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Relative Humidity and Activity Patterns of *Ixodes scapularis* (Acari: Ixodidae)

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Relative Humidity and Activity Patterns of *Ixodes scapularis* (Acari: Ixodidae)

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ABSTRACT Laboratory studies have shown clear relationships between relative humidity (RH) and the activity and survival of *Ixodes scapularis* Say (blacklegged tick). However, field studies have produced conflicting results. We examined this relationship using weekly tick count totals and hourly RH observations at three field sites, stratified by latitude, within the state of Rhode Island. Records of nymphal tick abundance were compared with several RH-related variables (e.g., RH at time of sampling and mean weekly daytime RH). In total, 825 nymphs were sampled in 2009, a year of greater precipitation, with a weighted average leaf litter RH recorded at time of sampling of 85.22%. Alternatively, 649 nymphs were collected in 2010, a year of relatively low precipitation, and a weighted average RH recorded at time of sampling was 75.51%. Negative binomial regression analysis of tick count totals identified cumulative hours <82% RH threshold as a significant factor observed in both years (2009: $P = 0.0037$; 2010: $P < 0.0001$). Mean weekly daytime RH did not significantly predict tick activity in either year. However, mean weekly daytime RH recorded with 1-wk lag before sample date was a significant variable ($P = 0.0016$) in 2010. These results suggest a lag effect between moisture availability and patterns of tick activity and abundance. Differences in the relative importance of each RH variable between years may have been due to abnormally wet summer conditions in 2009.

KEY WORDS *Ixodes scapularis*, relative humidity, tick activity

Lyme disease is the most commonly reported vector-borne disease in the United States, with the majority of reported cases concentrated in the heavily populated coastal northeastern United States. In this region, disease-causing bacteria, *Borrelia burgdorferi*, are transmitted to humans through the bite of an infected blacklegged tick (*Ixodes scapularis* Say). Lyme disease incidence is positively associated with blacklegged tick activity and abundance (Nicholson and Mather 1996, Kitron and Kazmierczak 1997, Stafford et al. 1998, Falco et al. 1999). Because Lyme disease remains a significant problem throughout the region and elsewhere, the ability to predict tick encounter risk from environmental determinants could potentially contribute to prevention programs by fostering better targeted public awareness and management interventions.

Year-to-year variability in Lyme disease risk has been hypothesized to be a result of fluctuating weather conditions influencing tick survival (Subak 2003, McCabe and Bunnell 2004). Because of their high surface area to volume ratio, blacklegged ticks are susceptible to desiccation when questing for hosts (Stafford 1994); temperature and relative humidity (RH), therefore, can be considered determining factors in their survival. Nymphal ticks can desiccate within 48 h if deprived of moisture, even though they are able to imbibe water moisture from partially saturated air (Needham and Teel 1991, Stafford 1994). Laboratory experiments have identified a critical threshold for tick survival (Stafford 1994, Rodgers et al. 2007). While experimental variables can be held constant within the laboratory setting, both temperature and RH fluctuate daily in the field. Rodgers and colleagues (2007) simulated field conditions in a laboratory experiment that modified the duration and level of RH. Ticks did not survive when exposed to suboptimal humidity conditions for long periods of time; however, the return of humid air within 4–8 h had a positive impact on survival (Rodgers et al. 2007). At <82% RH, the moisture deficit was too large for the ticks to easily extract water from partially saturated air. Tick survival declined when suboptimal RH conditions were held constant for an extended period of time, even when RH later increased (Rodgers et al. 2007).

