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**Black-Legged Tick Distributions, Small Mammal Abundances, Mast Production, and Vegetative Influences on Lyme Disease Apparent Prevalence on Fort Drum Military Installation, New York**

Samantha R. Fino

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**Black-legged tick distributions, small mammal abundances, mast production, and vegetative influences on Lyme disease apparent prevalence on Fort Drum Military Installation, New York**

**Samantha R. Fino, B. S.**

**Thesis submitted to the  
Davis College of Agriculture, Natural Resources and Design  
at West Virginia University  
in partial fulfillment of the requirements  
for the degree of**

**Master of Science  
In  
Wildlife and Fisheries Resources**

**John W. Edwards, PhD., Chair  
Sheldon F. Owen, PhD.  
Jeffrey Wimsatt, DVM, PhD., DACLAM  
Raymond E. Rainbolt, M.S.**

**Division of Forestry and Natural Resources**

**Morgantown, West Virginia  
2017**

**KEYWORDS: black-legged tick, *Borrelia burgdorferi*, cover type, diversity, *Ixodes scapularis*, Lyme disease, mast production, small mammals**

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## ABSTRACT

### **Black-legged tick distributions, small mammal abundances, mast production, and vegetative influences on Lyme disease apparent prevalence on Fort Drum Military Installation, New York**

**Samantha R. Fino**

Lyme disease is the most common infectious disease spread by black-legged ticks in the Northern Hemisphere. Lyme disease is a vector-borne zoonotic disease typically caused by bacterial spirochetes of the species *Borrelia burgdorferi*. The primary vector of Lyme disease in the Midwestern and eastern United States is *Ixodes scapularis*, the deer or black-legged tick. Although there are several preventative measures against ticks that carry Lyme disease, such as public education regarding personal protection (e.g., wearing light colored clothing, tucking pants into socks, wearing repellent, promptly inspecting oneself to remove ticks, getting pets vaccinated) and recommended control measures, it is important to understand how the disease is transmitted and which factors increase the potential risk of contracting the disease. Even with these preventative measures, which are not necessarily available worldwide, tick-borne diseases are increasing both in numbers and impact to the overall human population, and there are still several knowledge gaps and conflicting findings that need to be elucidated. For these reasons, there exists a need for further research on Lyme disease ecology to identify steps necessary to decrease disease prevalence and reduce human exposure. I conducted a field study on the Cantonment Area of Fort Drum Military Installation, New York, which is representative of a suburban community with multiple cover types. From May 2015–November 2016 I surveyed the Cantonment Area to evaluate the basic distributions of *Ixodes scapularis* and small mammal host species, their relationships with vegetative characteristics, and associated Lyme disease apparent

prevalence. This will allow resource managers to assess and communicate the likelihood of encountering a Lyme-positive tick and to take necessary actions to minimize that risk.

Specifically, our objective was to assess the apparent prevalence of Lyme disease based on the distributions and indices of abundance of the vector and host populations on Fort Drum.

I used tick drags to evaluate black-legged tick temporal and spatial distributions in six different cover types discriminated by developmental stage. Total index of tick abundance was related to (1) temperature, (2) humidity, (3) coarse woody debris, (4) leaf litter depth, (5) tree species richness (6) average tree dbh, and (7) patch size. Adult index of abundance was greatest in the spring and fall, while nymph index of abundance was greatest in early summer and larval index of abundance was greatest at the end of summer. Tick and Lyme-positive tick indices of abundance were greatest in the coniferous and mixed cover type and lowest in the shrub and deciduous cover type. Overall Lyme disease apparent prevalence on the Cantonment Area of Fort Drum was 35% (434/1246). These results provide objective criteria for understanding a baseline of tick distributions on a temporal and spatial scale, and assist in developing management recommendations to decrease Lyme disease apparent prevalence on the landscape.

I used Sherman and Tomahawk traps to capture individuals from the overall small mammal host community during June–August. The small mammal community was composed mostly of *Peromyscus* sp. (n = 79; 38%), chipmunk (n = 59; 28%), red squirrel (n = 33; 16%), gray squirrel (n = 18; 9%). Trapping success, as well as Simpson's and Shannon's indices of diversity were greatest in the developed and coniferous forest cover types. Indices of abundance of small mammals were greatest in the developed cover type, followed by coniferous forest. We modeled the relation between estimated index of abundance of ticks with the estimated index of abundance of all small mammal host species, as well as the relationship between estimated index

of abundance of Lyme-positive ticks and small mammal host Simpson's and Shannon's indices of diversity. Although *Peromyscus* sp. had a greater number of individuals with tick burdens, there was significantly greater estimated index of abundance of Lyme-positive tick burdens on chipmunks. Furthermore, a significantly greater proportion of sampled chipmunks (58%) had Lyme-positive ear punches.

My results suggest that habitat management in the coniferous and mixed forest that target vector and host habitat is necessary in order to decrease Lyme disease prevalence and reduce risk of human exposure. Recommendations such as removal of the leaf/pine litter and coarse woody debris, which provide stable microhabitat for ticks and small mammals alike, a selective cut of large conifer trees, allowing sunlight and wind penetration that encourages tick desiccation, and creating and mowing grassland barrier habitat between human developed areas and forested areas are possible solutions for decreasing Lyme disease prevalence and human risk of exposure on the landscape. Public education seminars regarding black-legged tick spatial and temporal distributions, as well as explaining recommended control measures for personal property should also be developed in order to communicate Lyme disease risk to residents on Fort Drum Military Installation.

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**CHAPTER 1**  
**LITERATURE REVIEW**

## LITERATURE REVIEW

### *Lyme disease (Borrelia burgdorferi) and other tick-borne diseases*

Lyme disease is the most common infectious disease spread by black-legged ticks (*Ixodes scapularis*) in the Northern Hemisphere (Berger 2014). Lyme disease is a vector-borne zoonotic disease typically caused by bacterial spirochetes of the species *Borrelia burgdorferi* (Burgdorfer et al. 1982, Johnson et al. 1984). The disease is spreading across North America (CDC 2014) but predominantly exists in the Northeast and upper Midwest (CDC 2013). The number of confirmed cases of Lyme disease increased from 11,700 in 1995 to 27,203 in 2013 (CDC 2014, CDC 2015c). There are more than 30,000 cases reported to the Center for Disease Control (CDC) annually, but the total number of people diagnosed is estimated to be 10 times higher and the number of unreported cases is likely higher still (CDC 2013). Lyme disease has been reported in all states except Hawaii, but the majority (96%) of the cases occur in 13 states of the Northeast and upper Midwest (CDC 2013). Infection rates in the southeastern and western states are between 1–5% (Lane et al. 1991, Ginsberg 1994). Although there are effective antibiotic treatments such as doxycycline, amoxicillin, or cefuroxime axetil, ceftriaxone and penicillin, that can alleviate symptoms in individuals with acute infections, previous unrecognized chronic Lyme disease can be difficult if not impossible to treat. Likewise, post-Lyme (autoimmune) sequelae have been reported (CDC 2015b). Although antibiotics alleviate the symptoms, in a subset of “nonresponders” there is likely no cure for the disease (CDC 2015d). It has been estimated that to significantly decrease the rate of transmission, black-legged tick densities, the primary vector of *Borrelia burgdorferi*, must be lowered so that humans get bitten <1 time a year to reduce the rates of human infection (Ginsberg 1994).

The primary vector of Lyme disease in the Midwestern and eastern United States is *Ixodes scapularis*, the deer or black-legged tick. The black-legged tick is located along the east coast, into the south and west into Texas, as well as in the upper Midwest. *Ixodes pacificus*, the western black-legged tick, located along the west coast and *Amblyomma americanus*, the Lone Star tick, located in the eastern half of the country except for the northern portions, can also transmit Lyme disease (Armstrong et al. 2001). The ability of a tick to transmit or contract *Borrelia burgdorferi* is dependent on the amount of time it is attached to the host. Potential risk for infection significantly declines if a tick is removed within 36–48 hours (CDC 2017b). *Borrelia burgdorferi* is ingested through a blood meal and resides in the midgut of the tick. During the tick's next blood meal, *Borrelia burgdorferi* detaches and penetrates the stomach lining into the hemocoel, or body cavity, and then migrates into the salivary glands. *Borrelia burgdorferi* is then passed to the host with the salivary fluid during a blood meal (Tilly et al. 2008).

