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ORIGINAL RESEARCH

Influence of Weather on Questing Strategy by *Amblyomma americanum* Nymphs

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Ticks are ectoparasites that feed exclusively on blood from vertebrate hosts using questing (host-seeking behaviors) strategies such as ambushing (sitting/waiting on vegetation for hosts to brush by) or active pursuit (chasing after hosts). Tick abundance is assessed with flagging/dragging and carbon dioxide (CO_2)-baited trap methods, which target ambushing and actively pursuing ticks, respectively. Many studies employ only one collection method; however, the lone star tick, *Amblyomma americanum*, uses both ambushing and active pursuit. Weather is an environmental factor whose effect on questing strategy remains unclear. We hypothesized that if *A. americanum* changes host-seeking behaviors in response to weather, then the success rate of collection methods will vary accordingly. Sampling events occurred 3 rounds in 3 plots within each of 14 sites—including Tyson Research Center—across St. Louis County, Franklin County, and Jefferson County, using both flagging/dragging and CO_2 traps (N=110). During each survey, we recorded temperature, relative humidity, wind speed, and cloud cover. Using generalized linear mixed models with a binomial distribution, we modeled the influence of weather variables on the probability of *A. americanum*, nymphs either ambushing or actively pursing hosts. Over the course of 4 months, we collected 2,255 *A. americanum* nymphs via flagging/dragging, and 1,682 via CO_2 traps. Saturation deficit, the "drying" power of the atmosphere, and visit round had the greatest influence on tick questing behavior. Active pursuit increased as saturation deficit increased, but ambushing increased over the questing season. Cloudy conditions promoted ambushing and sunny conditions promoted active pursuit. These results underscore how weather can confound tick population estimates due to variability in tick behavior. Future *A. americanum* studies should employ flagging/dragging and CO_2 traps simultaneously. As climate change extends tick questing seasons, understanding how weather influences tick questing strategies is crucial for accurate tick surveillance.

Ticks are small ectoparasites that feed on blood from vertebrate hosts. They have four distinct life stages: egg, larva, nymph, and adult. In each of the stages, ticks use behaviors known as questing to locate a host and feed on it. They feed once per life stage, each lasting anywhere from several months to a year, and use bloodmeals to molt or develop eggs [1]. During the feedings, ticks may be infected with disease-causing pathogens from their hosts, and they may also transmit these pathogens. Tick-borne diseases include Lyme disease, spotted fever rickettsioses, ehrlichiosis, and babesiosis [2]. The lone star tick, *Amblyomma americanum*, is a common tick species in Missouri. It transmits several human and animal pathogens, including agents of ehrlichiosis and tularemia [3, 4]. Tick-borne disease cases have more than tripled from around 20,000 cases in 2004 to over 70,000 cases in 2022 [2], [5]. As pathogens spread by *A. americanum* become more prevalent in the United States, it is crucial to understand questing behaviors of ticks, since a successful quest can transmit disease-causing pathogens to humans and other hosts [6]. Further, standard methods to estimate the abundance of free-living ticks rely on ticks exhibiting specific questing behaviors. Human-biting ticks commonly use two different questing methods: "ambushing," where a tick sits on vegetation and waits for a host to brush by, and "active pursuit," where a tick chases after a host [1]. To measure tick abundance, dragging or flagging methods target ambushing ticks and CO_2 traps collect actively pursuing ticks [7]. Dragging involves a cloth with a rope tied on two ends. For flagging, the user holds the end of a flag's pole and sweeps it in front of them. Both methods aim to brush through vegetation and collect ambushing ticks. CO_2 traps consist of a container of CO_2 and a fibrous cloth. The container of CO_2 mimics a host's breathing, which can trigger a tick to start chasing down the source of the CO_2, hence actively pursuing its host. Certain tick species of human health concern such as blacklegged ticks (Ixodes scapularis) are known to primarily use the ambushing behavior and therefore, they are typically collected through dragging/flagging. Notably, *A. americanum* are very flexible in their host-seeking strategies, using both ambushing and active pursuit, but many *A. americanum* population studies conventionally only use dragging/flagging or CO_2 traps, not both simultaneously [8]. Effective public health interventions for tick-borne diseases require a better understanding of tick questing behavior [9]. Therefore, more information is needed on factors that influence which questing strategy *A. americanum* use and how these factors may confound research and surveillance efforts. Little is known about how weather affects if *A. americanum* ambush or actively pursue hosts. Most studies on how abiotic conditions affect tick questing are conducted in labs, making it unclear how these results translate to natural conditions [10]. Previous research suggests that temperature, humidity, and wind speed, along with seasonal physiological variation, can affect *A. americanum* host-seeking frequencies, but there is a lack of studies on how these weather variables affect which questing behavior they use [10, 11]. In particular, temperature and humidity can be combined into one variable: saturation deficit, the drying power of the atmosphere. Higher saturation deficit indicates high temperature and low relative humidity. Studies have shown that *A. americanum* are more likely to quest at high saturation deficit since they can tolerate drier conditions [11], [12], [13]. The warming climate is likely to extend the questing period for ticks, making it all the more important to study how specific weather variables affect tick questing behavior [13]. High wind speeds can interfere with CO_2 trap effectiveness and cause fewer ticks to quest [7]. In terms of seasonal changes impacting tick questing, Mangan et al. (2022) found that there was an increase in *A. americanum* nymphs questing from spring to summer, though this was only observed in a forest habitat and not in field habitats. This study will examine how weather affects if questing *A. americanum* nymphs ambush or actively pursue a host. We hypothesized that if *A. americanum* changes questing behaviors in response to weather, then the success rate of collection methods will also change.