Prior field studies have demonstrated at least partial support for the influence of climate on questing populations of nymphal blacklegged ticks. Bertrand and Wilson (1996) found that blacklegged ticks suffered higher mortality rates in open fields than did ticks in

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edge or forested habitats. The authors reported that tick survival was negatively related to air temperature, vapor pressure deficit, and the coefficient of variation of RH. Likewise, Ginsberg and Zhioua (1996) found blacklegged tick survival to be higher in woodland than in open habitats. Additional field studies have found nymphal tick abundance to be significantly correlated with both temperature and RH (Vail and Smith 1998), and that these two weather factors also influenced both questing height and distance (Vail and Smith 2002). Lastly, extreme drought conditions have been responsible for reducing larval blacklegged tick populations in northern Illinois (Jones and Kitron 2000). Precipitation and temperature, however, have been reported as poor predictors of annual nymphal blacklegged tick abundance (Ostfeld et al. 2006, Schulze et al. 2009).

The purpose of this study was to examine the relationship of RH to *I. scapularis* activity under field conditions by applying the laboratory model developed by Rodgers et al. (2007) using tick activity samples at several field sites, along with RH values recorded at the leaf litter level where nymphal *I. scapularis* is active.

Materials and Methods

Study Areas. To validate the relationship between ground RH and tick activity and abundance, we established three study sites distributed across a latitudinal gradient in the state of Rhode Island. Bordered by the Atlantic Ocean and consisting of >640 km of coastline, Rhode Island is characterized by a moist continental climate. The mean annual temperature for the state is 10°C, while the mean annual precipitation (including rain and melted snow) is ≈1,000 mm, distributed evenly throughout the year (Mollis 2011). Stratified zones were determined using the southernmost and northernmost latitudes and dividing the difference into three equal regions. The three study areas included: Scituate Reservoir, Scituate, RI (northernmost region); Arcadia Management Area, Exeter, RI (central region); and Burlingame Management Area, Charlestown, RI (coastal region). All study areas were located in state-owned parks and conservation areas, as they contained suitable tick habitats and held the potential for human tick encounters. All study sites were contiguous mixed forest, consisting predominantly of white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), and white oak (*Quercus alba* L.). The sampling substrate across all sites was uniform leaf litter, consistent with the understory of a contiguous mixed forest.

Hierarchical Sampling Design. To ensure a robust number of observations and to account for bias that might occur in nymphal tick sampling practices by field collectors, a hierarchical sampling design was implemented (Fig. 1). The top hierarchy of sites consisted of four 500 by 500-m plots (250,000 m^2) established within relatively close proximity of each other at each of the three study areas. The subplots were 30 by 30 m (900 m^2) and the quadrats were 10 by 10 m (100 m^2). Sampling of the quadrats followed a randomized design without replacement, so that no 100 m^2 quadrat was revisited over the course of the field season. Global positioning system technology was used to locate each of the 10 900-m^2 subplots and prevent redundant directional sampling within each 100 m^2quadrat. Tick totals from each of the 10 900-m^2 subplots were summed to provide a single value for each of the four 250,000-m^2 plots across all three study sites ($n = 12$). Recorded measurements of tick abundance were standardized as total nymphal ticks per unit area.

Tick Sampling. Nymphal blacklegged ticks were sampled at all study areas using a standard flagging technique adapted from that described by Nicholson and Mather (1996). A 0.5-m^2 piece of white flannel attached to a wooden pole was used to flag forest floor leaf litter over 10-m linear transects within each study area. Simple tick counts were conducted for each 100-m^2 quadrant and totaled for each 250,000-m^2 area. All ticks were removed from the flags at the end of each 10-m drag and released immediately into leaf litter outside of the sampling area. A single sample consisted of five 10-m drags within each 100-m^2 quadrat. To reduce bias introduced by repeated sampling across sites, the date, time, and name of field collector were recorded, and an effort was made to prevent repeated sampling of individual locations by single field technicians. Weekly tick counts were recorded for each of the four 250,000-m^2 plots within the three study areas ($n = 12$).