Although there are several preventative measures against Lyme disease, such as public education regarding personal protection (e.g., wearing light colored clothing, tucking pants into socks, wearing repellent, promptly inspecting oneself to remove ticks, getting pets vaccinated) (Ginsberg 1994) and recommended control measures (Stafford 2004), it is important to understand how the disease is transmitted and which factors increase the potential risk of contracting the disease. Even with these preventative measures, which are not necessarily available worldwide, tick-borne diseases are increasing both in numbers and impact to the overall human population, and there are still several knowledge gaps and conflicting findings that need to be elucidated. For these reasons, there exists a need for further research on tick-



borne disease ecology to identify steps necessary to decrease disease prevalence and reduce human exposures.

There are several factors that influence the prevalence of Lyme disease on a landscape. Because individual black-legged ticks (*Ixodes scapularis*) spend 98% of their life off-host, environmental conditions, specifically temperature and humidity, determine tick distributions, host-seeking ability and success, and survival (Needham and Teel 1991, Fish 1993, Lindsay et al. 1995, Bertrand and Wilson 1996, Jones and Kitron 2000). If conditions put ticks at risk of desiccation they will not quest, which is the behavior where ticks climb vegetation and lay on their back with legs splayed in search of a host. The probability of encountering a host depends on host abundance and distribution (Ostfeld et al. 1995, Ostfeld et al. 1996c, Brunner and Ostfeld 2008) while successful feeding and transmission of the disease depends in large measure on host specificity (Van Buskirk and Ostfeld 1995, Wilder and Meikle 2006, LoGiudice et al. 2008). Density and diversity of host populations are heavily dependent on the availability of food resources, specifically mast or seed production (Ostfeld et al. 1996a, McCracken et al. 1999, McShea 2000, Elias et al. 2004). These contributors to the prevalence and risk of Lyme disease vary among cover types as a result of specific vegetation characteristics preferred by vector and host species.

#### *Black-legged tick (Ixodes scapularis)*

The complete life cycle of a black-legged tick spans about 2 years, has 4 developmental stages (egg, larva, nymph, adult), and requires 3 successful blood meals, each from a distinct vertebrate host (Hazler and Ostfeld 1995, Bertrand and Wilson 1996, Ostfeld et al. 1996a). About 2,000 eggs are laid by a gravid female and typically hatch midsummer with the exact timing

depending on the year. The larvae that hatch acquire their first blood meal from an animal in the following months; each feeding lasts 3–7 days. Fed larva will molt into a nymph after about a month and overwinter in leaf litter. The second blood meal is also from an animal and obtained during the following summer whereby the nymph molts into an adult in the fall (Ginsberg 1994, Shaw 2001). White-tailed deer (*Odocoileus virginianus*) are the primary hosts for adult *Ixodes scapularis* (Piesman et al. 1979, Anderson and Magnarelli 1980, Schulze et al. 1984, Spielman et al. 1985), which typically quest in the fall or the following spring (if finding a blood meal is unsuccessful before this) (Bertrand and Wilson 1996). Blood-fed adults will mate in the fall on deer, and females deposit egg masses under leaf litter. Larvae congregate in early summer primarily in forested habitat corresponding to locations occupied by white-tailed deer (Wilson et al. 1985, Maupin et al. 1991, Fish 1993, Ostfeld et al 1995). As a result of their life cycle, tick populations are often dominated by a particular developmental stage during different times of the year. Nymphs predominate in early to mid-summer while larvae predominate early spring and again in late summer (Mannelli et al. 1994, Ostfeld et al. 1995, Brunner and Ostfeld 2008). Different populations of black-legged ticks have two peaks of the nymph with the second being in late summer (Arsnoe et al. 2015). However, by fall, adults are the dominant developmental stage with the greatest abundance of tick populations found in oak woodlands favored by white-tailed deer (Ostfeld et al. 1995, Brunner and Ostfeld 2008). Ostfeld et al. (1996a) found that in deciduous forests of the eastern United States, larval densities were 10 times higher in oak (*Quercus* sp.) predominant forests than in any other habitats when acorn production was high and in maple (*Acer* sp.) predominated forests when acorn production was poor.

The prevalence of human Lyme disease is most directly influenced by the abundance of nymphs which is determined by the success of larvae from the previous year that were able to

feed on hosts without being compromised by biotic and abiotic influences on survivorship and molting success (Hazler and Ostfeld 1995). Spirochetes are not passed from adult female ticks to progeny efficiently, so larvae typically emerge free of *Borrelia burgdorferi* (Shaw 2001). Larval *Ixodes scapularis*, remaining within a few meters from the location of hatching (Daniels and Fish 1990, Stafford 1992), obtain *Borrelia burgdorferi* during their first blood meal if the host is infected (Anderson 1988, Lane et al. 1991). *Ixodes scapularis* can become infected by the host during any of their blood meals, and remain infected for the rest of their life cycle (Shaw 2001). Questing, infected nymphs are the greatest threat to humans because of their small size (1 mm) and difficulty of detection (Falco and Fish 1989, Ostfeld et al. 1996c, Schmidt et al. 1999). Additionally, peak nymphal tick activity occurs in the midsummer months when humans are more active in tick habitat (Lane et al. 1991, Barbour and Fish 1993, Shaw 2001).

#### *Vegetation and seasonal effects*

Environmental conditions, land cover, and landscape patterns, influence the abundance and distributions of vector hosts as well as vertebrate reservoirs of Lyme disease (Pavlovsky 1966, Randolph 1993, Ostfeld et al. 1996b, Kitron 1998, Hay et al. 2000, Lindgren et al. 2000). Temperature and humidity, largely influence and regulate tick population distributions, host-seeking ability, and tick survival (Jones and Kitron 2000, Lindsay et al. 1995). Because *Ixodes scapularis* spends about 98% of its life cycle off of the host, seasonal changes in temperature and humidity will greatly affect population growth and the spread of black-legged ticks (Needham and Teel 1991, Fish 1993, Bertrand and Wilson 1996). Measuring environmental conditions is important to characterize these potential influences on tick questing success and survivability in conjunction with sampling tick populations.

Methods to estimate the non-feeding tick population include the use of tick drags or flags constructed of a piece of light-colored cloth attached to wooden dowels with a rope handle that is dragged for a prescribed distance or time period to pick up questing ticks that attach to the fabric (Schulze and Jordan 2006). Drag sampling in dense herbaceous, shrub, or forested habitat, may underestimate the abundance of juvenile black-legged ticks that typically remain on or near the ground when questing because the cloth, by necessity, is dragged over taller vegetation (Ginsberg and Ewing 1989, Falco and Fish 1992, Schultze et al. 1997). Feeding tick populations can also be monitored by counting ticks on trapped small mammals (Schulze and Jordan 2006).

Seasonal changes in temperature and humidity will greatly affect the population growth and spread of black-legged ticks (Needham and Teel 1991, Fish 1993, Bertrand and Wilson 1996). Seasonal variables, such as cold temperatures and low humidity, not only slow development and growth rates of all stages in the life cycle (Needham and Teel 1991), but adverse conditions can prevent them from contributing to the spread of Lyme disease (Brownstein et al. 2003). Bertrand and Wilson (1996) found that increased temperatures and decreased relative humidity negatively affected development, oviposition, and hatching success, as well as overall survival. *Ixodes scapularis* is highly susceptible to desiccation when relative humidity drops below approximately 90% (Stafford 1994).