Methods

Field Data Collection

We sampled 14 sites in the St. Louis, Missouri region with a diversity of habitats (Fig. 1). All sites were predominantly characterized by deciduous forest and were located in three different counties: St. Louis County, Franklin County, and Jefferson County. Three sites at Tyson Research Center were indistinct habitat types (ForestGEO, Glades, Patchidor). The ForestGEO site is mostly oak-hickory forest with an understory mainly consisting of woody shrubs, such as pawpaw (*Asimina triloba*) and spicebush (*Lindera benzoin*) [14]. The Tyson Glades were grass dominated with encroaching Eastern Red Cedar. The Tyson Patchidor was an old field habitat, which is a grassland established on previously disturbed land. Three sites were conservation areas. Powder Valley Conservation was an oak-hickory forest habitat but situated within a suburban environment. Forest 44 Conservation Area was characterized by Ozark uplift, an uplifted plateau. The Pacific Palisades Conservation Area was primarily cropland and grassland. Three sites were county parks, with Kirkwood Park and Emenegger Nature Park situated in a suburban area and West Tyson County Park in a predominantly oak-hickory forest habitat in a rural area. Mastodon State Historic Site has several natural springs with open grassland and oak-hickory forest. Tyson Annex Property is predominantly native grasses near a creek. Finally, one site was a ranch. Long Meadow Rescue Ranch was an oak-hickory forest and has a high concentration of domesticated animals. At each site, 3 plots were established. Each plot consisted of sampling paths called transects totaling 750 meter long for flagging/dragging and a CO_2 trap location adjacent to the transect. We collected ticks from April through July of 2025 for a total of 3 visits using two collection methods during each visit. On average, there were about 31 days between each visit. Dragging, as the name entails, involves dragging a 1.5 square yard cloth with a rope tied on two ends. For flagging, a cloth is attached to the end of a pole and swept in front of the user. Both methods are commonly used to collect ambushing (sit and wait) ticks [7]. Since ticks are attracted to CO_2 emitted from their hosts, CO_2 traps were placed to target actively pursuing ticks [16]. For each CO_2 trap, a container of dry ice is placed in the center of a 1 square yard sheet of cloth [7]. CO_2 traps were set for one hour during the dragging/flagging of transects. We used a handheld weather meter (Kestrel®, Nielsen-Kellerman, USA) to record the temperature, relative humidity, and wind speed for each visit. In addition, we also recorded the cloud coverage as a categorical variable, which was either sunny, partially cloudy, or majority cloud cover. The ticks collected from each plot were transported back to a -80°C freezer to preserve specimen before identification using dichotomous keys for Ixodidae [17, 18]. Ticks were then sorted by species, sex, and life stage.

