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Seasonal activity patterns of host-seeking *Ixodes scapularis* (Acari: Ixodidae) in Minnesota, 2015–2017

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Abstract

As the primary vector of Lyme disease spirochetes and several other medically significant pathogens, *Ixodes scapularis* presents a threat to public health in the United States. The incidence of Lyme disease is growing rapidly in upper midwestern states, particularly Michigan, Minnesota, and Wisconsin. The probability of a tick bite, acarological risk, is affected by the phenology of host-seeking *I. scapularis*. Phenology has been well-studied in northeastern states, but not in the Upper Midwest. We conducted biweekly drag sampling across 4 woodland sites in Minnesota between April and November from 2015 to 2017. The majority of ticks collected were *I. scapularis* (82%). Adults were active throughout our entire 8-month collection season, with sporadic activity during the summer, larger peaks in activity observed in April, and less consistent and lower peaks observed in October. Nymphs were most active from May through August, with continuing low-level activity in October, and peak activity most commonly observed in June. The observed nymphal peak corresponded with the typical peak in reported human Lyme disease and anaplasmosis cases. These findings are consistent with previous studies from the Upper Midwest and highlight a risk of human exposure to *I. scapularis* at least from April through November. This information may aid in communicating the seasonality of acarological risk for those living in Minnesota and other upper midwestern states as well as being relevant to the assessment of the ecoepidemiology of Lyme disease and the modeling of transmission dynamics.

Keywords

Ixodes scapularis ; blacklegged tick; phenology; Minnesota; Lyme disease

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Supplementary Material

Supplementary material are available at *Journal of Medical Entomology* online.

Introduction

The blacklegged tick (*Ixodes scapularis*) and its associated pathogens pose an increasing public health threat in the United States, with established and expanding regional foci in the Northeast and Upper Midwest (Eisen et al. 2016, Eisen and Eisen 2018, Fleshman et al. 2021, 2022). *Ixodes scapularis* is a vector of 7 human pathogens that are known to circulate in the upper midwestern United States: *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae) sensu stricto and *Bo. mayonii* (Spirochaetales: Spirochaetaceae) (Lyme disease), *Bo. Miyamotoi* (Spirochaetales: Spirochaetaceae) (*Bo. miyamotoi* disease), *Anaplasma phagocytophilum* (Rickettsiales: Anaplasmataceae) (anaplasmosis), *Ehrlichia muris euclairensis* (Rickettsiales: Ehrlichiaeceae) (a form of ehrlichiosis), *Babesia microti* (Piroplasmida: Babesiidae) (babesiosis), and Powassan virus (a neuroinvasive viral disease) (Barbour et al. 2009, Pritt et al. 2011, 2016, Johnson et al. 2018b, Lehane et al. 2021, Fleshman et al. 2022). In order to define habitat types and geographic locations (e.g., counties) where persons are at risk for exposure to ticks and tickborne pathogens, several studies have explored changes in the distribution of *I. scapularis*, its associated pathogens, and acarological risk in the Upper Midwest (Lee et al. 2013, 2019, Robinson et al. 2015, Johnson et al. 2018a, 2018b, Foster et al. 2022). However, relatively few studies have been conducted in the region with the goal of describing the phenology of host-seeking *I. scapularis*, which provides information on when persons are at risk for tick bites (Neitzel et al. 1993, Brinkerhoff et al. 2011, Hamer et al. 2012, Diuk-Wasser et al. 2014, Stromdahl et al. 2014, Ogden et al. 2018).

The phenology of *I. scapularis* has been well-described in the northeastern United States, with an asynchronous pattern wherein nymphal activity precedes larval host-seeking. Peak host-seeking activity of nymphs is typically observed in early summer while peak host-seeking activity of larvae is most commonly observed in late summer (Piesman et al. 1987, Yuval and Spielman 1990, Ostfeld et al. 1996, Stafford et al. 1998, Falco et al. 1999, Simmons et al. 2015, Elias et al. 2020). Similar patterns have been observed in the Northeast for *I. scapularis* collected directly from humans through passive surveillance systems (Xu et al. 2016, Little et al. 2019, Rounsville et al. 2021). *Ixodes scapularis* nymphs are considered the most epidemiologically important life stage with adults also being capable of transmitting pathogens (Stafford et al. 1998, Pepin et al. 2012). The relative timing of nymphal and larval emergence is important as well as asynchronous peaks may promote the transmission of *Bo. burgdorferi* s.s., while synchronous peaks may increase the rate of co-feeding between life stages potentially facilitating the transmission of other pathogens (Ogden et al. 2007, Hassett and Thangamani 2021).

The phenology of questing *I. scapularis* in the Upper Midwest has received less attention by researchers than that in the Northeast, but *I. scapularis* phenology has generally been observed to be similar, with adults most active in the spring and fall and nymphs active in the early summer (Neitzel et al. 1993, Diuk-Wasser et al. 2014, Stromdahl et al. 2014, Ogden et al. 2018). Unlike northeastern *I. scapularis* populations, in the Upper Midwest, the larval peak has been observed to overlap with the nymphal peak in the early summer (Brinkerhoff et al. 2011, Hamer et al. 2012). Documenting when each life stage is questing for hosts aids in understanding seasonal variation in risk for tickborne diseases (Piesman et

al. 1987, Moore et al. 2014, Lin et al. 2019). We documented the host-seeking activity of *I. scapularis* at 4 geographically distinct woodland sites throughout Minnesota in order to improve our understanding of the temporal risk for exposure to *I. scapularis* nymphs and adults. We also aimed to assess the interannual and geographic variability in host-seeking phenology and determine the relative timing of the activity peaks for larvae and nymphs.

Materials and Methods

Site Description

Four geographically distinct sites on public land in Minnesota were chosen to assess host-seeking phenology of *I. scapularis*. These 4 sites were distributed across a latitudinal gradient and included 2 sites within the eastern broadleaf forest (Richard J. Dorer Memorial Hardwood (RJDMH hereafter) State Forest and William O'Brien State Park) and 2 sites within the Laurentian mixed forest (Itasca and St. Croix State Parks) (Fig. 1). Specific tick sampling transects at each site were identified based on accessibility, land manager recommendations, and a priori knowledge of *I. scapularis* established populations. Vegetation at all 4 sites is primarily deciduous, oak-dominated forest with dense leaf litter and understory, with the exception of the site at Itasca State Park, which is better described as mixed forest with hardwoods and pines. Specific tick sampling transects at each site were identified based on suitable *I. scapularis* habitat (i.e., wooded and brushy mesic areas with at least 50% canopy coverage) (Ostfeld et al. 1995, Guerra et al. 2002, Lubelczyk et al. 2004), accessibility, and land manager recommendations. We also collected temperature and precipitation data between April 1st and November 30th for each year. Data were collected from NOAA weather stations nearby each site, USC00210018 (Itasca), USC00211198 (RJDMH), USC00210190 (St. Croix), and USC00218450 (William O'Brien).