Ostfeld et al. (1995) and Bertrand and Wilson (1996) found that, overall, black-legged ticks experienced higher rates of mortality in open field habitats than in forested habitats because both air and soil temperature are higher and relative humidity is lower. Similarly, smaller fragments, or areas of habitat that are separated from other patches of habitat, with greater edge effects undergo more frequent tick extinctions due to greater environmental fluctuations and

harsher environmental conditions. In wetter years, questing behavior can occur higher up in the vegetation and hosts will likely be larger, thus affecting less reservoir-competent species such as squirrels (LoGuidice et al. 2008). Additionally, to better represent the desiccation risk, the average daily survival rate of black-legged ticks decreased as the vapor pressure deficit increased. Because ticks can accommodate fluctuating temperatures by seeking refuge under leaf litter, under conditions such as a higher vapor pressure, or the combination of both temperature and relative humidity, ground cover can serve as a compensating environmental factor (Bertrand and Wilson 1996).

Distributions of *Ixodes scapularis* among different habitat types have been extensively studied in a variety of locations. Although *Ixodes scapularis* has been found in all vegetation types, the highest densities are typically found in areas with trees (Daniel et al. 1977, Eisen et al. 2010, Dobson et al. 2011). Black-legged ticks are primarily detected in deciduous forest habitats of New England (Carey et al. 1980, Anderson and Magnarelli 1984), transition zones between coniferous and deciduous forest communities in Wisconsin (Godsey et al. 1987), and in dense woods of suburban Westchester County, New York (Maupin et al. 1991). Maupin et al. (1991) and Ostfeld et al. (1995) found, in general, that forested habitat types contained the highest densities of black-legged ticks compared to forest edge, shrubby or herbaceous habitat, respectively. In fact, forested habitats can maintain black-legged tick densities that are approximately 5 times greater than those in nearby open areas (Dobson et al. 2011). An area with dense woody vegetation inhibits wind, which in turn reduces saturation deficit (Gray 1991), enabling black-legged ticks to quest for longer periods of time (Perret et al. 2000) and at higher locations on vegetation, all while using less energy (Randolph and Storey 1999). Successional stage of the forest, or the forest's growth and maturity, also plays a role in suitability for ticks.

Sites with increased tree sapling density were correlated with a decreased probability of tick-host interactions because of increased light penetration. Reduced light: 1) prevents photolytic low strata shrub vegetation growth (Richburg et al. 2001), thus causing tick desiccation; 2) less complex stems that provide a less suitable questing substrate; 3) less leaf cover at ground level causing a less hospitable habitat due to an increased saturation deficit, and desiccating conditions (Lindsay et al. 1999, Schultze and Jordan 2005).

Additionally, areas with more ground covered by surface water, saturated soil, and inundated leaf litter all had low *Borrelia burgdorferi* prevalence because of unsuitable conditions for molting and overwintering (Prusiniski et al. 2006), while sandy, well-drained soils provided improved habitat (Kitron et al. 1992, Glass et al. 1994). Tick densities are positively correlated with underlying sedimentary bedrock that is associated with increased particle size (Curtis 1959, Guerra et al. 2002). Although, leaf litter provides a more suitable microhabitat, which explains why black-legged ticks are more abundant in deciduous forests than in coniferous forests (Curtis 1959, Guerra et al. 2002), excessive moisture is negatively associated with *Ixodes scapularis* populations (Zhioua et al. 1999, Guerra et al. 2002). Soils with increased acidity and a high proportion of clay retain a greater amount of moisture, which can enhance the growth of fungi and entomophagous nematodes that negatively affect tick populations (Zhioua et al. 1999, Gerra et al. 2002). Furthermore, soil types influence the type of vegetation, and oak species prefer sandier soils (Curtis 1959, Guerra et al. 2002).

Although black-legged ticks are primarily found in woodlands and edge areas (Carey et al. 1980, Ginsberg and Ewing, 1989, Stafford and Magnarelli 1993), an uneven distribution of black-legged ticks may occur if there exists differential mortality of black-legged tick stages

among habitat types, differential natality rates across habitat types, movements by the black-legged ticks themselves, and similar such movements by their vertebrate hosts (Ostfeld et al. 1995). Abundance of larvae tick populations were greatest in forested habitats dominated by maple during the summer months, but forested habitats dominated by either maple or oak habitats support nymph tick populations that were about equal in abundance (Ostfeld et al. 1995). Although environmental conditions may significantly influence the maintenance of reproducing populations, factors such as host density and species composition might have a greater influence controlling tick population size and tick infection rates (Brownstein et al. 2003).

#### *Tick-host interactions*

Tick-host interactions leading to disease contraction and transmission are based on the strength of the host's immune response to tick antigens in the saliva as well as the ability of the tick to evade the immune response. While feeding, there are periodic interruptions for salivation that trigger a host immune response resulting in decreased feeding success or even rejection (Sonenshine 1993). Therefore, heightened host immune and grooming responses are expected when there is a higher tick feeding density, which will reduce the quality or the quantity of each blood meal, as well as overall feeding success (Ostfeld et al. 1995, Brossard and Wikel 2004). Hazler and Ostfeld (1995) and Allan and Appel (1993) suggest that the host may develop resistance against *Ixodes scapularis* as the weight and percentage of engorged black-legged ticks decreased on pre-exposed hosts compared to naïve hosts. However, black-legged tick saliva contains anti-inflammatory and immunosuppressive agents that suppress host inflammatory responses and prevent hemostasis. Therefore, higher tick densities on a host may actually facilitate feeding (Ribeiro et al. 1985, Davidar et al. 1989).

There are over 60 vertebrate species (Shaw 2001), approximately 29 species of mammals, 49 species of birds, and even some reptile species, that can serve as hosts for *Ixodes scapularis*, suggesting they are indiscriminate during host selection (Oliver 1989, James and Oliver 1990, Reed 1993, Schmidt 1999). In the Northeast, the most important host of immature black-legged ticks, particularly as relates to Lyme disease transmission, is the white-footed mouse (*Peromyscus leucopus*) (Bosler et al. 1984, Levine et al. 1985, Anderson et al. 1987, Magnarelli et al. 1988, Mather et al. 1989, Anderson and Magnarelli 1993, Apperson 1993, Levin and Fish 1998). This reflects not only its high abundance, widespread distribution, and frequency of tick parasitism, but also because it is the most competent reservoir of the Lyme disease spirochete. Hence black-legged ticks feeding on this species have a high probability of becoming infected with *Borrelia burgdorferi* during a blood meal from an infected individual (Shaw 2001); likewise these same ticks have a higher molting success into the next developmental stage compared to the same species of ticks feeding on other hosts (Davidar et al. 1989, James & Oliver 1990, Mannelli et al. 1993, Mather & Ginsberg 1994). Schmidt and Ostfeld (2000) reported this host's reservoir competence at > 90% based on newly molted nymphs; and Mather (1993) reported between 40–80% of larvae feeding on an infected *Peromyscus leucopus* obtain *Borrelia burgdorferi*. The primary attachment site on white-footed mice is located on the auditory pinnae (Main et al. 1982). Finally, Ostfeld and Keesing (2012) found that white-footed mice were less likely to remove feeding ticks than other species of rodents or shrews.

The abundance and proportion of host-seeking and host feeding by black-legged ticks is influenced by population density and the distribution of the host species. The diversity and abundance of host species may help to assess the risk of Lyme disease to the human population (Ostfeld et al. 1995). The abundance of host-seeking ticks, as well as tick burdens on hosts, and



their distributions are directly related to host densities (Ostfeld et al. 1995, Brunner and Ostfeld 2008). However, while tick density is a function of host density, spirochete prevalence is a function of each host's reservoir competence (Van Buskirk and Ostfeld 1998). Ostfeld et al. (1995, 1996c) found that the probability of a black-legged tick encountering a host as well as the proportion of the total number of black-legged ticks attached to an individual white-footed mouse increases dramatically at higher population densities, such as above 10 mice per hectare. Van Buskirk and Ostfeld (1995, 1998) found that a highly infected tick population is maintained when the density of mice is at or above 20 per hectare for juveniles and white-tailed deer populations reach 5 per hectare for adults. At higher densities, although individual mice may experience a density-dependent reduction in their home range, the population will occupy a greater proportion of the landscape and therefore questing black-legged ticks maintain higher feeding success rates (Wolff 1985, Ostfeld et al. 1996c, Brunner and Ostfeld 2008). Although *Peromyscus* are territorial (Sadleir 1965, Healey 1967, Metzgar 1971, Fairbairn 1978, Wolff et al. 1983), which conceivably could contribute to the regulation of population densities, and even black-legged tick densities, under such circumstances, population densities of mice still appear to increase and expand in the presence of environmentally suitable habitats (Adler and Wilson 1987). A greater population of *Peromyscus leucopus* will provide increased opportunities for larvae to successfully feed and acquire *Borrelia burgdorferi*, resulting in a high abundance of infected nymphs and a greater risk to human populations the following year (Ostfeld et al. 2001).