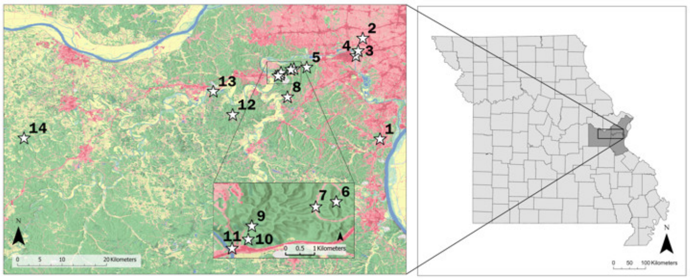

Fig. 1 | Map of the 14 sampling sites. 1. Mastodon State Historic Site, 2. Kirkwood Park, 3. Powder Valley Conservation Nature Center, 4. Emmenegger Nature Park, 5. Forest 44 Conservation Area, 6. ForestGEO TRC1, 7. Patchidor TRC2, 8. Pleasant Valley Nature Preserve, 9. West Tyson County Park, 10. Glades TRC3, 11. Route 66 State Park, 12. Sandstone Creek-Annex, 13. Pacific Palisades Conservation Area, 14. Longmeadow Rescue Ranch. These encompass part of the urbanization gradient that transitions from urban to rural areas in St. Louis, as shown by the National Land Cover Dataset (NLCD) [15]. The green, yellow, and red covers indicate forest, agriculture, and urban areas, respectively. On the right side of the figure with the Missouri counties in light grey, the sampled counties, St. Louis County, Franklin County, and Jefferson County, are shaded in dark grey.

Statistical analyses

We filtered collection data to include only *A. americanum* nymphs identified at all sites with a maximum of 3 visits, where each visit used both flagging/dragging and CO_2 traps. The nymphal stage is the most important life stage for tick-borne disease risk, because they are small enough to evade detection, have a greater likelihood of being infected from their first blood meal as larvae, and reach peak questing from spring to summer when humans are more likely to engage in outdoor activities and animal hosts are more active [19]. We used the temperature and relative humidity measurements from each visit to calculate saturation deficit—the "drying" power of the atmosphere—using the following formula from Randolph and Storey (1999):

$$SD = \left(1 - \frac{RH}{100}\right) 4.9463e^{0.0621\mathrm{T}}$$

where SD is saturation deficit, RH is relative humidity in mmHG, and T is temperature in Celsius. Each row of sampling event data consisted of the site, plot, number of *A. americanum* nymphs on

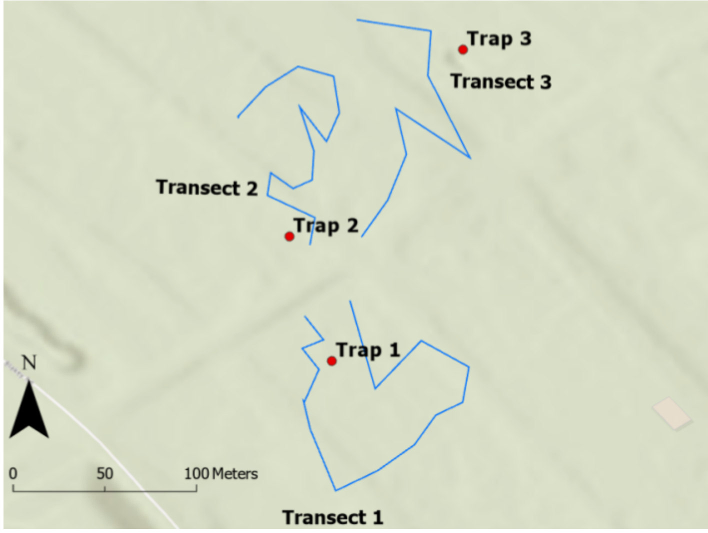

Fig. 2 | Example of 3 plots with their respective transect and CO_2 trap location at Route 66 State Park. Each transect averages 250 meters long, totaling to 750 meters of transects for each site.