Tick Collections

Distance-based drag sampling was performed in which 2 samplers pulled a modified 1 m² white canvas cloth with weighted fingers over the ground to collect host-seeking *I. scapularis* (Siegel et al. 1991). In total, 750 m² were sampled at each site on each sampling occasion. Samplers stopped every 15 m to inspect the drag cloths and their clothing. Samplers wore light colored clothing taped to closed toe boots. Ticks found on researchers were also counted towards the total. Ticks of all life stages collected were returned to the transect of collection after being identified in the field by trained researchers. Atypical ticks of all life stages were collected for morphologic identification to the species level using published taxonomic keys (Keirans and Litwak 1989, Durdens and Keirans 1996, Coley 2015). The species, life stage, and number of ticks collected were recorded for each 15 m section of the transects. Sites were sampled every 2 weeks from April through November in 2015, 2016, and 2017. Tick dragging was only performed under favorable weather conditions for tick activity (i.e., no rain or snow cover with ambient air temperatures ≥ 4 °C). Transects were marked with flagging tape to ensure researchers sampled the same area on each visit and between years. Minor deviations were made on rare occasions when the route was impassable (i.e., downed tree or flooding).

Data Analysis

Peak densities for *I. scapularis* nymphs and adults were defined as the observed maximum number collected during our collection periods (April–November) per 750 m² collection divided by year, site, and life stage. Onset and cessation of nymphal host-seeking activity was defined as the first and last occasion nymphs were collected per collection period. The distribution of host-seeking adults was bimodal. Therefore, onset and cessation of adult host-seeking was defined as the earliest and latest dates of activity first in the spring (April–June) and then in the fall (October–November) within each calendar year. The *I. scapularis* nymph data had exponential increases and decreases on each site for most years. Separate models were constructed during the increasing phases of the peaks as well as the decreasing phases. We used the output from the models between the first collection day to the peak (increasing) of each site and from those peaks to the last collection day (decreasing) to predict the dates between which activity peaks were at 25% and 50% of their maximums (Eisen et al. 2002). All data used for the linear models were log-transformed, with +1 added to account for zeros. This allowed our data to conform with the assumption of normality and account for the exponential nature of the data. Normality was visually assessed by examining quantile–quantile plots of the model residuals. We also compared the AIC values of models using transformed and untransformed datasets. The transformed data sets performed significantly better ($\Delta AIC > 2$) for all models. These analyses were conducted for each site with all years (2015, 2016, 2017) combined. Data analyses were performed using the base package in R (v. 4.0.3) (R Core Team 2022). Our full dataset can be found as Supplemental Materials. In Fig. 2, density data are expressed as the percentage of ticks that are active per life stage at a given time point relative to the total numbers collected per life stage per year. This normalization of the data allowed us to directly compare phenology between life stages, years, and sites. We recognize that drag sampling does not accurately estimate larval abundance but expressing abundance as a percentage of totals collected provides reasonable estimates of seasonal host-seeking activity (Ginsberg et al. 2020).

Results

Site Visits and Weather Data

Over the 3 yr of study, a total of 46 visits were made each to St. Croix and William O'Brien State Parks. There were 47 visits to RJDMH State Forest and 48 visits to Itasca State Park. A total of 3,273 ticks were collected and identified by staff on transects with the majority (82%) of ticks being identified as *I. scapularis* (41% larvae, 34% adults, and 24% nymphs). An additional 14% of ticks were identified to be *Dermacentor variabilis* (Acari: Ixodidae) (93% adults and 7% larvae) and 4% were *D. albipictus*, all of which were larvae. The number of *I. scapularis* found on transects varied by life stage, collection date, and site. The average density of adults and nymphs collected per visit across all sites and years was 0.64 adults per 100 m² and 0.47 nymphs per 100 m² (Table 1). There was limited variation, with mean minimum temperature varying by no more than 4.8 °C and mean maximum varied by no more than (3.0 °C). There was a north-to-south gradient in temperature, with Itasca being the coldest and RJDMH being the warmest. Average cumulative precipitation was similar (699–801 mm) across 3 sites (Itasca, RJDMH, William O'Brien), but was lower on Itasca at

500 mm. Overall, 2016 was a wetter year, with the difference being most notable on Itasca and RJD MH.

Ixodes scapularis Activity

A peak in adult *I. scapularis* activity was generally observed in the spring, with a second smaller peak observed in the fall in some years. In some years, we did not observe a fall increase in host-seeking adult densities, as occurred at St. Croix in 2017 or Itasca in 2015, among others (Fig. 2). Adult *I. scapularis* were generally active across a broad range of dates, with the potential to be collected throughout the field season (April–November). The earliest collection of adults was on April 3, while the latest was on November 19. Nymphal questing activity was unimodal with most observations of peak activity occurring in between May and July (Table 2, Fig. 2), but they were often still collected in the fall through October. The earliest collection of nymphs was on April 21, while the latest was on November 3 (Table 2, Fig. 2). Our larval data are somewhat limited as activity was low or undetected in some years on several sites, specifically in Itasca and RJD MH in 2016 and 2017 as well as in William O'Brien in 2017. Among sites where activity was detected, the timing of peak larval host-seeking activity varied, generally occurring sometime between June and September. The timing of these peaks relative to those of *I. scapularis* nymphs also varied across sites and years, but often resulted in overlapping activity between nymphs and larvae (Fig. 2).

Generally, the increasing phase occurred more rapidly than the decreasing phase of the nymph activity peaks, with nymphs being collected in the fall through October, but rarely before May (Table 2, Fig. 2). This is reflected in the dates wherein nymphs are estimated to be at 25% and 50% of their peaks based upon our linear models (Table 3). Across sites and years, nymphs are estimated to be at 50% of their peak between June 2 and August 4, and 25% of their peak between May 14 and August 27 (Table 4). As with the observed peak densities, there is variation between sites and different years.

