (BSA, 2024). Additionally, an on-going study has used 4-poster™ devices to treat deer with a permethrin-based acaricide to examine its effects on tick abundance. The stations may impact tick abundance in a radius of up to 300m away (Wong et al., n.d.), but the closest station was over 1,000m from the selected study area.

2.2. Sampling Design

Across the study site, eight 3-m x 15-m plots were randomly established in the interior region of the *Quercus*-dominated pitch pine-oak forest to prevent large discrepancies between site variables (Fig. 1). The plots were located at least 20m from the road to reduce potential edge effects associated with wildlife movement and tick abundance along recreational trails and roads (Adams et al., 2024; Mols et al., 2022; Van Gestel et al., 2021). Field measurements of vegetation structure, microclimatic conditions, tick-host TO, and tick abundance were collected over a three-week period in July 2025 (Table 1). At each plot, a camera trap recorded host TO for at least two weeks across the entire plot, vegetative variables were measured once throughout the study at a $1m^2$, and tick sampling occurred weekly. Microclimate data was collected actively at the time of tick sampling and passively through the deployment and rotation of passive recording devices. To account for tick abundance at the $1m^2$, each plot with a camera was considered to hold 15 "microplots" that were located along a 15m transect in the center of the 3-m x 15-m plot (Fig. 1). There were three "subplots" located every 5m for characterizing the spatial placement of tick hosts.

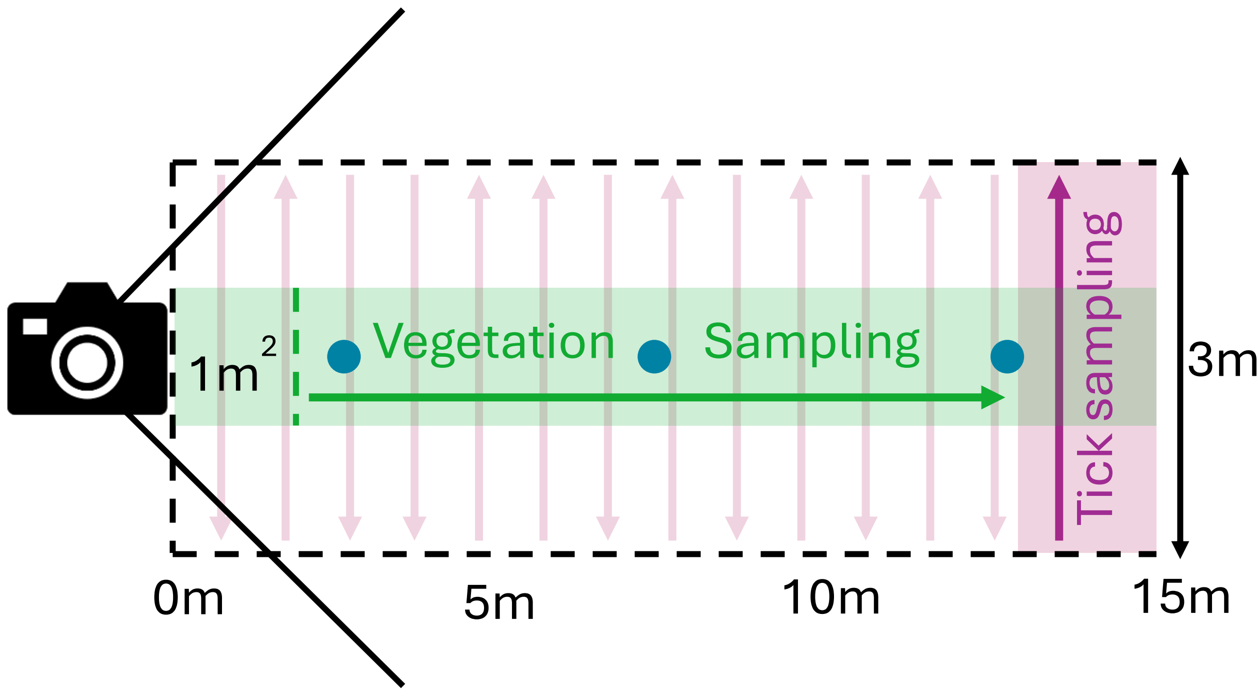

Figure 1. Visualization of plot sampling design. The camera captured wildlife motion across the entire plot. Vegetation sampling was conducted at each of the 15 microplots within the larger plot, which were placed along the inner $1m^2$ of the plot, while tick dragging was completed across $3m^2$. Microclimate data was collected at the center of each subplot, located from 0m to 5m, 5m to 10m, and 10m to 15m. every 5m.