traps or transect, cloud coverage, wind speed, the hour a trap was collected or a transect was complete, and saturation deficit. We used logistic regression in R to assess the odds that lone star nymphs were collected from flags/drags or CO_2 traps at each plot and to determine which variables best predicted those odds. Continuous variables—saturation deficit and wind speed—were centered and scaled prior to modeling. We created 11 generalized linear mixed models (GLMMs) with different combinations of predictor variables, setting site as a random effect for all models. We compared models using Akaike's Information Criterion for small samples in order to prevent overfitting (AICc) [20]. Prior to constructing models, we tested for correlations among covariates; time of day and saturation deficit were strongly correlated (Pearson correlation coefficient, r=0.706). Therefore, we created two global models with one of each variable to avoid having correlated variables in the same model. Statistical analysis was conducted in R version 4.5.1, and the packages lme4 and MuMIn were used for creating the GLMMs and evaluating the GLMMs, respectively [20], [21], [22]. To evaluate the fit of our models, we used the Diagnostics for HierArchical Regression Models (DHARMa) package to test for overdispersion and evaluate residuals between our model's predictions and the observational data [23]. Finally, the ggeffects package was used to calculate the prediction responses from our best model by computing marginal predictions for ticks' questing strategy while controlling for cloud coverage, wind speed, saturation deficit, and visit round [24].

Results

Overall, we collected and identified 8,669 *Amblyomma americanum*, 18 *Dermacentor variabilis*, 10 *Ixodes scapularis*, and 1 *Haemaphysalis longicornis*. A total of 3,937 *A. americanum* nymphs were collected, with 2,255 via flagging/dragging, and 1,682 *A. americanum* nymphs via CO_2 traps (Table 1). According to standard tick surveillance protocol, survey were not conducted during rainy or extremely windy conditions (greater than 20 mph) [7]. Over 80% of our visits were during sunny conditions.

Site	EMG	F44	KWP	LMR	MSP	PAC	PVC	PVP	R66	TAP	TRC 1	TRC 2	TRC 3	WT P	Total
Transect total	222	465	9	138	0	6	64	11	158	126	317	373	151	215	2,255
Trap total	122	111	38	16	2	0	11	16	54	213	277	426	275	121	1,682
Total	344	576	47	154	2	6	75	27	212	339	594	799	426	336	3,937

Table 1 | Summary of total A. americanum nymphs collected on transects (flagging/dragging) and CO_2 traps for each site. Sample counts for transect and trap totals across sites were roughly equal (2,255 vs. 1,682), demonstrating that we had similar active pursuit and ambushing sample effort overall.

Out of the 11 GLMMs, the global GLMM with saturation deficit, wind speed, cloud coverage, and visit round had the lowest AICc value by more than 15 ΔAICc, indicating the best relative model fit. A smaller AICc value indicates a better fit model [20]. This GLMM was also the only model with a weight, the numerical value representing the importance of a model variable, greater than 0, indicating that it has the highest likelihood of being the best model of the set for predicting tick questing strategy (Weight = 1) (Table 2). The weight is the numerical value representing the importance of a model variable [20]. To verify the fit of our best model, an overdispersion and uniformity test was conducted on the two global models using DHARMa. Overdispersion tests evaluate the variability of observations residuals to simulation residuals, and a significant test ($p<0.05$) indicates that a model has overestimated variability. Uniformity tests evaluate the distribution of residuals, and a significant test indicates that residuals substantially deviate from a uniform distribution. The dispersion test was non-significant ($p=0.79$). For the Kolmogorov-Smirnov uniformity test (KS test), which measures the difference in data distribution between two independent models, the p-value was also non-significant ($p=0.20$) (Fig. 3). Saturation deficit, cloud coverage, and visit had a significant p-value ($p<0.001$). The odds ratios (OR) of of saturation deficit is greater than 1 (OR=1.78, Table 3), indicating that an increase in saturation deficit was associated with higher odds of active pursuit. Meanwhile the odds of active pursuit decreased over the course of three visits from 0.09 to 0.02 (Table 3).