Dermacentor variabilis Activity

Dermacentor variabilis adults were active primarily in May and June across all sites and years. The earliest they were detected at any site was April 13 with the latest collection being on August 21. We did not have sufficient data for *D. variabilis* larvae and nymphs to provide any information regarding their activity peaks.

Discussion

We documented the seasonal host-seeking activity of *I. scapularis* by life stage in 4 field sites across Minnesota. Generally, in the context of Lyme disease in the eastern United States, *I. scapularis* nymphs are considered the most epidemiologically important life stage (Stafford et al. 1998, Pepin et al. 2012). Our data suggest that nymphs were active between May and August, with peak activity occurring in June and July. Of the confirmed Lyme disease cases reported in Minnesota, cases typically begin to be reported in May, peak in June, and continue into August (Moore et al. 2014). Specifically, of the 876 Lyme disease cases reported in 2018 with known illness onset dates, illness onsets peaked from June

through August (MDH 2022). This indicates likely tick exposure in late May through July, which aligns with the nymphal activity peaks we observed. Some of the variability in tick densities observed both within and between sites may be due to variation in field conditions or the time of day for sampling (Schulze and Jordan 2003). It is also possible that the dates for the 25% and 50% activity peaks calculated using our linear models are slightly inaccurate, as it is possible that we missed the true peak of nymphal activity, which would shift the dates predicted by our models. Despite this, our estimated activity dates largely match those of the observed peaks (Table 4) and align with previous observations for nymph activity in the Upper Midwest (Neitzel et al. 1993, Diuk-Wasser et al. 2014, Stromdahl et al. 2014, Ogden et al. 2018).

The phenology of immature *I. scapularis* can play an important role in pathogen transmission dynamics, with *Bo. burgdorferi* s.s. being particularly notable, as hosts can remain capable of infecting ticks for long periods of time (Lindsay et al. 1997). If nymphs emerge early in the season, prior to larvae, they can infect a larger portion of the reservoir host population before the larvae feed, facilitating the transmission of *Bo. burgdorferi* s.s. between generations of *I. scapularis* (Ogden et al. 2007). This phenological pattern is common in northeastern *I. scapularis* populations (Carey et al. 1981, Wilson and Spielman 1985, Schulze et al. 1986). Here, as previously observed (Brinkerhoff et al. 2011, Hamer et al. 2012), our data suggest that the activity peaks for *I. scapularis* nymphs and larvae in the Upper Midwest can overlap. Despite this, the infection prevalence of *Bo. burgdorferi* in *I. scapularis* is similar in the Northeast (Prusinski et al. 2014, Feldman et al. 2015, Lehane et al. 2021) and Upper Midwest (Johnson et al. 2018a, Lehane et al. 2021). It has been hypothesized that asynchronous peaks for the activity of larvae and nymphs facilitate increased transmission of *Bo. burgdorferi* (Ogden et al. 2007) but it is possible that different strains of *Bo. burgdorferi* dominate depending upon the timing of the larval and nymphal activity peaks (Gatewood et al. 2012, Hamer et al. 2012, Arsnoe et al. 2015). It is also possible that the transmission of other pathogens, like Powassan virus, may be facilitated by co-feeding (Hassett and Thangamani 2021). Ultimately, more research is needed regarding the impact of larval and nymphal phenology on the transmission of different *Bo. burgdorferi* strains and other *I. scapularis*-associated pathogens, particularly considering the variability observed in larval densities when drag cloths are the collection instrument.

Synchronicity between the activity peaks of the 2 life stages varied by year and collection site. Larvae were not consistently detected across all 4 sites and years of study, despite other life stages being present. Our data from the 2 sites with sufficient larval collections to observe patterns suggest that the larval and nymphal activity peaks can be synchronous (e.g., Itasca in 2017), with little evidence for a late summer larval peak (Fig. 2), as is often observed in northeastern populations (Carey et al. 1981, Wilson and Spielman 1985, Schulze et al. 1986). Larvae and nymphs have been observed feeding concurrently on small mammals in the Upper Midwest (Caporale et al. 2005). Our larval data should be interpreted with caution as drag sampling is not the best method for estimating larval tick densities due to their questing height (Mejlon and Jaenson 1997), patchy distribution (Daniels and Fish 1990), and strong effect of weather conditions on their questing activity (Schulze et al. 1997, Ginsberg et al. 2020). It is also possible that other *Ixodes* species were included in our *I. scapularis* counts, as ticks were identified in the field without the use of a microscope,

but previous work in Minnesota has shown that other *Ixodes* species are rarely collected (Johnson et al. 2018b). Despite these limitations, the overlapping activity of larvae and nymphs observed here matches previous observations of synchronous activity between the 2 life stages from the Upper Midwest (Brinkerhoff et al. 2011, Hamer et al. 2012).

While there was some variation between sites and years, adult *I. scapularis* host-seeking activity was generally bimodal with peak activity observed in the spring and a smaller peak in the fall. Sampling was not performed in the winter, so it is possible that adult *I. scapularis* were actively host-seeking when there was limited snow cover and temperatures were above the activity threshold temperature of 4 °C (Duffy and Campbell, 1994). There was no appreciable north-to-south pattern in activity across sites. There was also limited variation in temperature between years, so we cannot evaluate the effect of temperature on tick activity patterns. There was higher precipitation in 2016 on the Itasca and RJDMH sites, but we did not observe any consistent effect on *I. scapularis* activity. *Dermacentor variabilis* is an important vector for the agents of Rocky Mountain Spotted Fever (*Rickettsia rickettsii*) and tularemia (*Francisella tularensis*). Cases of both diseases are rare in Minnesota, but do occur occasionally. This species was not the focus of this study as their primary habitat of moist and humid forest-grassland ecotones (Sonenshine and Stout 1968, Sonenshine and Levy 1972) were not directly targeted, yet adult host-seeking *D. variabilis* were still encountered in our wooded sites in Minnesota. Their activity peaked in June, and few were collected after August. This adult tick activity coincided with adult *I. scapularis* activity in the spring and early summer, but we did not observe *D. variabilis* questing behavior in the fall.