2.2.1. Vegetation Structure

At each plot, fifteen $1m^2$ quadrats were sampled once during the study period. The quadrats were established within the center of the plot for vegetative factors that may influence tick and host behavior (Fig. 1). The percent cover of fine and coarse woody debris (FWD and CWD, respectively), bare ground, leaf litter, herbaceous plants, and shrubby plants; type of leaf litter; depth of leaf litter; maximum vegetation height; and canopy cover at 0.2m and maximum vegetation height were measured for each quadrat within each plot. The Daubenmire method was used for cover estimation (Daubenmire, 1959). Woody debris was defined as FWD when the largest end remained under 10-cm in diameter and as CWD when the diameter was equal to or larger than 10-cm (Harmon and Sexton, 1996).

Table 1. Predictor variables used for modelling the abundance of ticks at a 1m^2 scale.

Parameter	Unit
Vegetation Structure	
CWD	%
FWD	%
Bare ground	%
Leaf litter	%
Herbaceous plants	%
Shrubby plants	%
Leaf litter type	Categorical
Leaf litter depth	cm
Maximum vegetation height	cm
Canopy cover	%
Microclimate Conditions	
Temperature	C
Relative humidity	%
Tick-host Temporal Occurrence	
Temporal occurrence	sec

* CWD and FWD stands for coarse and fine woody debris, respectively

2.2.2. Microclimate Conditions

Because tick hosts move through the environment throughout the day and night, a passive approach to recording microclimatic conditions was also employed. Three iButtons (DS1923-F5# Hygrochron Temperature and Humidity Data Logger, iButtonLink Technology, Whitewater, WI) were placed in the plots on a rotational schedule over the course of the study. Each iButton was wrapped in a thin cheesecloth, tied with flagging tape, and staked into the ground. The devices collected high-resolution humidity and temperature data at a 20-minute rate at the center of each subplot, which was the 2.5m, 7.5m, and 12.5m mark along the center transect of each plot (Fig. 1). An iButton was deployed for two days before it was transferred to a different plot, and two iButtons were never placed in the same plot during the same 2-day sampling window. Each plot was measured once with three measurements of microclimate data on different sampling dates and different subplot-level locations (2.5m, 7.5m, 12.5m).

2.2.3. Tick Abundance

Ticks were sampled once at each plot during favorable questing conditions, with low wind speeds, dry vegetation, and during peak tick abundance according to their seasonal phenology in Long Island (*unpublished data*, Gilvarg, S.). A drag cloth was constructed with a 1-m x 1-m cotton corduroy attached to a wooden dowel of 1” diameter and a 1m rope fastened around the ends of the dowel (Salomon et al., 2020; Eisen et al., 2019). At each plot, 15 1m wide transects were dragged for 3m. Although vegetation was sampled with quadrats at a $1m^2$ scale, ticks were sampled along 1-m x 3-m transects to ensure the entirety of the vegetation quadrat was sampled (Fig. 1). The cloth drag was examined thoroughly after each $3m^2$ transect. Ticks were identified in the field using morphological traits (Lindquist et al., 2016) and were not collected for further inspection or molecular analyses. The number of questing ticks were identified and recorded by species and life stage.

2.2.4. Tick-host Temporal Occurrence

Cameras (either Moultrie A-900i, Reconyx HC600, or Moultrie M-50i) were deployed at each transect for at least 2 weeks. Each camera was placed in a random cardinal direction at 1m above the ground on a live tree. Cameras were set on high sensitivity, and recorded burst of 3 photographs with a 10 or 15 second time lapse between consecutive activations, depending on the camera model. Although a carnivore bait tablet was placed in view of one camera as part of a coyote colonization monitoring project, no carnivores were photographed at this location, and it was unlikely to have influenced deer presence. For each plot, all photos captured were examined for deer presence. If deer were present, the time of total occurrence in the photos was summed using the photo time stamps and time burst setting of the camera. Each deer observation was also categorized by distance from the camera, using flagging set up along the subplots (Fig. 1).