Model	k	Delta AICc	Weight
Saturation deficit, Wind speed, Cloud coverage, Visit	8	0.0000	1
Wind speed, Cloud coverage, Time, Visit	8	15.7728	0
Time, Wind speed, Cloud coverage	4	292.5378	0
Saturation deficit, Wind speed, Cloud coverage	6	681.2117	0
Saturation deficit, Cloud coverage	5	752.6353	0
Wind speed, Cloud coverage	6	754.9056	0
Wind speed, Saturation deficit	4	788.2680	0
Wind speed	5	790.3165	0
Saturation deficit	4	1869.3244	0
Cloud coverage	3	1875.1804	0
Time	3	1972.6638	0
Visit	3	1984.7157	0
Intercept only	2	2005.1367	0

Table 2 | Summary of 11 models' variables, number of parameters (k), delta AICc, and weights. The model with saturation deficit, wind speed, cloud coverage, and visit had the lowest AICc and a weight of 1.

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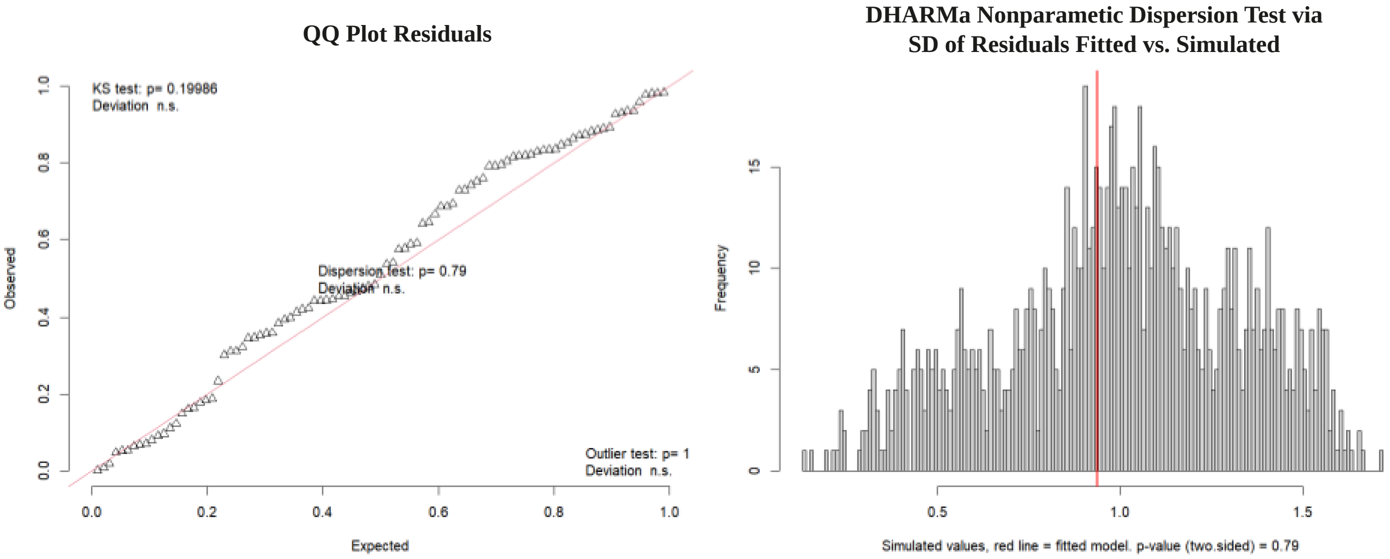

Fig. 3 | Assessment of data normality and dispersion. The linear trend of the QQ plot indicates that the data aligns well with the distribution. The nonparametric dispersion test displays the simulations as gray lines and the fitted model as a red line, and the roughly symmetric distribution suggests equal dispersion.

Probability of active pursuit over ambush			
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.04	0.01 – 0.18	**<0.001**
Saturation deficit	1.78	1.49 – 2.13	**<0.001**
Wind speed	0.93	0.77 – 1.12	0.455
Partial cloud cover	402.87	141.82 – 1144.45	**<0.001**
Sunny	59.22	29.01 – 120.88	**<0.001**
Visit 2	0.09	0.06 – 0.14	**<0.001**
Visit 3	0.02	0.01 – 0.03	**<0.001**
Random Effects			
σ^2	0.08		
$\tau_{00\ \text{site}}$	5.88		
ICC	0.99		
N_{site}	14		
Observations	95		
Marginal R^2 / Conditional R^2	0.545 / 0.994		

Table 3 | Summary of our best model displaying the exponentiated odds ratios, calculated based on coefficient estimates for each predictor variable Odds ratios greater than 1 indicate increased odds of active pursuit while odds ratios less than 1 indicate increased odds of ambushing.