Sampling of nymphal blacklegged ticks was conducted, weather permitting, during the 0900 and 1800 hours at all study sites on a weekly basis during the summers of 2009 and 2010. Sampling at all three study areas began on 16 June 2009 (because of an unprecedented month of extensive heavy rain prohibiting sampling at all sites before that date), and ended on 26 August 2009. This resulted in a total of 10 wk of observations ($n = 40$ tick counts per site with a cumulative total of 120 observations across all three sites). In 2010, sampling was initiated on 27 May and completed on 11 August. Intended sampling design was only scheduled to last 9 wk, but the first quadrat within each subplot was resampled in 2009, as were the first two quadrats in 2010, as the weather conditions and nymphal tick activity were still conducive to sampling. In both years, sampling was terminated when cumulative tick counts for each 250,000-m^2 plot were at or near zero.

RH Loggers. A network of 12 HOBO H8 Pro Series (no. H08-032-08) Temp/RH Data Loggers (Onset Computer Corp., Bourne, MA) were deployed in each of the four plots within each of the three study areas used in this analysis from 16 June to 26 August 2009, and from 27 May to 11 August 2010. Each logger (15.24 cm in height by 21.34 cm in width by 18.80 cm in diameter) was mounted on a 0.91-m galvanized steel pole driven 5.08 cm into the ground, suspended 0.1 m above ground and fitted with a radiation shield (no. 7714, Davis Instruments Corp., Hayward, CA) to pro-