Other small mammals abundant in deciduous eastern forests include the eastern chipmunk, *Tamias striatus*, as well as the short-tailed shrew, *Blarina brevicauda*, and the masked shrew, *Sorex cinereus*, and represent other major hosts for *Ixodes scapularis* nymphs (Schmidt et al. 1999, Shaw 2001, Brisson et al. 2008). These species in aggregate, along with

*Peromyscus* sp., contribute 80–90% of *Borrelia* infected ticks (Brisson et al. 2008). Chipmunks and shrews, however, are slightly less competent reservoirs and less efficient compared to mice at infecting black-legged ticks; it is believed this is due to protective physiological immune responses possessed by these hosts to the pathogen (Nupp and Swihart 2000, Ostfeld and Keesing 2000a, Anderson et al. 2003, Wilder and Meikle 2006). Schmidt et al. (1991) and Shaw (2001) determined that larval tick burdens are about 3 times higher on white-footed mice than on chipmunks in the same environment potentially due to their immunoresponse differences, however, larval burdens on mice decreased with increasing chipmunk abundance and burdens of nymphs on chipmunks declined with increasing mice abundance. Furthermore, male mice have larger burdens of ticks compared to females (Davidar et al. 1989, Schmidt et al. 1999, Perkins et al. 2003) and younger mice have a greater burdens compared to adults; these trends were not consistently found in chipmunks (Brunner and Ostfeld 2008). While black-legged ticks are thought of as opportunistic, Mannelli et al (1993) and Brunner and Ostfeld (2008) found *Ixodes scapularis* prefer different rodent hosts based on developmental stage potentially due to their questing height on the vegetation, with larvae preferring mice and nymphs preferring chipmunks, allowing for the most efficient reservoir to influence the abundance of infected nymphs and thus also the risk of infection by maintaining lower disease prevalences compared to an area occupied by only mice (Brisson et al. 2008).

The spread of Lyme disease is also dependent on host abundance, host-tick encounter rates, and the ability of the preferred host to transmit the agent to a feeding tick (Shaw 2001). Although mice were found to be more efficient groomers than chipmunks, their higher tick burdens counteract this ability (Shaw 2001). Additionally, allogrooming of young by mothers may also facilitate removal of ticks, however, this does not seem to be true for nymphs feeding

on juvenile mice (Brunner and Ostfeld 2008). Keesing et al. (2009) found that certain species such as opossums (*Didelphis virginiana*) and squirrels (*Sciurus* sp.) have a more effective species-specific immune response, allowing these individuals to kill between 83–96% of tick burdens while increased grooming reduces infestations. Only 3% and 15% of ticks that feed on opossums and squirrels, respectively, are successful (Keesing et al. 2009). Yet, squirrels receive 5 to 37 times as many infected tick bites compared to other host species (Randolph and Craine 1995), however, they are more effective groomers. Vertebrate species such as squirrels, deer, voles, raccoons, opossums and skunks are considered to be dilution hosts because they are poor reservoirs for *Borrelia burgdorferi* (Levi et al. 2016, LoGiudice et al. 2003, Brisson and Dykhuizen 2004). Because *Ixodes scapularis* can feed on many hosts, the ability to make a choice of hosts in the wild is only possible if potential hosts are abundant and the probability of specific host encounters is high. However, black-legged ticks are opportunistic and will attach to the first host they encounter (Shaw 2001). Thus, tick burdens will be more frequent on the most abundant host of the community, and in the Northeast, that host is the white-footed mouse. Similarly, when there is a high proportion of competent reservoir hosts for *Borrelia burgdorferi*, the potential risk of encountering an infected black-legged tick is greater (Keesing et al. 2009).

Ostfeld and Keesing (2000b) suggest the reason behind the increased reservoir competence of *Peromyscus* is because of its disproportionate, abundant population density in the community, and therefore more frequent and higher tick burdens that lead to successful molting. As a result, specialization on the most abundant host would allow increased survival of *Ixodes scapularis*. *Borrelia burgdorferi* may also have adapted to a specific vertebrate species to increase its reservoir competence (Shaw 2001). White-footed mice appear to better adapt to anthropogenic changes and forest fragmentation (LoGiudice et al. 2008) while coincidentally,

these habitats cannot sustain a diversity of competitors and predators (Nupp and Swihart 1996, Krohne and Hoch 1999, Rosenblatt et al. 1999). In fact, *Peromyscus leucopus* densities have been found to rapidly increase in patch sizes <2 ha (Nupp and Swihart 1996, Krohne and Hoch 1999), and concentrate on edges of these patches in the absence of abundant mast (Ostfeld et al. 1995); conversely, densities decrease as distance from the edge increases (Horobik et al. 2001). As a result, nymphal infection prevalence increases with decreasing patch size (Allen et al. 2003). Similarly, there is a strong correlation between habitat fragmentation and both tick density and infection prevalence (Steere et al. 1978, Falco and Fish 1988, Frank et al. 1998, Ostfeld and Keesing 2000b, Brownstein et al. 2005). One reason for this is that white-tailed deer prefer edge habitat (Leopold 1933), and concomitantly, this results in the adult ticks dropping off and laying eggs at these sites. More importantly, it has been hypothesized that to reduce the risk of human exposure to Lyme disease, an increase in diversity of hosts, many of which are less competent reservoirs, will replace tick meals from mice and decrease infected black-legged tick associated prevalence (Van Buskirk and Ostfeld 1995, Rosenblatt et al. 1999, Ostfeld and Keesing 2000a, Ostfeld and Keesing 2000b). Brunner and Ostfeld (2008) found that as chipmunk densities declined, tick burdens on mice increased. Similarly, if the populations of competitor and predator species declined, more resources become available for mice populations and their reproductive success, survival and abundance will increase (Ostfeld and Keesing 2000, Schmidt and Ostfeld 2001, Keesling et al. 2009). As black-legged ticks are generalists and opportunistic in nature, a species-rich habitat with equal frequencies of host species would be expected to decrease the potential risk of encountering an infected black-legged tick (LoGiudice et al. 2008). However, in areas with high forest fragmentation, mice dominate the landscape near human communities increasing the risk of exposure.

### *Habitat selection of host species*

Human development often causes patchy landscapes, which in turn influences the distributions and abundances of wildlife species and their ectoparasites. Although Mannelli et al. (1994) found that habitat type did not play a significant role in the abundance of black-legged ticks on white-footed mice, Maupin et al. (1991) and Adler et al. (1992) both found that tick burdens on white-footed mice increased with density of woody vegetation and decreased with herbaceous vegetation. Other studies have found an increased probability of tick-host interactions and elevated tick burdens occur in areas with dense shrubby understory, specifically increased vegetation density at the lowest strata, including snags and coarse woody debris, due to its stable microclimate, increased relative humidity, and reduced predation risk for both black-legged ticks and hosts, all of which promote tick survival (Ginsberg and Ewing 1989, Adler et al. 1992, Goddard 1992, Stafford 1994, Lindsay et al. 1999, Schmidt et al. 1999, Lubelczyk et al. 2004, Prusiniski et al. 2006). Woody debris and brush piles, common in forested habitats, also provide the above benefits and have been found to increase overwinter survival in small mammals (Carey and Johnson 1995, Loeb 1996, Davis et al. 2010). Although the density of *Peromyscus* increases with denser woody vegetation (Myton 1974, Adler and Wilson 1987), Prusiniski et al. (2006) found that as density of woody vegetation and shrub coverage increased, small mammal diversity decreased; however, there was still a high occurrence of *Borrelia burgdorferi* infection due to the mice population. Regardless, because individual ticks can only move a few meters themselves (Falco and Fish 1989, Carroll and Schmidtman 1996), the abundance and dispersal of black-legged ticks across habitat types is heavily reliant on host distributions and movements, which are determined by patch size and juxtaposition (Ostfeld et al. 1995, Van Buskirk and Ostfeld 1998).