Our model predicted that the probability of active pursuit decreased over the course of visits, and ticks were least likely to use active pursuit under majority cloud cover conditions (Fig. 4). The probability of active pursuit shows a slight decrease with increasing wind speed, while the probability of active pursuit increases as saturation deficit increases, but slows down starting around 12.9 mmHg (Fig. 5).

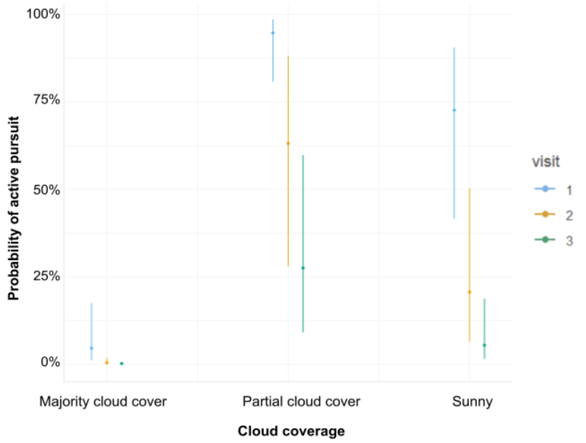

Fig. 4 | Probability of active pursuit over ambush as a function of cloud coverage and visit. Points represent model-predicted mean response and lines represent 95% confidence intervals. For each coverage, visits 1, 2, and 3 are the blue, yellow, and green plots, respectively.

Discussion

The best prediction model for *A. americanum* nymph questing behavior used saturation deficit, wind speed, cloud coverage, and visit. As saturation deficit increased, *A. americanum* nymphs were more likely to actively pursue hosts. Increasing wind speed decreased the probability of active pursuit. During majority cloud cover, the possibility of an *A. americanum* nymph ambushing its host was greater than 75% for all visits. Interestingly, the cloud coverage with the highest probability of *A. americanum* nymphs actively pursuing a host was partial cloud cover. However, the confidence intervals overlapped, which may indicate that the difference in cloud coverage is not significant. One reason for a stronger response during partial cloud coverage could be that is the optimal condition for *A. americanum* nymphs to chase after their hosts, since there is a balance of enough humidity, warm enough temperatures, and shade to risk spending energy on movement. Eisen et al. (2016) found that when there is low humidity, black-legged ticks (*Ixodes scapularis*) and western black-legged ticks (Ixodes pacificus) will spend more time re-hydrating, which could take away their energy from chasing a host. Increasing saturation deficit increased the probability of *A. americanum* nymphs actively pursuing, albeit slowing down at higher saturation deficit, which aligns with our results. Towards the end of July, the probability of *A. americanum* nymphs actively pursuing decreased. Saturation deficit was a better predictor of *A. americanum* nymph questing behavior than the time of day. Marshall (2025) suggested that the temperature, a variable in saturation deficit, previously experienced by ticks may also impact their movement, or whether they actively pursue or ambush a host. Future studies could expand on this finding by studying the questing strategies of wild ticks after being exposed to a range of temperatures. At higher wind speeds, ticks may be less likely to actively pursue hosts because they can stabilize themselves while mounting on a vegetation stem, albeit at a lower height than they usually would [26].