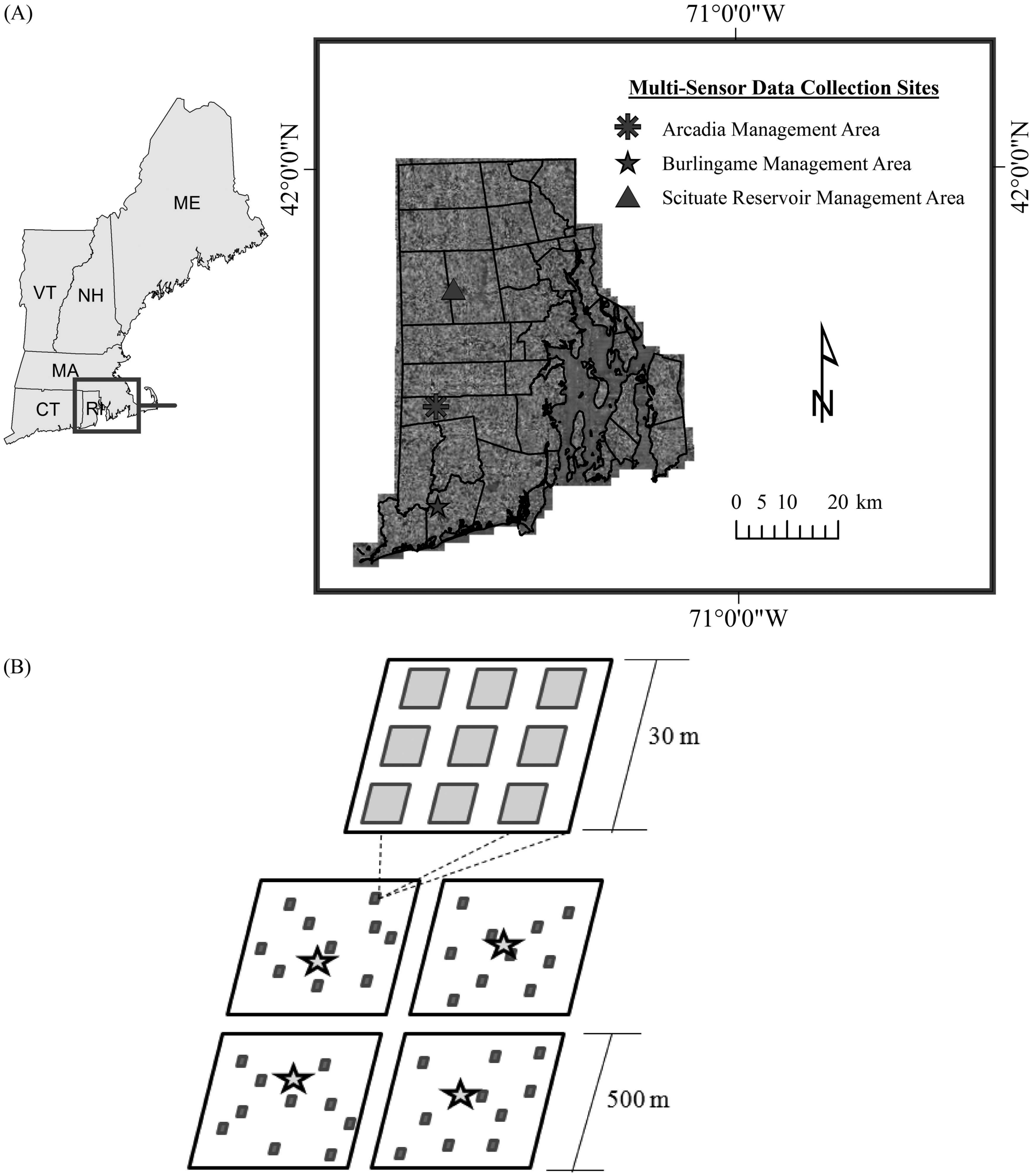

Fig. 1. (A) The study area of Rhode Island. Symbols indicate field study sites, distributed across a latitudinal gradient. All sites were located on state-owned forest management areas and suitable (contiguous, mixed forest) tick habitat. (B) Hierarchical sampling design implemented at each of the three study sites to ensure a robust number of observations were collected and to account for bias that might occur in nymphal tick sampling practices by field collectors. Stars represent approximate location of RH logger.

tect from both solar radiation and rainfall. Hourly RH data were transferred from each logger at weekly intervals using a portable data shuttle (HOBO H9 Shuttle, Onset Computer Corp., Bourne, MA). Retrieval of observations from the RH logger network corresponded with weekly sampling of nymphal ticks. All data were downloaded and imported into Excel (Microsoft Corp., Redmond, WA) for analysis. RH in leaf litter is high at night, often 100%, so our RH readings were limited to daytime hours to evaluate the role of RH during the dry peak sun hours in the afternoon (Rodgers et al. 2007). Moisture availability is not a limiting factor during evening and mornings, therefore RH parameter values were restricted to daytime only. Weekly averages of RH were calculated from individual loggers for each 250,000-m^2 sampling plot within each study area (n = 12 values for each week, corresponding to nymphal tick counts for the same number of sites) for both years. Temperature and additional RH values derived from hourly observations (e.g., minimum, maximum RH, total hours <82% threshold, etc.) were calculated for all plots on a weekly basis for each study area for each year.

Statistical Analysis. Because initial Poisson regression of tick sampling data demonstrated significant dispersion (>1), a negative binomial regression model was applied to account for overdispersion. To examine the relationship between suboptimal RH and tick abundance, total hours per 7-d period before sampling below a prescribed 82% RH threshold (Rodgers et al. 2007) were calculated. Negative binomial regression was used to evaluate the relationship between weekly nymphal tick counts and the following environmental variables: 1) day of year (DoY); 2) mean daytime (0800–2000 hours) logger RH recorded 7 d before sample date (AvgWklyDaytimeLgRH7); 3) total hours <82% RH threshold recorded by logger 7 d before sampling (HrsSub7 d); 4) cumulative (seasonal) total hours <82% RH threshold recorded by logger 7 d before sampling (CumHrsSub7 d); 5) maximum RH 7 d before sampling (MaxRH); 6) minimum RH 7 d before sampling (MinRH); 7) range of RH 7 d before sampling (RHRange); 8) maximum daily hours <82% RH threshold 7 d before sampling (SubHrsMax); 9) minimum daily hours <82% RH threshold 7 d before sampling (SubHrsMin); 10) range in daily hours <82% RH threshold (SubHrsRange); 11) logger RH at time of sampling (LgToS); 12) mean weekly daytime (0800–2000 hours) logger RH recorded, with 1-wk lag (consisting of days 8–14) before sampling date (AvgRH14); and 13) temperature at time of sampling (TempToS). Because a central component of this study was to identify environmental factors influencing tick activity, postpeak nymphal tick abundance values were used for analysis. Postpeak refers to the period of time in the nymphal tick's life cycle where abundance values for the season are stable or just starting to decline. This decline occurs over several weeks while ticks are questing for hosts and allows us to examine the role of RH on activity, while accounting for the effects of recruitment on the current nymphal questing population (Daniels et al. 2000). An offset term, number of observations, was used to account for differences in number of sampling sites across study plots. Differences in the number of sampling sites across study plots was due to accessibility or weather-related discontinuation of sampling of some 900-m^2 subplots on the day of sampling. Because of the contrasting nature of the two years observed (2009 characterized by historical rain events and greater tick abundance vs. 2010 with drier conditions and relatively half of the prior year's tick abundance totals), it was decided to analyze both the years separately. All statistical analyses were performed in SAS version 9.2 (SAS Institute Inc. Cary, NC).