Previous tick surveillance efforts in Minnesota have demonstrated that the range of *I. scapularis* is expanding and each of its 7 associated human pathogens have been detected in host-seeking nymphs and adults (Johnson et al. 2018b, Lehane et al. 2020). Our findings are consistent with previous studies (Brinkerhoff et al. 2011, Hamer et al. 2012) and highlight a risk of human exposure to *I. scapularis* at least from April through November. In areas where *I. scapularis* is emerging, the public may consider ticks a threat predominantly in the summer, although they are active throughout the spring, fall, and potentially the winter. The potential for exposure to infected *I. scapularis* throughout the spring, summer, and fall is important to relay in public health messaging so people can incorporate tick bite prevention measures and awareness into their daily routines throughout the year.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Arsnoe IM, Hickling GJ, Ginsberg HS, McElreath R, Tsao JI. Different populations of blacklegged tick nymphs exhibit differences in questing behavior that have implications for human Lyme disease risk. *PLoS One*. 2015;10(5):e0127450. 10.1371/journal.pone.0127450 [PubMed: 25996603]
- Barbour AG, Bunikis J, Travinsky B, Hoen AG, Diuk-Wasser MA, Fish D, Tsao JI. Niche partitioning of *Borrelia burgdorferi* and *Borrelia miyamotoi* in the same tick vector and mammalian reservoir species. *Am J Trop Med Hyg*. 2009;81(6):1120–1131. 10.4269/ajtmh.2009.09-0208 [PubMed: 19996447]
- Brinkerhoff RJ, Folsom-O’Keefe CM, Streby HM, Bent SJ, Tsao K, Diuk-Wasser MA. Regional variation in immature *Ixodes scapularis* parasitism on North American songbirds: implications for transmission of the Lyme pathogen, *Borrelia burgdorferi*. *J Med Entomol*. 2011;48:422–428. [PubMed: 21485384]
- Caporale DA, Johnson CM, Millard BJ. Presence of *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae) in southern Kettle Moraine State Forest, Wisconsin, and characterization of strain W97F51. *J Med Entomol*. 2005;42(3):457–472. 10.1093/jmedent/42.3.457 [PubMed: 15962800]
- Carey MG, Carey AB, Main AJ, Krinsky WL, Sprance HE. *Ixodes dammini* (Acari: Ixodidae) in forests in Connecticut. *J Med Entomol*. 1981;18(2):175–176. 10.1093/jmedent/18.2.175 [PubMed: 7288840]
- Coley K. Identification guide to larval stages of ticks of medical importance in the USA. University Honors Program Theses, Paper 110; 2015.
- Daniels TJ, Fish D. Spatial distribution and dispersal of unfed larval *Ixodes dammini* (Acari: Ixodidae) in southern New York. *Environ Entomol*. 1990;19(4):1029–1033. 10.1093/ee/19.4.1029
- Diuk-Wasser MA, Gatewood AG, Cortinas MR, Yaremych-Hamer S, Tsao J, Kitron U, Hickling G, Brownstein JS, Walker E, Piesman J, et al. Spatiotemporal patterns of host-seeking *Ixodes scapularis* nymphs (Acari: Ixodidae) in the United States. *J Med Entomol*. 2014;43:166–176.
- Duffy DC, Campbell SR. Ambient air temperature as a predictor of activity of adult *Ixodes scapularis* (Acari: Ixodidae). *J Med Ent*. 1994;31(1):178–180.
- Durden LA, Keirans JE. Nymphs of the genus *Ixodes* (Acari: Ixodidae) of the United States: taxonomy, identification. Key, distribution, hosts, and medical/veterinary importance. Annapolis (MD): Entomological Society of America; 1996.
- Eisen L, Eisen RJ, Lane RS. Seasonal activity patterns of *Ixodes pacificus* nymphs in relation to climatic conditions. *Med Vet Entomol*. 2002;16(3):235–244. 10.1046/j.1365-2915.2002.00372.x [PubMed: 12243224]
- Eisen RJ, Eisen L. The blacklegged tick, *Ixodes scapularis*: an increasing public health concern. *Trends Parasitol*. 2018;34(4):295–309. 10.1016/j.pt.2017.12.006 [PubMed: 29336985]
- Eisen RJ, Eisen L, Beard CB. County-scale distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the continental United States. *J Med Entomol*. 2016;53(2):349–386. 10.1093/jme/tjv237 [PubMed: 26783367]
- Elias SP, Maasch KA, Anderson NT, Rand PW, Lacombe EH, Robich RM, Lubelczyk CB, Smith RP. Decoupling of blacklegged tick abundance and Lyme disease incidence in Southern Maine, USA. *J Med Entomol*. 2020;57(3):755–765. 10.1093/jme/tjz218 [PubMed: 31808817]
- Falco RC, McKenna DF, Daniels TJ, Nadelman RB, Nowakowski J, Fish D, Wormser GP. Temporal relation between *Ixodes scapularis* abundance and risk for Lyme disease associated with erythema migrans. *Am J Epidemiol*. 1999;149(8):771–776. 10.1093/oxfordjournals.aje.a009886 [PubMed: 10206627]
- Feldman KA, Connally NP, Hojgaard A, Jones EH, White JL, Hinckley AF. Abundance and infection rates of *Ixodes scapularis* nymphs collected from residential properties in Lyme disease-endemic

areas of Connecticut, Maryland, and New York. *J Vector Ecol.* 2015;40(1):198–201. 10.1111/jvec.12153 [PubMed: 26047204]