*Peromyscus leucopus* are primarily dense woodland inhabitants (Baker 1968, Kaufman and Fleharty 1974, Bee et al. 1981, Kamler and Pennock 2004, Stancampiano and Schnell 2004). However, they can occupy a range of microhabitat types at high population densities, and are classified as habitat generalists (Adler et al. 1984, Clark et al. 1987, Seamon and Adler 1996, Kamler and Pennock 2004) and even thrive in low-diversity and degraded forest fragments (Nupp and Swihart 1996, Allen et al. 2003, LoGiudice et al. 2008, Keesing et al. 2009).

*Peromyscus* is the only competent host species to be captured in all habitat types (Ostfeld et al. 1995). They are also known to more readily expand their range from forested habitat into small patches of shrubby or herbaceous habitat (Grant 1972, M'Closkey and Lajoie 1975, Ostfeld et al. 1995), compared to large patches of herbaceous habitat where competition with voles exists (Abramsky et al. 1979, Grant 1972). Movements of this sort may represent expanded access to foraging areas, dispersal routes, or a spillover that occurs at high population densities (Stancampiano and Schnell 2004). Ostfeld et al. (1995) and Dobson et al. (2011) suggested that black-legged ticks disperse when they attach to a host in small herbaceous patches in or near adjacent forests, but then drop off when the host is no longer in these areas. This would explain the presence of black-legged ticks on lawns (Maupin et al. 1991, Carroll et al. 1992, Stafford and Magnarelli 1993) or in areas with short grass where humans more often spend time, compared to dense vegetation (Dobson et al. 2011). However, Boyard et al. (2007, 2008) found that as the distance from forests increased, there was a decrease in the relative abundance of black-legged ticks because *Peromyscus leucopus* prefer forested habitats. *Peromyscus maniculatus*, the North American deer mouse, primarily utilize open grasslands (Kaufman and Fleharty 1974, Bee et al. 1981, Stancampiano and Schnell 2004), but may frequent mixed forests (Graves et al. 1988, Choate et al. 1994, Garmen et al. 1994). Even so, both species of *Peromyscus* occur in mid-

successional vegetation along edge (Kamler 1998), *Peromyscus leucopus* is more often encountered in transitional areas because of their potential to utilize a greater variety of microhabitats (Kamler and Pennock 2004). However, both of these species can serve as hosts for black-legged ticks in areas with a high level of human contact. The distribution of black-legged ticks across various habitat types is dependent on host species' movements, which are markedly influenced by mast production (Ostfeld et al. 1995).

Jones et al. (1998) and Wolff (1996) suggest that there are higher densities of *Ixodes scapularis* in forests because abundant seeds and fruits from the vegetation attract a wide diversity as well as a high abundance of host species. The diets of *Peromyscus* and *Tamias*, as well as species of *Sciurus*, vary with season. More fleshy fruit, specifically blueberries (*Vaccinium* sp.), raspberries and blackberries (*Rubus* sp.), are eaten in the summer whereas more nuts, specifically acorns (*Quercus* sp.), hickory nuts (*Carya* sp.), beechnuts (*Fagus* sp.), and ripening seeds, are eaten in the fall and winter reflecting seasonal availability (Hamilton 1941, Whitaker 1966, Wolff et al. 1985). Diet is supplemented with arthropods throughout the year (Wolff et al. 1985). The population density and breeding season abundance of mice has been found to be directly correlated to the previous year's mast index and acorn abundance, as acorns are a staple of their diet (Wolff 1996, Ostfeld et al. 1996a, McCracken et al. 1999, McShea 2000, Elias et al. 2004). In fact, years with a high mast index even allowed *Peromyscus* to breed over the winter in response to an excess of stored acorns (Pucek et al. 1993, Ostfeld 1996a). A similar relationship of mast production influencing the abundance and distribution of white-tailed deer has also been examined (Jones et al. 1998). A high mast index also attracts more deer, which often carry large numbers of adult male and female ticks, and result in a large population of larvae the following year (Ostfeld 1996a, Wolff 1996, Jones et al. 1998, Ostfeld et al. 2001).

Jones et al. (1998) found that deer spend eight times as long feeding in oak stands during a year of high mast production compared to a year with poor mast production. As a result, tick burdens on hosts will increase even though many desiccate while questing or get consumed when the host grooms. In contrast, nuts from hickory (*Carya* sp.) trees are too hard to be utilized by mice and more often attract squirrels. In years with an abundance of hickory mast production, the squirrel-to-mouse ratio is high (LoGiudice et al. 2008). When there is high mast index and acorn abundance, host species will experience greater reproductive success and thus a population increase, allowing for more opportunities and a higher success for a large population of questing larval black-legged ticks in the following year, which then leads to large population of infected nymphs the following year (Wolff 1996, Jones et al. 1998, Ostfeld et al. 2001). These factors increase infection prevalence and amplify the risk to the human population (Ostfeld et al. 2001). Jones et al. (1998) found that the density of host-seeking larval black-legged ticks and the number of ticks attached to mice was directly correlated with the abundance of acorns, and therefore acorn production was a good indicator of Lyme disease risk 2-years hence. Additionally, years of poor acorn production influence the movement of hosts out of forest habitats and into marginal areas (Van Buskirk and Ostfeld 1998).

Non-native and invasive species in human developed areas may also influence the distribution of host species indirectly through food preference. Eckert (2012) found that *Peromyscus maniculatus* preferred the seeds of non-native non-invasive blue spruce (*Picea pungens*) over native white spruce (*Picea glauca*). Nowalk (2007) conducted a similar experiment to examine the relative seed preference of *Peromyscus maniculatus* for invasive species when presented with native species of the same genus. No consistent preference for native or invasive seeds was found across all genera (Nowalk 2007). Pearson et al. (2011) found



that *Peromyscus maniculatus* avoided consuming the seeds of strongly invasive *Centaurea stoebe* relative to the other 12 weakly invasive and native species tested and weakly invasive species experienced a greater release from seed predation compared to strongly invasive species, but this was not the case for native species (Pearson et al. 2011). Knight et al. (2007) found that mice avoid common buckthorn (*Rhamnus cathartica*), which is an invasive species typically found in shrubby habitat. Based on the various results, it seems that *Peromyscus* species are opportunistic generalists.

Mast production is influenced by several factors. While the timing and amount of mast production varies across species, the total amount of mast produced also depends on tree density; likewise, mast production can be heavily influenced and cued by environmental conditions. Several tree species are sensitive to weather conditions and mast-seeding is strongly correlated to water availability and air temperature. As a result, many species have considerable interannual variability in mast production, and individual species have different abiotic requirements and functional strategies when stressed (Kelly et al. 2013). For example, dryer conditions during a specific year may cause a decline in mast production in deciduous forests, while alternatively, warmer temperatures during a specific year may cause declines in mast production in coniferous forests (Perez-Ramos et al. 2015). Diminished rainfall will impact subsequent floral initiation and acorn development (Sork et al. 1993, Koenig et al. 1994, Koenig and Knops 2013). Additionally, environmental conditions favoring wet and warm weather during the spring immediately prior to acorn maturation is an important influence on mast production because it allows for flower pollination and fertilization leading to acorn development (Olson and Boyce 1971). Intense wind, late frost, prolonged rain, and cold temperatures negatively affect the opening of the anthers and the dissemination of pollen (Sharp and Chisman 1961). Additionally,

the loss of fruits often occurs because of premature abscission (Olson and Boyce 1971). It may not be extreme weather conditions that affect masting, but rather a drastic change from one year to the next (Kelly et al. 2013). However, there has yet to be a study that identifies a single environmental influence of acorn production (Koenig and Knops 2013). Although extreme weather conditions may affect acorn production, quick changes in environmental conditions also negatively affect masting (Koenig et al. 2013).