2.3. Statistical Analysis

The number of ticks was modelled using a generalized linear mixed model with a binomial distribution in R software (R Core Team, 2025). The response variable was the total number of ticks collected at a $1m^2$ plot. A list of ten candidate models was created, including a global and null model and eight models with various predictors based on their hypothesized influence to determining tick distribution (Table 2). The variables were checked for correlation, and the model assumptions were checked by examining the diagnostics of the global model using the following R packages: lme4 (Bates et al., 2015), correlation (Makowski et al., 2020, 2022), performance (Lüdecke et al., 2021), easystats (Lüdecke et al., 2022), DHARMa (Hartig et al., 2024), and MuMIn (Bartoń, 2025). Different random effects were tested on the global model, and the only random effect included across all candidate models was the $1m^2$ microplot. Model selection was performed using Akaike Information Criterion (AIC), and the model with the lowest AIC was selected as the most parsimonious model (Akaike, 1973).

Table 2. List of ten candidate models used for modelling the abundance of ticks at a $1m^2$ scale, where CWD corresponds to coarse woody debris, FWD to fine woody debris, BARE to bare ground cover, LIT_COV to leaf litter cover, HERB to herbaceous cover, SHRUB to shrub cover, LIT_DEP to leaf litter depth, MVH to maximum vegetation height, CAN_GRD to canopy cover

at 0.2m, CAN_MVH to canopy cover at maximum vegetation height, THO to tick-host temporal occurrence, TEMP to average temperature, AVG_RH to average relative humidity, SD_RH to standard deviation of relative humidity, and RAND_MICRO to the random effect as the 1m^2 microplot.

Model #	***Hypothesis (higher abundance of ticks)***	***Model parameters***
Global	All parameters contribute to tick abundance.	CWD + FWD + BARE + LIT_COV + HERB + SHRUB + LIT_DEP + MVH + CAN_GRD + CAN_MVH + THO + TEMP + AVG_RH + SD_RH + RAND_MICRO
Null	Tick abundance is not supported by any parameters	1 + RAND_MICRO
1	High CWD + high litter and shrub cover + low vegetation height + high canopy cover + high tick-host temporal occurrence + low temperatures + high relative humidity	CWD + LIT_COV + SHRUB + MVH + CAN_GRD + THO + TEMP + AVG_RH + RAND_MICRO
2	High CWD + high shrub cover + high tick-host temporal occurrence + low temperatures + high relative humidity	CWD + SHRUB + THO + TEMP + AVG_RH + RAND_MICRO
3	High FWD + high litter cover + low herbaceous cover + high tick-host temporal occurrence + low temperatures + high relative humidity	FWD + LIT_COV + HERB + THO + TEMP + AVG_RH + RAND_MICRO
4	High litter cover + low vegetation height + high canopy cover + low temperature + high relative humidity	LIT_COVER + MVH + CAN_GRD + TEMP + AVG_RH + RAND_MICRO
5	High canopy cover + high shrub cover + low herbaceous cover + high tick-host temporal occurrence + low temperature + high relative humdity	CAN_MVH + SHRUB + HERB + THO + TEMP + AVG_RH + RAND_MICRO
6	High FWD + low bare ground + high canopy cover + low temperature + high relative humidity + low deviation of relative humidity	FWD + BARE + CAN_GRD + TEMP + AVG_RH + SD_RH + RAND_MICRO
7	High CWD + high tick-host temporal occurrence + high relative humdity	CWD + THO + AVG_RH + RAND_MICRO
8	High shrub cover + low vegetation height + high tick-host temporal occurrence	SHRUB + MVH + THO + RAND_MICRO

3. Results

The null model containing the random effect of the $1m^2$ microplot and no predictor variables was the most parsimonious model for determining tick abundance at a $1m^2$ resolution (Table 3). Except for the null model, the models failed to converge due to the high model complexity and low sample size (n = 60 microplots across five plots). The predicted mean total counts of ticks at each site were considerably different across the five plots, indicating that variation in tick abundance may be attributable to site-level random effects (Fig. 3).