Results

In total, 825 nymphs were collected in 2009 (Arcadia = 234; Burlingame = 229; Scituate = 362). Mean tick abundance within each 250,000-m^2 plot, across all study sites was 9.16 (±7.38). The weighted average RH recorded at the time of sampling was 85.22% (Arcadia = 84.5%; Burlingame = 84.5%; Scituate = 87.12%). Average weekly daytime RH across all study sites ranged from 66.10 to 98.99%, and temperature varied from 16.76 to 29.5°C between 29 June and 26 August 2009. Median total hours subthreshold (82%) RH recorded 7 d before sampling were greatest at Arcadia (26 h) in 2009, while Burlingame and Scituate only recorded 13 and 16 total hours, respectively.

In 2010, 649 nymphs were collected (Arcadia = 122; Burlingame = 113; Scituate = 414). Mean tick abundance within each 250,000-m^2 plot, across all study sites was 5.23 (±4.17). Weighted average RH recorded at time of sampling was 75.51% (Arcadia = 72.5%; Burlingame = 77.61%; Scituate = 77.33%). Average weekly daytime RH, across all study sites, ranged from 52.65 to 99.34%, and temperature varied from 14.85 to 36.13°C between 28 May and 11 August 2010. Median total hours subthreshold (82%) RH recorded 7 d before sampling was also greatest at Arcadia (49 h) in 2010, while Burlingame and Scituate recorded 33.5 and 24.5 h, respectively. Precipitation varied between years sampled. The summer of 2009 was characterized by much wetter conditions as sampling during the first campaign was delayed by excessive rains from mid-May to mid-June. In contrast, the summer of 2010 was characterized by drier conditions. Total rainfall for the summer of 2010 (28 May–6 September) was lower (34.09 cm) than the summer of 2009 (43.79 cm; Parris and Russo 2010).

Negative binomial regression analysis of tick count totals identified cumulative hours <82% RH threshold to be a significant factor observed in both years (2009: P = 0.0037; 2010: P ‹ 0.0001; Table 1). TempToS also was negatively associated with tick abundance in both years (2009: P = 0.0008; 2010: P = 0.0394). MinRH and RHRange demonstrated borderline significance in 2009 (MinRH: P = 0.0877; RHRange: P = 0.0879), but were not significant in 2010 (MinRH: P = 0.8981; RHRange: P = 0.9689). In 2010, the variable AvgRH14 also was significant (P = 0.0016), but was not significant in 2009 (P = 0.1118). All other RH variables investigated in this analysis were not significant predictors of weekly tick abundance (Table 1), including LgToS for both years (2009: P = 0.1379; 2010: P = 0.2414). The total number of nymphs sampled differed among study areas in both years (2009: χ^2 (2, N = 90) = 17.08; P = 0.0002; 2010: χ^2 (2, N = 121) = 56.50; $P < 0.0001$).