Soft mast production (e.g., berries) is also affected by similar environmental factors. Both hard and soft mast producers benefit from larger and well-developed crowns, or an open or edge habitat, allowing for a greater rate of photosynthesis. Although light intensity and soil nutrient concentrations are positively correlated with larger mast crops, temperature and rainfall seem to be the more important. Warmer temperatures in the spring followed by cooler temperatures in the summer produce a more abundant mast crop, however a lack of moisture will reduce overall production. As found with hard mast production, frost and freezing during flowering will significantly impact total annual mast production. Genetics and age may also play a role in both hard and soft mast production (Weeks 1999).

## **CHAPTER 2**

### **LYME DISEASE (*BORRELIA BURGDORFERI*) APPARENT PREVALENCE AND BLACK-LEGGED TICK (*IXODES SCAPULARIS*) DISTRIBUTIONS ON A TEMPORAL AND SPATIAL SCALE ON FORT DRUM MILITARY INSTALLATION, NEW YORK**

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**Lyme Disease (*Borrelia burgdorferi*) Apparent Prevalence and Black-legged Tick (*Ixodes scapularis*) Temporal and Spatial Distributions on Fort Drum Military Installation, New York**

SAMANTHA R. FINO, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

JOHN W. EDWARDS, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

SHELDON F. OWEN, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

JEFFERY WIMSATT, School of Medicine, West Virginia University, Morgantown, WV 26506,  
USA

RAYMOND E. RAINBOLT, Natural Resources Branch, US Army, Fort Drum, NY 13602, USA

MEAGAN MARSHALL, Public Health Command, US Army, Fort Meade, MD 20755, USA

**ABSTRACT**

Lyme disease (*Borrelia burgdorferi*) is the most common infectious vector-borne zoonotic disease spread by black-legged ticks (*Ixodes scapularis*) in the Northern hemisphere. The objective of this study was to determine if tick abundance and *Borrelia burgdorferi* apparent prevalence in ticks are associated with time of year, abiotic factors, and vegetation

characteristics at Fort Drum Military Installation. Questing ticks were collected using a 1-m<sup>2</sup> tick drag in 3 grids per cover type (coniferous forest, deciduous forest, developed, grassland, mixed forest, shrub forest) each consisting of 3 50-m transects and tested with a real-time PCR multiplex for *Borrelia burgdorferi*. Overall Lyme disease apparent prevalence was estimated to be 35%. Both tick and *B. burgdorferi*-positive tick indices of abundance were highest in coniferous forest during April and November, largely due to the adult developmental stage peak, and correspondingly, lowest in the shrub and deciduous forests during August and September dominated by the larval developmental stage peak. Knowledge of the basic spatial and temporal patterns of *Ixodes scapularis* will allow resource managers to better assess and communicate the potential risk of exposure and contraction of Lyme disease to the human population, as well as develop habitat management practices to decrease prevalence of Lyme disease and other tick-borne illnesses on the landscape.

**KEYWORDS** black-legged tick, *Borrelia burgdorferi*, cover type, *Ixodes scapularis*, Lyme disease

## **INTRODUCTION**

Lyme disease is caused by the bacterial spirochete, *Borrelia burgdorferi*, and is commonly spread by contact with black-legged ticks (*Ixodes scapularis*). There are more than 30,000 cases reported to the Center for Disease Control (CDC) annually, but the total number of people diagnosed is estimated to be 10 times higher (Berger 2014) and the number of unreported cases is likely higher still (CDC 2013). One method to substantially decrease the rate of transmission is to decrease black-legged tick densities in order to prevent human-tick interactions (Ginsberg 1994).

Environmental conditions, land cover, and landscape patterns influence the abundance and distributions of vectors and vertebrate hosts of Lyme disease (Pavlovsky 1966, Randolph 1993, Ostfeld et al. 1996b, Kitron 1998, Hay et al. 2000, Lindgren et al. 2000). Temperature and humidity largely influence and regulate tick population distributions, host-seeking ability, and tick survival (Jones and Kitron 2000, Lindsay et al. 1995). Variability within a season, such as cold temperatures and low humidity, can slow developmental success and growth rates of all stages in the tick life cycle (Needham and Teel 1991). In addition, adverse conditions can also cause black-legged ticks to freeze or desiccate, limiting their distribution and survival, and thus preventing them from contributing to the spread of Lyme disease (Brownstein et al. 2003). Bertrand and Wilson (1996) found that increasing temperatures and decreasing relative humidity negatively affected development, oviposition, and hatching success, as well as overall survival. *Ixodes scapularis* is highly susceptible to desiccation when relative humidity drops below approximately 90% (Stafford 1994). Alternatively, when there are higher temperatures and humidity, questing behavior can occur higher up on vegetation (LoGuidice et al. 2008). Because *Ixodes scapularis* spends about 98% of its life cycle off of a host, seasonal changes in temperature and humidity will greatly affect population growth and the spread of black-legged ticks (Needham and Teel 1991, Fish 1993, Bertrand and Wilson 1996).

Although *Ixodes scapularis* has been found in all vegetation types, the highest densities are typically recorded in forested areas (Daniel et al. 1977, Eisen et al. 2010, Dobson et al. 2011). Black-legged ticks are primarily detected in deciduous forest habitats in New England (Carey et al. 1980, Anderson and Magnarelli 1984), transition zones between coniferous and deciduous forest communities in Wisconsin (Godsey et al. 1987), and in dense woods of suburban Westchester County, New York (Maupin et al. 1991). Maupin et al. (1991) and

Ostfeld et al. (1995) found that forested vegetation types contained the highest densities of black-legged ticks compared to forest edge, shrubby or herbaceous vegetation, respectively. Dense woody vegetation inhibits wind, which in turn reduces saturation deficit (Gray 1991), enabling black-legged ticks to quest for longer periods of time (Perret et al. 2000) and at higher locations on vegetation, all while using less energy (Randolph and Storey 1999). Successional stage of the forest, or the forest's growth and maturity, also plays a role in suitability for ticks. Increased light penetration promotes tick desiccation and supports less suitable questing substrate (Lindsay et al. 1999, Schultze and Jordan 2005). Leaf litter and coarse woody debris provide a more suitable microhabitat, where ticks can tolerate fluctuating temperatures by seeking refuge (Curtis 1959, Guerra et al. 2002).

Military installations in the Northeast contain large tracts of forested lands suitable for *Ixodes scapularis*. Although the branch of military and specific mission may differ among installations, the potential for exposure of active duty personnel to Lyme disease while training or to personnel and family members while engaged in recreational activities is a growing concern for the Department of Defense (Piacentino and Schwartz 2002). Fort Drum Military Installation near Watertown, New York is the largest (433 km<sup>2</sup>) in the Northeast and is home to approximately 19,605 active duty soldiers and their families. The U.S. Army Public Health Command Human Tick Test Kit Program reported an increase in Lyme disease incidences of 5.7% from 2006–2012 on Fort Drum (Rossi et al. 2015). Of recorded Lyme diagnoses, Fort Drum had 38 absolute incident cases of Lyme disease during 2004–2013, making it one of the highest in the nation (Hurt and Dorsey 2014).

The potential risk for Fort Drum personnel and their dependents to be exposed to Lyme disease via encounters with infected ticks warrants research to better manage the level of risk. Knowledge of the basic spatial and temporal patterns of *Ixodes scapularis* will allow resource managers to assess and communicate the likelihood of encountering a Lyme-positive tick and to take necessary actions to minimize that risk. Specifically, our objective was to assess the potential risk of Lyme disease based on the distributions and densities of the vector populations on Fort Drum.

## **STUDY AREA**

Our study was conducted on the Cantonment Area of Fort Drum located in Jefferson County, New York (44.05° N, 75.77° W) (Dobony and Rainbolt 2008, INRMP 2011) (Figure 1.1). Fort Drum (43,422 ha) is located in the Great Lake Plains region, also known as the Erie-Ontario lowlands, between the Tug Hill Plateau and the edge of the Adirondack Mountains. Elevation on Fort Drum ranges from approximately 125–245 m. Soils in the Cantonment Area are generally classified as sand, silt loam, and silty clay (Web Soil Survey 2015). The annual average temperature was -10.14 °C in 2015 and -4.94 °C in 2016. The total precipitation was 9.88 cm of rainfall and 151.08 cm of snowfall in 2015 and 6.02 cm of rainfall and 58.70 cm of snowfall in 2016 (U.S. Climate Data 2015, 2016).