- Fleshman AC, Foster E, Maes SE, Eisen RJ. Reported county-level distribution of seven human pathogens detected in host-seeking *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the contiguous United States. *J Med Entomol.* 2022;59(4):1328–1335. [PubMed: 35583265]
- Fleshman AC, Graham CB, Maes SE, Foster E, Eisen RJ. Reported county-level distribution of Lyme disease spirochetes, *Borrelia burgdorferi* sensu stricto and *Borrelia mayonii* (Spirochaetales: Spirochaetaceae), in host-seeking *Ixodes scapularis* and *Ixodes pacificus* ticks (Acari: Ixodidae) in the contiguous United States. *J Med Entomol.* 2021;58(3):1219–1233. 10.1093/jme/tjaa283 [PubMed: 33600574]
- Foster E, Burtis J, Sidge JL, Tsao JI, Bjork J, Liu G, Neitzel DF, Lee X, Paskewitz S, Caporale D, et al. Inter-annual variation in prevalence of *Borrelia burgdorferi* sensu stricto and *Anaplasma phagocytophilum* in host-seeking *Ixodes scapularis* (Acari: Ixodidae) at long-term surveillance sites in the upper midwestern United States: Implications for public health practice. *Ticks Tick Borne Dis.* 2022;13(2):101886. 10.1016/j.ttbdis.2021.101886 [PubMed: 34929604]
- Gatewood AG, Liebman KA, Vourc'h G, Bunikis J, Hamer SA, Corinas R, Melton F, Cislo P, Kirton U, Tsao J, et al. Climate and tick seasonality are predictors of *Borrelia burgdorferi* genotype distribution. *Appl Environ Microbiol.* 2012;75:2476–2483.
- Ginsberg HS, Rulison EL, Miller JL, Pang G, Arsnoe IM, Hickling GJ, Ogden NH, LeBrun RA, Tsao JI. Local abundance of *Ixodes scapularis* in forests: effects of environmental moisture, vegetation characteristics, and host abundance. *Ticks Tick Borne Dis.* 2020;11(1):101271. 10.1016/j.ttbdis.2019.101271 [PubMed: 31677969]
- Guerra M, Walker E, Jones C, Paskewitz S, Cortinas MR, Stancil A, Beck L, Bobo M, Kitron U. Predicting the risk of Lyme disease: habitat suitability for *Ixodes scapularis* in the north central United States. *Emerg Infect Dis.* 2002;8(3):289–297. 10.3201/eid0803.010166 [PubMed: 11927027]
- Hamer SA, Hickling GJ, Sidge JL, Walker ED, Tsao JI. Synchronous phenology of juvenile *Ixodes scapularis*, vertebrate host relationships, and associated patterns of *Borrelia burgdorferi* ribotypes in the Midwestern United States. *Ticks Tick Borne Dis.* 2012;3(2):65–74. 10.1016/j.ttbdis.2011.11.004 [PubMed: 22297162]
- Hassett EM, Thangamani S. Ecology of Powassan Virus in the United States. *Microorganisms.* 2021;9(11):2317. 10.3390/microorganisms9112317 [PubMed: 34835443]
- Johnson TL, Boegler KA, Clark RJ, Delorey MJ, Bjork JK, Dorr FM, Schiffman EK, Neitzel DF, Monaghan AJ, Eisen RJ. An acarological risk model predicting the density and distribution of host-seeking *Ixodes scapularis* nymphs in Minnesota. *Am J Trop Med.* 2018a;98:1671.
- Johnson TL, Graham CB, Maes SE, Hojgaard A, Fleshman A, Boegler KA, Delory MJ, Slater KS, Karpathy SE, Bjork JK, et al. Prevalence and distribution of seven human pathogens in host-seeking *Ixodes scapularis* (Acari: Ixodidae) nymphs in Minnesota, USA. *Ticks Tick Borne Dis.* 2018b;9(6):1499–1507. 10.1016/j.ttbdis.2018.07.009 [PubMed: 30055987]
- Keirans JE, Litwak TR. Pictorial key to the adults of hard ticks, family Ixodidae (Ixodida: Ixodoidea), east of the Mississippi river. *J Med Entomol.* 1989;26(5):435–448. 10.1093/jmedent/26.5.435 [PubMed: 2795615]
- Lee X, Hardy K, Johnson DH, Paskewitz SM. Hunter-killed deer surveillance to assess changes in the prevalence and distribution of *Ixodes scapularis* (Acari: Ixodidae) in Wisconsin. *J Med Entomol.* 2013;50(3):632–639. 10.1603/me12234 [PubMed: 23802460]
- Lee X, Murphy DS, Hoang Johnson D, Paskewitz SM. Passive animal surveillance to identify ticks in Wisconsin, 2011–2017. *Insects.* 2019;10(9):289. 10.3390/insects10090289 [PubMed: 31500362]
- Lehane A, Maes SE, Graham CB, Jones E, Delorey M, Eisen RJ. Prevalence of single and coinfections of human pathogens in *Ixodes* ticks from five geographical regions in the United States, 2013–2019. *Ticks Tick Borne Dis.* 2021;12(2):101637. 10.1016/j.ttbdis.2020.101637 [PubMed: 33360805]
- Lin S, Shrestha S, Prusinski MA, White JL, Lukacik G, Smith M, Jianhai L, Backenson B. The effects of multiyear and seasonal weather factors on incidence of Lyme disease and its vector in New York State. *Sci Total Environ.* 2019;665:1182–1188. [PubMed: 30893749]