Multiple negative binomial regression of all significant climatic variables, using a significance cut-off value of 0.20, identified one best-fit model for each year of the two years studied, using Akaike's informa-

Table 1. Exploratory analysis with individual variables

Variable of interest	2009		2010	
	Estimate	*P* value	Estimate	*P* value
DoY	−0.0179	<0.0001***	−0.0084	0.0014***
AvgWklyDaytimeLgRH7	0.0102	0.3761	0.0097	0.2007
HrsSub7 d	−0.0031	0.4754	−0.0025	0.4286
CumHrsSub7 d	−0.0052	<0.0001***	−0.0014	0.0037***
MaxRH	0.1751	0.7256	0.0372	0.4673
MinRH	0.0099	0.0877*	0.0008	0.8981
RHRange	−0.0099	0.0879*	−0.0003	0.9689
SubHrsMAX	−0.0101	0.6089	0.0313	0.3166
SubHrsMIN	−0.0711	0.5153	−0.0018	0.9445
SubHrsRange	0.0084	0.6792	0.0201	0.4058
LgToS	0.0097	0.1379	−0.0043	0.2414
AvgRH14	0.0183	0.1118	0.0264	0.0016***
TempToS	−0.0518	0.0008***	−0.0195	0.0394**

Negative binomial regression with offset term (log number of sampling sites per pixel) of total nymphs sampled per pixel (postpeak) and variables of observed relative humidity in 2009 and 2010. *P* values are result of negative binomial regression of each variable individually.
*Significant at $P < 0.10$; ** significant at $P < 0.05$; *** significant at $P < 0.01$.

tion criterion (AIC; Akaike 1974; Tables 2 and 3). The variables MinRH and RHRange demonstrated high (>10) variance of inflation values, indicating multicollinearity. The parameter MinRH was deemed a more biologically relevant variable than RHRange because of its interpretation as a measure of limited moisture availability, and therefore was selected for inclusion into model development while RHRange was excluded. In 2009, a three-parameter model including AvgRH14, DoY, and MinRH provided the best-fit (AIC: 436.62; Table 2). Alternatively, a two-parameter model including AvgRH14 and TempToS gave the best-fit for 2010 (AIC: 478.73) in 2010 (Table 3). The variable AvgRH14 was identified as a component in both best-fit models in both years. The overall goodness-of-fit of both models was determined by log-likelihood ratio index using McFadden's pseudo R^2, and was equal to 0.2833 and 0.3086, respectively (McFadden 1974). A McFadden's pseudo R^2 between 0.2 and 0.4, like that determined using the three-parameter 2009 model, is considered a particularly good model fit and corresponds approximately to values of 0.7 and 0.9 in ordinary least squares regression (Domencich and McFadden 1975).

Discussion

The statistically significant relationship between cumulative hours of suboptimal (<82%) RH and nymphal *I. scapularis* activity supports the laboratory results of Rodgers et al. (2007) and confirms the influence of sustained periods of suboptimal RH on nymphal blacklegged tick activity in the field. Rodgers and colleagues (2007) reported a threshold (critical equilibrium activity; see Knulle and Rudolph 1982) of 82% RH, below which the moisture deficit would be too large for *I. scapularis* nymphs to easily extract moisture from the air. In addition, there was a significant negative relationship between TempToS and total nymphs sampled, which could result from a decrease in questing during the warmer parts of the day owing to increased water loss, forcing ticks to seek shelter in the depths of the leaf litter to rehydrate. The significant effect of AvgRH14, but not the RH recorded the week of sampling, could result from a lag time in the relationship between suboptimal RH and tick activity levels during drier summers (e.g., 2010). This is likely due more to its effect on tick mortality, than questing activity. Questing ticks may be able to submerge into the lower leaf litter layer to rehydrate during periods of suboptimal humidity, but will be unable to recover if this duration is too long. It is reasonable to suggest that this would not happen instantaneously and could be demonstrated with a 1-wk lag. Indeed, the accumulation of suboptimal moisture conditions has a negative impact on tick survival and has been identified as a significant predictive variable