The Cantonment Area is approximately 4,000 ha and consists of 30% developed, 30% grassland, 9% mixed forest, 5% coniferous forest, 8% shrub, and 18% deciduous forest (Figure 1.2). The developed areas (Appendix 23) included those that were in close proximity to human infrastructure and buildings. All buildings, residential homes, land navigation courses, parks and green spaces, such as lawns, and recreation areas were considered developed. These areas were



often surrounded by mowed grass (Poaceae) and/or adjacent to forest edges. The grassland cover type areas (Appendix 24) were without human development and often included fields containing grasses, wildflowers and other herbaceous plants. Common species included: *Carex* sp., *Cirsium* sp., *Cyperus* sp., *Juncus* sp., *Panicum* sp., *Aster* sp., *Centaurea* sp., *Galium* sp., *Megalodonta* sp., *Polygonum* sp., *Potamogeton* sp., *Solidago* sp., *Trillium* spp, and *Veronica* sp. (Fort Drum 2009).

The remaining four cover types also occurred in areas separated from human development but used for military training exercises. The shrub cover type (Appendix 26) was characterized by woody plants <8 m tall. This type was densely vegetated with both native and invasive species, and contained *Cornus* sp., *Lonicera* sp., *Malus* sp., *Rhamnus* sp., *Salix* sp., *Vaccinium* sp., *Viburnum* sp. (Fort Drum 2009). Unlike the shrub cover type, deciduous, coniferous and mixed cover types included trees that were >8 m tall. The deciduous cover type (Appendix 22) contained *Acer* sp., *Carya* sp., *Fagus* sp., *Fraxinus* sp., *Nyssa* sp., *Populus* sp., *Rubus* sp., among others (Fort Drum 2009). Dominant herbaceous plants in this cover type included *Caulophyllum* sp. and *Gallium* sp. (Fort Drum 2009). The ground was covered in leaf litter and coarse woody debris, and as a result, the soil was typically rich in organic matter. Coniferous cover type (Appendix 21) contained evergreen species such as *Picea* sp., *Pinus* sp., *Tsuga* sp., among others (Fort Drum 2009). The ground was covered in needle litter and coarse woody debris. The mixed cover type (Appendix 25) contained species present in both deciduous and coniferous cover types.

## **METHODS**

### **Off-host tick collection**

Field sampling occurred within the study area from April 2015 through November 2016. Non-feeding tick populations were estimated using a tick-drag method. Rulison et al. (2013) found that neither flagging nor dragging demonstrated a clear advantage for sampling *Ixodes scapularis* but due to efficacy tick drags have been historically used on Fort Drum. The tick-drag device was a 1-m<sup>2</sup> corduroy cloth to which questing ticks come in contact and are removed from the vegetation. The cloth was dragged on the ground along 50-m transects and checked every 10-m (approximately 30 seconds) to prevent losing ticks that drop off (Insect Diagnostic Laboratory 2012). Each tick-drag plot consisted of 3 parallel transects 10 m apart (Appendix 28). Three tick-drag plots were established in each of 6 cover types. Directional azimuths for the three tick-drag plots in each cover type were determined randomly as follows (in degrees): 335, 225, and 100 for coniferous, 160, 28, and 260 for deciduous, 70, 245, and 295 for grassland, 109, 28, and 15 for developed, 285, 325, and 40 for mixed, and 200, 170, and 190 for shrub. Ticks were removed from the tick drag using tape, identified by species, stage and gender, transferred into empty plastic vials using tweezers which were sterilized using 70% rubbing alcohol, stored in a freezer at -18 °C, and sent with ice packs to the Army Public Health Command at Fort Meade, MD for diagnostic testing. Tick drags were conducted biweekly and temperature, humidity, wind speed and barometric pressure were recorded from the local weather station at the time of each tick drag grid.

### ***Borrelia burgdorferi* detection**

Once received by Fort Meade, ticks were identified and individually placed in 100 µL of Tissue Lysis Buffer (Qiagen, Valencia, CA). Ticks were macerated by the addition of a 5mm borosilicate bead on the Qiagen Tissue Lyser for 3 minutes at a frequency of 20 beats per second.

Samples were spun down and an additional 400uL of buffer was added to each. Samples were then incubated with the addition of proteinase K prior to nucleic acid purification according to kit directions with the DNeasy Blood & Tissue Kit (Qiagen). Starting material for isolation was 200uL of the incubated tick lysate and purified nucleic acids were eluted with 100 µL of elution buffer. The macerated ticks, remaining lysate and purified nucleic acids were stored at -80°C for future analysis.

Purified nucleic acid preparations from individual *Ixodes scapularis* ticks were screened for *Borrelia* and *Anaplasma* species by a multiplex assay targeting the 23S rRNA and *msp2* genes of *Borrelia* and *Anaplasma*, respectively as described by Courtney et al. (2004). In addition, the samples determined positive for *Borrelia* species were further confirmed as *Borrelia burgdorferi* using qPCR targeting the N40.seq gene (Straubinger 2000) and the 16s rDNA of *B. miyamotoi* (Tsao et al. 2004). Likewise, *Anaplasma* species positive samples were further tested with a qPCR singleplex targeting a 106-bp fragment of the 16s rRNA gene (Pusterla et al. 1999). All qPCR assays were performed using the LightCycler FastStart DNA Master HybProbe kit (Roche) on the Roche LightCycler 2.0 or LightCycler® 480 Probes Master (Roche) on the Roche LightCycler 480.

In 2016, a 20% subsample, by developmental stage, cover type and month, was tested at the WVU Wildlife Genomics Laboratory for confirmation testing and method validation. DNA was extracted using Thermo Fisher Scientific Genomic DNA Purification Kit® and followed manufacturer recommendations for extraction. Extracted DNA were stored at -80°C for future analysis. Individual *Ixodes scapularis* ticks were screened for *Borrelia* species by a multiplex assay targeting the 23S rRNA gene of *Borrelia* using Tawman with fluorescent probes as adapted

from Courtney et al. (2004). We ran a qPCR as described in Appendix 1 for detect *Borrelia burgdorferi* presence.

### **Vegetation surveys**

Vegetation measurements in each cover type were conducted in summer 2016 (Appendix 19). We established 16 plots per cover type. Each plot was 0.04 ha with two nested plots, one 0.01 ha and the other 0.001 ha (Figure 2.1). In the 0.04-ha plot, species, crown class (USDA Forest Service 2002), and diameter at breast height (dbh) for all trees greater than 8 cm dbh was recorded. The number and height of snags, and their diameter and decay stage (score of 1–9; Maser et al. 1979, Thomas et al. 1979) within the 0.04-ha plot was also recorded. A canopy cover measurement was taken in the center of the plot, and at 10 m in each cardinal direction, to calculate an average canopy cover estimate. The 0.04-ha plot was divided into quadrants. Mid-story cover/vegetation density was measured using a cover board (Interagency Handbook 1996) in the nested 0.01-ha quadrant plot that was in the north direction. The cover board was placed in the corner and the observer was on the opposite corner. Percentage of mid-story cover was recorded for all corners of the north 0.01-ha quadrant to calculate an average. Also within the nested 0.01-ha quadrant, coarse woody debris was classified into a decay classes (score of 1–5; Maser et al. 1979, Thomas et al. 1979) and length and diameter was measured for calculation of volume. Coarse woody debris was considered as any downed log > 10 cm in diameter (Harmon et al. 1986, Spies and Cline 1988, Loeb 1996, Butts and McComb 2000). In a nested 0.001-ha plot, leaf litter depth and composition of vegetative ground cover, measured by relative abundance of stems, were recorded. An average leaf litter depth was determined from measurements taken in each corner of the 0.001 ha plot. The 0.04 ha plots were 30 m away from

each corner of the small mammal trapping grids on the same azimuths of its transects. In the event that the azimuth from the trapping grid led to a location that was uncharacteristic of that cover type, a random azimuth that did not overlap with another vegetation plot was used. In the developed cover type, vegetation plots were 30 m in the north direction from every fourth small mammal trapping point because trapping stations were not in a grid for this cover type. No sampling occurred in small mammal trapping grids because of our disturbance of vegetation during small mammal trapping.