- Lindsay LR, Barker IK, Surgeoner GA, McEwen SA, Campbell GD. Duration of *Borrelia burgdorferi* infectivity in white-footed mice for the tick vector *Ixodes scapularis* under laboratory and field conditions in Ontario. *J Wildl Dis.* 1997;33(4):766–775. 10.7589/0090-3558-33.4.766 [PubMed: 9391960]
- Little EA, Anderson JF, Stafford KC, Eisen L, Eisen RJ, Molaei G. Predicting spatiotemporal patterns of Lyme disease incidence from passively collected surveillance data for *Borrelia burgdorferi* sensu lato-infected *Ixodes scapularis* ticks. *Ticks Tick Borne Dis.* 2019;10(5):970–980. 10.1016/j.ttbdis.2019.04.010 [PubMed: 31101553]
- Lubelczyk CB, Elias SP, Rand PW, Holman MS, Lacombe EH, Smith RP. Habitat associations of *Ixodes scapularis* (Acari: Ixodidae) in Maine. *Environ Entomol.* 2004;33(4):900–906. 10.1603/0046-225x-33.4.900
- MDH. Minnesota Department of Health. Lyme Disease Statistics. 2022 [accessed 2022 Jun 24]. <https://www.health.state.mn.us/diseases/lyme/statistics.html#:~:text=In%202018%2C%2095%20confirmed%20Lyme,evidence%20of%20infection%20were%20reported.>
- Mejlon HA, Jaenson TG. Questing behaviour of *Ixodes ricinus* ticks (Acari: Ixodidae). *Exp Appl Acarol.* 1997;21:747–754.
- Moore SM, Eisen RJ, Monaghan A, Mead P. Meteorological influences on the seasonality of Lyme disease in the United States. *Am J Trop Med Hyg.* 2014;90(3):486–496. 10.4269/ajtmh.13-0180 [PubMed: 24470565]
- Neitzel DF, Jarnefeld JL, Sjogren RD. An *Ixodes scapularis* (deer tick) distribution study in the Minneapolis-St. Paul, Minnesota area. *Soc Vect Ecol.* 1993;18:67–73.
- Ogden NH, Bigras-Poulin M, O'Callaghan CJ, Barker IK, Kurtenbach K, Lindsay LR, Charron DF. Vector seasonality, host infection dynamics and fitness of pathogens transmitted by the tick *Ixodes scapularis*. *Parasitology.* 2007;134(Pt 2):209–227. 10.1017/S0031182006001417 [PubMed: 17032476]
- Ogden NH, Pang G, Ginsberg HS, Hickling GJ, Burke RL, Beati L, Tsao JI. Evidence for geographic variation in life-cycle processes affecting phenology of the Lyme disease vector *Ixodes scapularis* (Acari: Ixodidae) in the United States. *J Med Entomol.* 2018;55(6):1386–1401. 10.1093/jme/tjy104 [PubMed: 29986046]
- Ostfeld RS, Cepeda OM, Hazler KR, Miller MC. Ecology of Lyme disease: habitat associations of ticks (*Ixodes scapularis*) in a rural landscape. *Ecol Appl.* 1995;5(2):353–361. 10.2307/1942027
- Ostfeld RS, Hazler KR, Cepeda OM. Temporal and spatial dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a rural landscape. *J Med Entomol.* 1996;33(1):90–95. 10.1093/jmedent/33.1.90 [PubMed: 8906910]
- Pepin KM, Eisen RJ, Mead PS, Piesman J, Fish D, Hoen AG, Barbour AG, Hamer S, Diuk-Wasser MA. Geographic variation in the relationship between human Lyme disease incidence and density of infected host-seeking *Ixodes scapularis* nymphs in the Eastern United States. *Am J Trop Med.* 2012;86:1062.
- Piesman J, Mather TN, Dammin GJ, Telford SR, Lastavica CC, Spielman A. Seasonal variation of transmission risk of Lyme disease and human babesiosis. *Am J Epidemiol.* 1987;126(6):1187–1189. 10.1093/oxfordjournals.aje.a114757 [PubMed: 3687924]
- Pritt BS, Respicio-Kingry LB, Sloan LM, Schriefer ME, Replogle AJ, Bjork J, Liu G, Kingry LC, Mead PS, Neitzel DF, et al. *Borrelia mayonii* sp. nov., a member of the *Borrelia burgdorferi* sensu lato complex, detected in patients and ticks in the upper midwestern United States. *Int J Syst Evol.* 2016;66:4878.
- Pritt BS, Sloan LM, Johnson DKH, Munderloh UG, Paskewitz SM, McElroy KM, McFadden JD, Binnicker MJ, Neitzel DF, Liu G, et al. Emergence of a new pathogenic Ehrlichia species, Wisconsin and Minnesota, 2009. *NEJM.* 2011;365:422–429. [PubMed: 21812671]
- Prusinski MA, Kokas JE, Hukey KT, Kogut SJ, Lee J, Backenson PB. Prevalence of *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae), *Anaplasma phagocytophilum* (Rickettsiales: Anaplasmataceae), and *Babesia microti* (Piroplasmida: Babesiidae) in *Ixodes scapularis* (acari: Ixodidae) collected from recreational lands in the Hudson Valley region, New York state. *J Med Entomol.* 2014;51(1):226–236. 10.1603/me13101 [PubMed: 24605473]

- R Core Team. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; 2022. <https://www.R-project.org/>.
- Robinson SJ, Neitzel DF, Moen RA, Craft ME, Hamilton KE, Johnson LB, Mulla DJ, Munderloh UG, Redig PT, Smith KE, et al. Disease risk in a dynamic environment: the spread of tick-borne pathogens in Minnesota, USA. *EcoHealth*. 2015;12(1):152–163. 10.1007/s10393-014-0979-y [PubMed: 25281302]
- Rounsville TF, Dill GM, Bryant AM, Desjardins CC, Dill JF. Statewide passive surveillance of *Ixodes scapularis* and associated pathogens in Maine. *Vector Borne Zoonotic Dis*. 2021;21(6):406–412. 10.1089/vbz.2020.2724 [PubMed: 33661033]
- Schulze TL, Bowen GS, Lakat MF, Parkin WE, Shisler JK. Seasonal abundance and hosts of *Ixodes dammini* (Acari: Ixodidae) and other ixodid ticks from an endemic Lyme disease focus in New Jersey, USA. *J Med Entomol*. 1986;23(1):105–109. 10.1093/jmedent/23.1.105 [PubMed: 3950921]
- Schulze TL, Jordan RA. Meteorologically mediated diurnal questing of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae) nymphs. *J Med Entomol*. 2003;40(4):395–402. 10.1603/0022-2585-40.4.395 [PubMed: 14680102]
- Schulze TL, Jordan RA, Hung RW. Biases associated with several sampling methods used to estimate abundance of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *J Med Entomol*. 1997;34(6):615–623. 10.1093/jmedent/34.6.615 [PubMed: 9439115]
- Siegel JP, Kitron U, Bouseman JK. Spatial and temporal distribution of *Ixodes dammini* (Acari: Ixodidae) in a northwestern Illinois state park. *J Med Entomol*. 1991;28(1):101–104. 10.1093/jmedent/28.1.101 [PubMed: 2033600]
- Simmons TW, Shea J, Myers-Claypole MA, Kruse R, Hutchinson ML. Seasonal activity, density, and collection efficiency of the blacklegged tick (*Ixodes scapularis*) (Acari: Ixodidae) in Mid-Western Pennsylvania. *J Med Entomol*. 2015;52(6):1260–1269. 10.1093/jme/tjv132 [PubMed: 26336271]
- Sonenshine DE, Levy GF. Ecology of the American dog tick, *Dermacentor variabilis*, in a study area in Virginia. 2. distribution in relation to vegetative types. *Ann Entomol Soc*. 1972;65:1175–1182.
- Sonenshine DE, Stout IJ. Use of old-field habitats by the American dog tick, *Dermacentor variabilis*. *Ann Entomol Soc*. 1968;61:679–686.
- Stafford KC, Cartter ML, Magnarelli LA, Ertel SH, Mshar PA. Temporal correlations between tick abundance and prevalence of ticks infected with *Borrelia burgdorferi* and increasing incidence of Lyme disease. *J Clin Microbiol*. 1998;36(5):1240–1244. 10.1128/JCM.36.5.1240-1244.1998 [PubMed: 9574684]
- Stromdahl E, Hamer S, Jenkins S, Sloan L, Williamson P, Foster E, Nadolny R, Elkins C, Vince M, Pritt B. Comparison of phenology and pathogen prevalence, including infection with the *Ehrlichia muris*-like (EML) agent, of *Ixodes scapularis* removed from soldiers in the midwestern and the northeastern United States over a 15 year period (1997-2012). *Parasites Vectors*. 2014;7:1–12. [PubMed: 24411014]
- Wilson ML, Spielman A. Seasonal activity of immature *Ixodes dammini* (Acari: Ixodidae). *J Med Entomol*. 1985;22(4):408–414. 10.1093/jmedent/22.4.408 [PubMed: 4045938]
- Xu G, Mather TN, Hollingsworth CS, Rich SM. Passive surveillance of *Ixodes scapularis* (Say), their biting activity, and associated pathogens in Massachusetts. *Vector Borne Zoonotic Dis*. 2016;16(8):520–527. 10.1089/vbz.2015.1912 [PubMed: 27248292]
- Yuval B, Spielman A. Duration and regulation of the developmental cycle of *Ixodes dammini* (Acari: Ixodidae). *J. Medical Entomol*. 1990;27(2):196–201.