Table 2. Multiple negative binomial regression and five best-fit models using AIC selection of the most significant variables for year 2009

Model evaluation (2009)	Total variables	AvgRH14 (*P* value)	CumHrsSub7 d (*P* value)	DoY (*P* value)	LgToS (*P* value)	MinRH (*P* value)	AIC	McFadden pseudo R^2
AvgRH14, DoY, MinRH	3	**0.0767**		**0.001**		**0.0038**	**436.6223**	**0.2822**
AvgRH14, CumHrsSub7 d, DoY, MinRH	4	0.4374	0.2206	0.0189		0.0433	437.3113	0.2815
AvgRH14, DoY, LgToS, MinRH	4	0.0759		0.0001	0.6629	0.0228	438.4319	0.2821
AvgRH14, CumHrsSub7 d, DoY, LgToS, MinRH	5	0.4315	0.2235	0.0182	0.6798	0.1087	438.9234	0.2815
AvgRH14, CumHrsSub7 d, DoY	3	0.5852	0.0188	0.1092			439.0456	0.2833

Bold values highlight the smallest AIC value and indicate best-fit model. *P* values are a result of negative binomial regression.

Table 3. Multiple negative binomial regression and five best-fit models using AIC selection of most significant variables for year 2010

Model evaluation (2010)	Total variables	AvgRH14 (*P* value)	CumHrsSub7 d (*P* value)	DoY (*P* value)	TempToS (*P* value)	AIC	McFadden pseudo R^2
AvgRH14, TempToS	**2**	**0.0008**			**0.0095**	**478.7334**	**0.3086**
AvgRH14, CumHrsSub7 d, TempToS	3	0.0009	0.6371		0.0348	480.5104	0.0645
AvgRH14, DoY, TempToS	3	0.0009		0.9171	0.0238	480.7226	0.3125
AvgRH14, DoY, CumHrsSub7 d, TempToS	4	0.0049	0.3973	0.4757	0.0293	481.9957	0.3117
AvgRH14, CumHrsSub7 d	2	0.0024	0.0945			501.9808	0.3196

Bold values highlight the smallest AIC value and indicate best-fit model. *P* values are a result of negative binomial regression.

of seasonal nymphal tick abundance (Berger et al. 2014).

Vail and Smith (1998) identified a positive relationship between RH recorded at the leaf litter surface on days of drag sampling and nymphal blacklegged tick activity. The authors estimated tick host-seeking behavior by fitting drag-sample data to an exponential curve to account for seasonal changes in population density; residuals around this fitted curve were regressed against leaf litter RH measurements explaining 44% of the variance (Vail and Smith 1998). Likewise, multiple regression of temperature and RH explained 51% of the variance in field data samples ($R^2 = 0.51$; $P = 0.04$; Vail and Smith 1998). The lack of association between RH recorded at the leaf litter surface on days of sampling in our current study is likely due to the fact that mean RH at time of sampling was near or above the threshold in both years (2009: 84.38%; 2010: 75.35%). While 75% RH is considered below the threshold, it is still on the upper end of the tick survival model constructed by Rodgers and colleagues (2007).