Our finding that less ticks actively pursue hosts also aligns with Center for Disease Control tick collection guidelines, which advises against CO_2 traps during extremely windy conditions due to limited tick questing [2]. Windy conditions may also deter ticks from active pursuit because there is increased evaporated water-loss, resulting in higher desiccation risk [26]. The decline in active pursuit across all three visits demonstrates that physiology may also play a role in questing behavior. Ticks need to survive for long periods between each blood meal and therefore need to balance questing with minimizing energy expenditure [1]. Mangan et al. (2022) found that the time *A. americanum* nymphs spend questing relative to energy use decreased from spring to summer. There was an observed increase in *A. americanum* nymphs both ambushing and actively pursuing from spring to summer, though this increase was only observed in a forest habitat and not in field habitats, though the reason remains unclear. Since active pursuit requires more energy than ambushing, our findings reflect a similar trend. One limitation of this study is that we did not conduct 3 visits using both drags/flags and CO_2 traps for all sites. In addition, we did not survey sites during rainy and very windy days (over 8 mph winds) per standard tick collection protocols, so due to the period of time we conducted tick surveys (April to July) and avoiding rainy and extremely windy days per standard tick collection protocols, over 80% of our visits were sunny, which may have biased the model. Future studies could conduct multiple collection methods for all survey sites across a longer period that encompasses a more proportional distribution of cloud coverage. Another potential study could also collect data on how rain affects tick questing behavior, as previous research suggests the number of *A. americanum* nymphs ambushing decreases after a rainfall event [27]. Our study suggests that weather factors influence tick questing behavior, and that for tick species with flexible questing strategies like *A. americanum*, reliance on a single collection method during surveys may bias estimates of tick abundance. Based on our results, we recommend that both dragging/flagging and CO_2 traps should be used simultaneously when surveying *A. americanum* populations. Tick questing strategy needs to be an important consideration when surveying tick species, especially for species like *A. americanum* that have flexible questing strategies. Moreover, climate change is expected to extend questing activity periods for many tick species, including *A. americanum*, since warmer summers and shorter winters facilitate tick activity. Therefore, this is also predicted to increase the risk of tick contact [28]. Characterizing how environmental factors like weather affect tick questing behavior can improve public health surveillance and interventions for reducing tick-borne disease transmission.

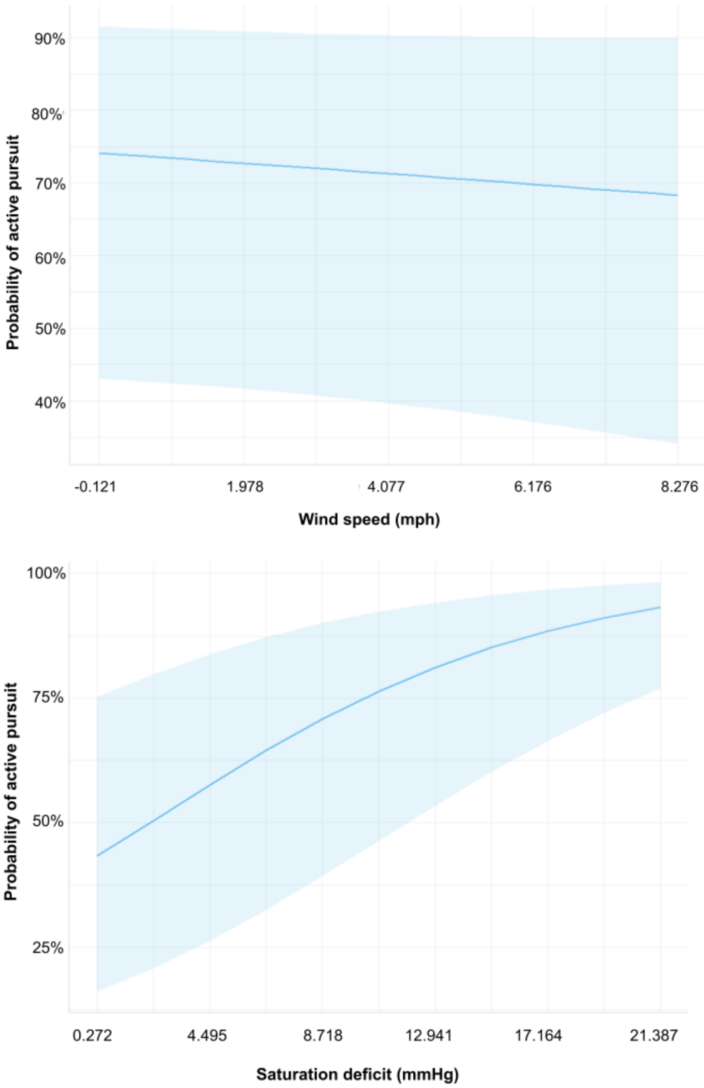

Fig. 5 | Probability of active pursuit over ambush as a function of wind speed and saturation deficit. Lines represent model-predicted mean response and shaded areas represent 95% confidence intervals. Visit 1 and sunny conditions were held constant for wind speed (left) and saturation deficit (right).

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