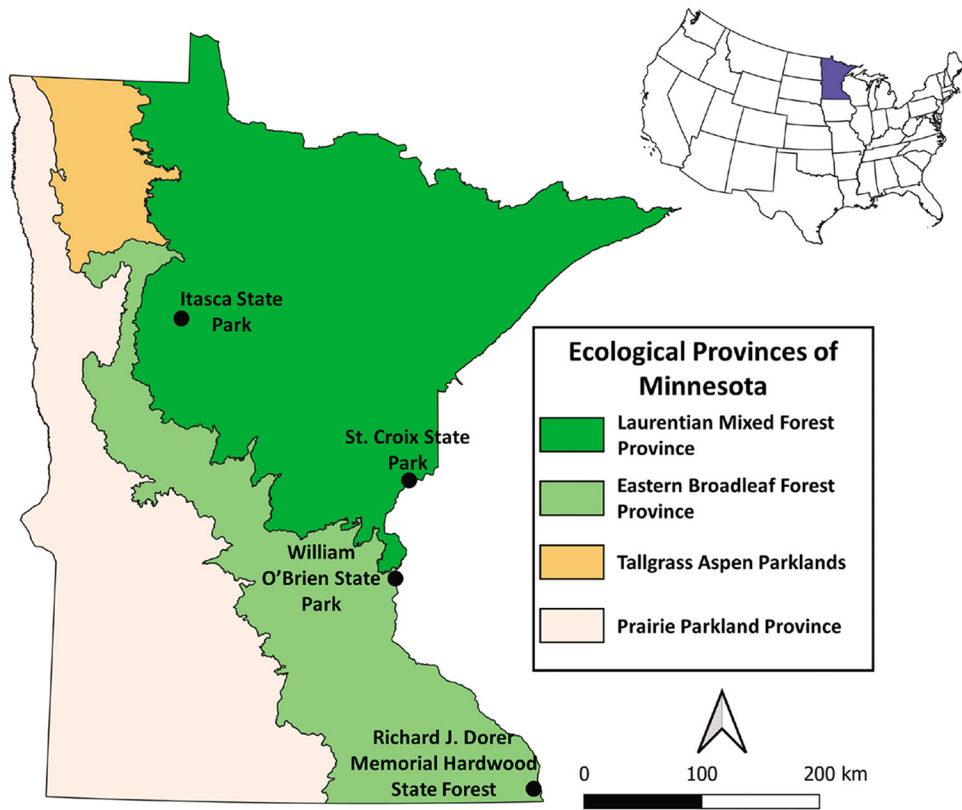


Fig. 1. Locations of the 4 collection sites in Minnesota. Minnesota is highlighted on the map of the lower 48 states.

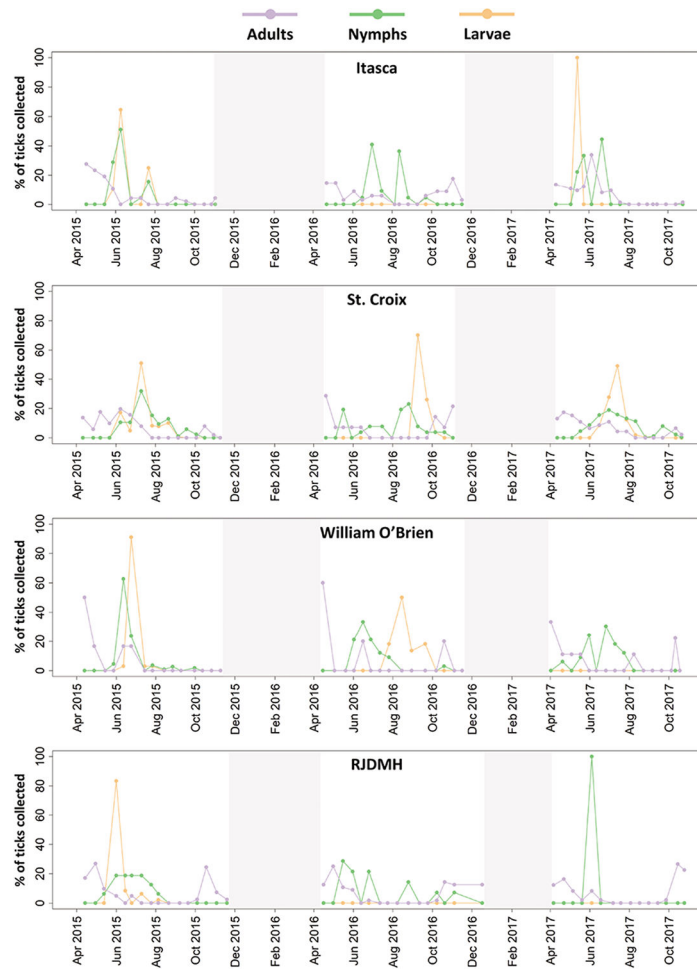


Fig. 2. Activity of *I. scapularis* adults (purple) nymphs (green), and larvae (orange) on each of the 4 collection sites (St. Croix, Itasca, RJDMH, William O'Brien) between 2015 and 2017. Data are presented as the percentage of ticks of each life stage collected within a season that were collected on each collection date. Shaded sections represent periods when no tick sampling occurred.