The results of our study indicate that the cumulative number of hours below the RH threshold (82%) is a significant environmental parameter influencing patterns of nymphal tick activity. It might be that annual variability in nymphal tick abundance and Lyme disease risk can be explained by periods of suboptimal RH exposure (Berger et al. 2014). We suggest that in years where moisture is not limiting (e.g., 2009), ticks are able to descend into the leaf litter layer to rehydrate when needed and can resume questing for a host. Alternatively, in drier years, it may be more difficult for host-seeking ticks to find refuge and rehydrate within the leaf litter layer, resulting in decreased nymphal activity and possible mortality as a result of desiccation. In the process of selection of the best-fit models for each year of study, multiple negative binomial regression demonstrated climatic variables contributed more to the model than DoY, indicating that a RH variable was more indicative of nymphal activity than the tick's natural seasonal decline (indicated by DoY). The variable AvgRH14 was identified as a factor in both best-fit models (Tables 2 and 3), suggesting it is an important contributor to patterns of nymphal tick abundance and, as it is recorded before population estimates, could be used in the development of a predictive disease risk model. A likely reason for AvgRH14 being borderline significant in 2009 and significant in 2010 (Table 1) may be because of a difference in the number of samples taken in both seasons. Because of the extreme rain events of 2009, AvgRH14 values were missing for some sampling days and so unavailable for model development. During the relatively wetter sampling season, the greater moisture availability did not impose a strong desiccation stress on nymphal tick questing activity (Table 1).

The fact that our results demonstrate one best-fit model for each of the two years studied, we propose that it is a result of the contrasting weather differences experienced by questing ticks between both years. During years (e.g., 2009) where moisture availability is not limiting and mean weekly daytime RH values are above threshold (84.38%), age (indicated by the variable DoY) and MinRH will contribute more to AvgRH14 in predicting seasonal tick activity and abundance. Alternatively, during relatively drier years (e.g., 2010) where questing ticks are under more stress, a simpler model that includes temperature at time of sampling (TempToS) will be more suitable. Both models, however, demonstrate the role of microclimatic environmental variables on nymphal tick activity and abundance.

While the total number of sampled nymphal ticks differed among study areas in both years, study areas did not differ in terms of site characteristics (e.g., forest cover, land-use, etc.). One distinguishing feature of the Scituate study site, however, is its location adjacent to the state's water reservoir. We hypothesized that the results in this location, and the fact that the two 500-m^2 plots located within the closest proximity to the shores of the reservoir were also those that generally reported higher values of tick abundance and activity, was likely because of the increased availability of moisture within the environment.

The relationship between microclimatic environmental factors and the behavioral activity and abundance of *I. scapularis* is very complex. It is possible that host abundance patterns may have played a role in tick abundance between years, and because it has not been accounted for within this field study, provides a limitation of our findings. Despite this limitation, evidence of the presence of white-tailed deer (e.g., animal itself, or deer scat) was found across all sampling site locations and is assumed to be relatively uniform across all sites.

Studies that have not found significant relationships between moisture availability and *I. scapularis* activity have used general climate indexes or coarse scale (e.g., monthly and yearly) precipitation values (Ostfeld et al. 2006, Schulze et al. 2009), and have not considered both the level and the duration of suboptimal RH exposure on tick survival in combination. The relationship between nymphal blacklegged tick activity and its environment is both complex and characterized by interactions among several variables. It is likely that simple weather indexes such as the Palmer Hydrological Drought Index or precipitation cannot reliably predict tick abundance and Lyme disease risk because these variables are too coarse to capture this complex relationship.

Future studies should investigate the timing of extended periods of suboptimal RH, as events early in the nymph's expected life-cycle could have a significant negative impact on both blacklegged nymph survival and Lyme disease risk. Perret et al. (2004) reported that abrupt declines in questing *Ixodes ricinus* L. ticks, the primary vector of Lyme disease in Europe, coincided with drought events, defined by either declines in maximum RH (mostly occurring at night) or increases in maximum saturation deficit (mostly recorded during the day). After a brief drought event in June, the nymphal tick populations examined in the study by Perret et al. (2004) were unable to recover even partially. Identifying tick-adverse RH events, and related tick mortality, could potentially be helpful in explaining spatial distributions of blacklegged ticks as well as frequently observed interannual variability in nymphal blacklegged tick populations. Monitoring or modeling RH in blacklegged tick habitat also could be used in predicting seasonal risk for Lyme disease and other infections transmitted by blacklegged ticks.

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