Table 3. Model results of ten candidate models used to determine the influence of predictors on tick abundance on a fine scale; df is degrees of freedom; logLik is log likelihood

Model #	df	logLik	AICc	Delta AICc	Weight
null	3	-123.44	253.22	0.00	1
2	8	-127.37	272.92	19.71	0
6	9	-126.11	272.99	19.77	0
3	9	-126.13	273.03	19.81	0
4	8	-127.52	273.23	20.01	0
5	9	-127.20	275.16	21.94	0
8	6	-131.33	275.89	22.68	0
7	6	-132.45	278.14	24.93	0
1	11	-126.67	279.52	26.31	0
global	17	-124.77	294.28	41.06	0

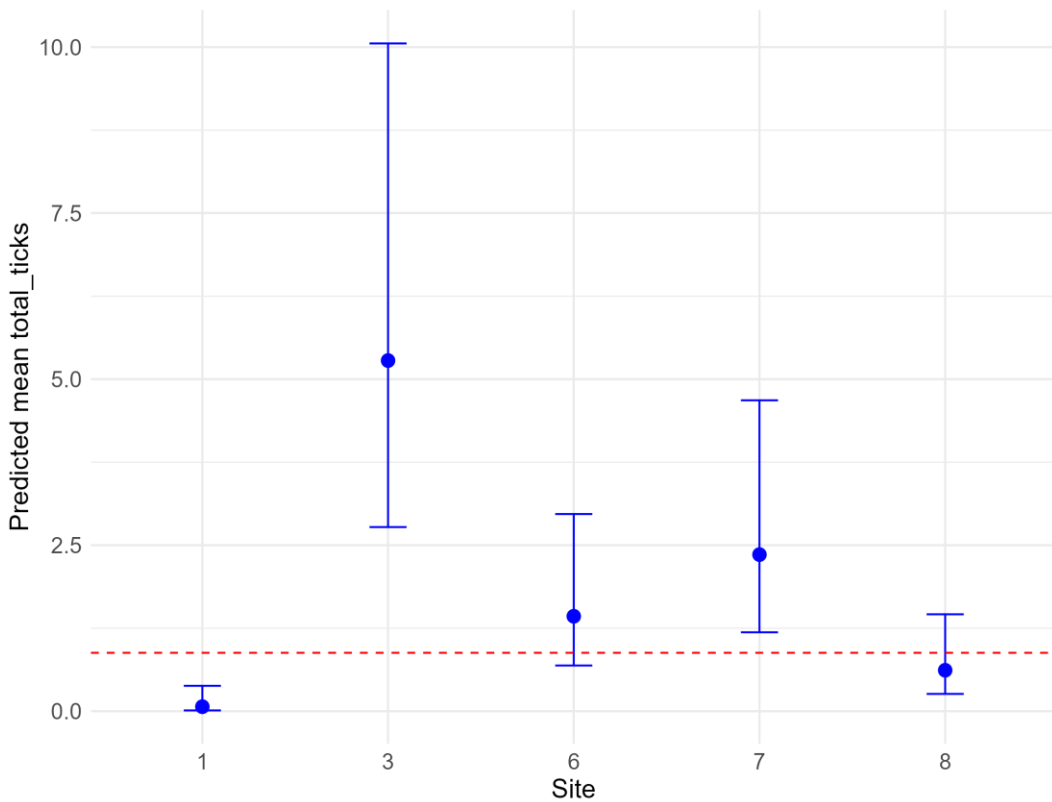

Figure 3. Predicted mean number of ticks with microplot-level ($1m^2$) error bars for each plot, demonstrating how each plot differs in the number of ticks compared to the overall mean (red horizontal line).

4. Discussion

The fine-scale spatial distribution of ticks is determined by multiple ecological factors, including tick-host temporal occurrence, vegetative structure, and microclimatic conditions. The top model indicated that only random effects contributed to tick abundance at the$1m^2$ scale. However, the interpretability of the results was constrained by the high model complexity and low amount of data sampled (n = 60 $1m^2$ microplots across five plots). Despite the limitations of the results, this study offers an integrative approach to exploring the relative influence of these components on tick distribution at fine spatial scales. The methodology builds upon recent work that has employed camera traps to understand tick abundance (Hofmeester et al., 2017; Vada et al., 2024) and examined abiotic factors to predict fine-scale tick distribution (Van Horn et al., 2018; Adams, 2025). Specifically, the methodology created in this study provides a comprehensive sampling design that incorporates potential predictors of tick abundance beyond host occurrence, including fine-scale vegetation and microclimate data, and data collection that contributes quantifiable measures of data. This study highlights the need for applying integrative approaches to understand local tick spatial distributions and to inform targeted management of ticks and tick-borne diseases.

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