Maximum and average densities (per 100 m²) and total number of *I. scapularis* adults and nymphs on each of the 4 sites located in Minnesota between 2015 and 2017

Table 1.

Life stage	Avg/max	Year	Itasca State Park	St. Croix State Park	William O'Brien State Park	RJDMH State Forest	All sites	
Adults	Average (per visit)	2015	0.78	0.88	0.27	0.60	0.64	
		2016	0.58	0.46	0.05	0.97	0.52	
	Maximum (per visit)	2017	0.92	1.04	0.14	1.01	0.77	
		All Years	0.76	0.79	0.15	0.84	0.64	
	Total number of ticks collected	2015	3.47	2.93	1.87	2.67	3.47	
		2016	1.33	2.53	0.40	3.07	3.07	
		2017	4.27	2.27	0.67	3.60	4.27	
		All Years	4.27	2.93	1.87	3.60	4.27	
	Nymphs	Average (per visit)	2015	45	85	110	16	256
			2016	22	26	33	14	95
Maximum (per visit)		2017	9	265	33	2	309	
		All Years	76	376	176	32	660	
Total number of ticks collected		2015	0.38	0.71	0.98	0.13	0.55	
		2016	0.18	0.23	0.29	0.12	0.20	
		2017	0.08	2.36	0.28	0.02	0.67	
		All Years	0.21	1.09	0.50	0.09	0.47	
Total number of ticks collected		2015	3.07	3.60	9.20	0.40	9.20	
		2016	1.20	0.80	1.47	0.53	1.47	
	2017	0.53	6.67	1.33	0.27	6.67		
	All Years	3.07	6.67	9.20	0.53	9.20		
Total number of ticks collected	2015	47	51	6	41	145		
	2016	34	14	5	56	109		
	2017	74	46	9	49	178		
	All Years	155	111	20	146	432		

The "all years" column shows the densities of each site averaged across all 3 collection years.

Table 2.

The dates when the first, last, and peak for *I. scapularis* adults and nymphs that were collected across sites and years during our collection period (April–November)

Site	Year	First collection	Peak collection	Last collection
<i>Adults</i>				
Itasca	2015	April 17	April 30/September 2	November 2
	2016	April 22	May 5/November 3	November 17
	2017	April 12	June 7/October 25	October 25
St. Croix	<i>All Years</i>	<i>April 12</i>	<i>June 7/November 3</i>	<i>November 17</i>
	2015	April 11	June 8/October 16	October 30
	2016	April 20	April 20/October 6	November 2
William O'Brien	2017	April 13	April 13/October 13	October 22
	<i>All Years</i>	<i>April 11</i>	<i>June 8/October 16</i>	<i>November 2</i>
	2015	April 13	June 12/NA	June 24
RJD MH	2016	April 15	April 15/October 16	October 19
	2017	April 3	April 3/October 12	October 19
	<i>All Years</i>	<i>April 3</i>	<i>April 3/October 12</i>	<i>October 19</i>
Nymphs	2015	April 14	April 30/October 18	November 19
	2016	April 16	May 1/October 20	November 17
	2017	April 7	April 23/October 16	October 26
Itasca	<i>All Years</i>	<i>April 7</i>	<i>May 1/October 16</i>	<i>November 19</i>
	2015	May 28	June 9	July 22
	2016	June 16	July 1	September 22
St. Croix	2017	May 15	June 22	June 22
	<i>All Years</i>	<i>May 15</i>	<i>June 9</i>	<i>September 22</i>
	2015	June 8	July 10	October 3
William O'Brien	2016	May 17	Aug 26	October 20
	2017	May 19	July 2	October 22
	<i>All Years</i>	<i>May 17</i>	<i>July 2</i>	<i>October 22</i>
2015	May 28	June 12	September 30	

Site	Year	First collection	Peak collection	Last collection
	2016	June 2	June 16	October 19
	2017	April 21	June 27	July 25
	<i>All Years</i>	<i>April 21</i>	<i>June 12</i>	<i>October 19</i>
RJDMH	2015	May 13	June 15	Aug 5
	2016	May 15	May 15	November 3
	2017	June 5	June 5	June 5
	<i>All Years</i>	<i>May 13</i>	<i>May 15</i>	<i>November 3</i>

There are 2 peak dates for adults showing a peak between April and July and a second peak between August and November. No adults were collected in the fall on William O'Brien in 2015, so the second adult peak is labeled "NA". The "all years" rows show the earliest start and latest end for the season on each site, as well as the date of the highest peak density across all 3 years.

The output from the linear models for the “increasing” (early season) and “decreasing” (late season) phases of *I. scapularis* nymphal host-seeking activity across all years within each site (St. Croix, Itasca, RIDMH, William O’Brien)

Table 3.

Site	Intercept increase/decrease	Slope increase/decrease	r ² increase/decrease	df increase/decrease	P-value increase/decrease
Itasca	2.53/2.63	0.02/-0.01	0.337/0.263	14/30	0.018/0.003
St. Croix	-2.06/8.59	0.02/-0.03	0.284/0.611	22/21	0.007/<0.001
William O’Brien	-1.65/5.91	0.02/-0.02	0.467/0.603	15/27	0.003/<0.001
RIDMH	-2.57/1.74	0.02/-0.01	0.661/0.254	13/29	<0.001/0.004

All data were log-transformed to conform with the assumptions of normality and homoscedasticity.

Table 4.

Estimated start and end dates between which *I. scapularis* nymphal densities will be at 25 and 50% of their peak based upon the linear models for the “increasing” (early season) and “decreasing” (late season) phases

Site	25%	50%	Dates of recorded peak density
Itasca	June 2–August 16	June 23–July 12	2015: June 9
			2016: July 1
St. Croix	June 25–August 27	Jul 18–August 4	2017: June 22
			2015: July 10
			2016: August 26
William O’Brien	May 14–August 27	Jun 2–July 24	2017: July 2
			2015: June 12
			2016: June 16
RJDMH	May 18–August 6	Jun 5–July 11	2017: June 27
			2015: June 15
			2016: May 16
			2017: June 5

The 25% peak represent moderate seasonal risk for bites from *I. scapularis* nymphs and 50% of the peak represents high risk. Other dates represent lower, but a still present risk, of tick bites.