### **Statistical Analysis**

Summary statistics for each developmental stage were calculated on a temporal and spatial scale for both tick count and positive-*Borrelia burgdorferi* tick-count data. Infection apparent prevalence was estimated for each developmental stage, as well as for each cover type. We used a Poisson distribution to model-estimated index of abundance of black-legged ticks (adults, nymphs, larvae) among cover types and months.  $Y_i$  denoted estimated index of abundance, which we modeled as a Poisson random variable:  $y_i \sim \text{Poisson}(\lambda_i)$  because data were formatted as count data. We conducted parametric bootstrapped pairwise comparisons with a 95% confidence interval to observe any statistical differences in estimated index of abundance among months or cover types. This was done for both tick count data and positive-*Borrelia burgdorferi* tick count data in Program R x64 3.0.2.

We modeled estimated index of abundance of black-legged ticks (response variable) as a function of predictor variables month, year, cover type, temperature, humidity, wind speed, pressure, as well as various vegetative characteristics (Table 2.1). An initial pairwise comparison analysis indicated that months of April, June, October and November 2015 were statistically

different from months of April, June, October and November 2016. As a result, we used sum-to-zero coding with year effect and the predictive variables year and month were interaction terms in the model (Yandell 1997). All other predictor variables (environmental and vegetative) were additive, as the relationship with estimated index of abundance did not change in different months, cover types, or for tick developmental stage. For index of abundance of each developmental stage, we only used the predictor variables of year, month and cover type as our focus was on the spatial and temporal distributions for each developmental stage. We developed the following models: (1) estimated index of abundance of adult ticks (Table 2.4), (2) estimated index of abundance of nymphs (Table 2.5), (3) estimated index of abundance of larvae (Table 2.6), (4) total estimated index of abundance of ticks (Tables 2.2 and 2.3), (5) estimated index of abundance of *B. burgdorferi*-positive adults (Table 2.7), and (6) estimated index of abundance of *B. burgdorferi*-positive nymphs (Table 2.8). We chose to model *B. burgdorferi*-positive count data instead of apparent prevalence because infection rate can be misleading as a result of sample size. Model selection for total index of abundance of ticks was based on the Wald's test ( $p < 0.05$ ) and lowest relative AICc score (highest relative AICc weight). The top model (Tables 2.2 and 2.3) for estimated index of abundance of total tick count data was used to predict estimated index of abundance as a function of significant environmental and vegetative predictor variables as these variables do not influence spirochete apparent prevalence in the population, but rather estimated index of abundance of questing ticks themselves (regardless of developmental stage). The predictor variables month, year and cover type were not included in evaluation of models because our focus was on the relationship between these environmental and vegetative predictor variables with total index of abundance of ticks. Because several of these vegetative characteristics had high collinearity of a  $r$  value  $> 0.70$  (Appendix 20), we ran each vegetative

characteristic as an independent model and then selected the top models that did not have vegetative predictor variables that had high covariance with previously selected vegetative characteristics. Lastly, using ArcGIS®, the influence of patch size (m<sup>2</sup>) on total tick index of abundance was also examined. The combination of vegetative characteristics and environmental predictor variables comprised the top model. An alpha level of 0.05 was used in data analyses.

## RESULTS

Overall estimated apparent prevalence of *Borrelia burgdorferi* in the black-legged tick population on Fort Drum was approximately 35% based on adult and nymph count data (Table 2.11). Approximately 48% of adults and 18% of nymphs were infected with *Borrelia burgdorferi* (Table 2.11). Our subsample had similar apparent prevalence estimates of 48% for adults, 18% for nymphs and 36% overall positive for *Borrelia burgdorferi*. The coniferous cover type had the greatest estimated black-legged tick index of abundance while the shrub and deciduous cover types had the lowest (Figs. 2.2–2.4). Estimated adult black-legged tick index of abundance was greatest in November and lowest in July and August (Fig. 2.2). The coniferous cover type had the highest estimated adult black-legged tick indices of abundance while the deciduous cover type had the lowest (Fig. 2.2). Estimated nymph index of abundance was greatest in June and lowest in April, October and November (Fig. 2.3). The coniferous cover type had the highest estimated nymph index of abundance while the shrub cover type had the lowest (Fig. 2.3). Estimated larval index of abundance was greatest in August and September and lowest in April and November (Fig. 2.4). The mixed cover type had the greatest estimated larval index of abundance while the shrub cover type had the lowest (Fig. 2.4).

While estimated tick indices of abundance were highest in November and April due to adults (Fig. 2.2), in June due to nymphs (Fig. 2.3), in August and September due to larvae (Fig. 2.4), estimated Lyme disease-positive tick indices of abundance were highest in November, April, and October due to adults (Fig. 2.5), followed by June due to nymphs (Fig. 2.6), and lowest in August and September due to larvae (Figs. 2.5 and 2.6). Lyme disease-positive index of abundance was greatest in the coniferous forest and lowest in the deciduous forest cover type for adults (Fig. 2.5) and in developed cover type for nymphs (Fig. 2.6). No questing ticks were detected in the grassland cover type. Estimated indices of abundance of Lyme-positive ticks follows the same significance trends as tick indices of abundance (Table 2.9 and 2.10). Probability of recovering (via tick drags) positive-*Borrelia burgdorferi* ticks was greatest in the coniferous cover type for adult and nymph developmental stages, and lowest in the deciduous forest type for adults and in the developed cover type for nymphs (Table 2.12).

Tick indices of abundance on Fort Drum increased as both temperature and humidity increased (Wald test  $p = <0.001$  and  $p = <0.001$ , respectively). The slope coefficient for temperature predicted a 3.0% increase in expected tick count with a 1°C increase in temperature (Fig. 2.7). The slope coefficient for humidity predicted a 28.0% increase in expected tick count with a 1% increase in relative humidity (Fig. 2.8). These results indicate that humidity is a more influential factor on tick index of abundance than temperature.

Tick index of abundance increased as both leaf litter depth, tree species richness, and average tree dbh increased (Wald test  $p \leq 0.001$  for all), and decreased as coarse woody debris decay and patch size increased (Wald test  $p \leq 0.001$  for both). The slope coefficient for leaf litter depth predicted a 10.8% increase in expected tick count with a 1-cm increase in leaf litter depth



(Fig. 2.10). The slope coefficient for tree species richness predicted a 26.7% increase in expected tick count with each additional tree species (Fig. 2.11). The slope coefficient for average tree dbh predicted a 0.69% increase in expected tick count with each additional tree species (Fig. 2.12). The slope coefficient for coarse woody debris decay predicted a 33.7% decrease in expected tick count with a 1-unit increase in decay on a scale of 1–5 (Fig. 2.9). Because cover type was not a predictive variable in this model, the slopes and influence of the predictive environmental and vegetative variables on total tick index of abundance is constant throughout cover types (Table 2.3). Tick index of abundance increased as patch size decreased. The slope coefficient for patch size predicted a 0.65% decrease in expected tick count with a 1-m<sup>2</sup> increase in patch size (Fig. 2.13). These results indicate that environmental and vegetative characteristics are more influential factor on tick index of abundance than cover type.

## **DISCUSSION**

The overall infection apparent prevalence among ticks on Fort Drum Military Installation was approximately 35%. Adults had a higher infection incidence of approximately 48% compared to that of nymphs at approximately 18%, likely due to the possibility of more vector-host interactions and exposure to the spirochete during their previous two blood meals (Hazler and Ostfeld 1995, Bertrand and Wilson 1996, Ostfeld et al. 1996a). The temporal peaks in occurrence and number of *B. burgdorferi*-positive adults, nymphs and larvae followed the expected trends reported in the literature; adults peak in spring (April) and fall (October and November), while nymphs peak early summer (June) (Ginsberg 1994, Bertrand and Wilson 1996, Shaw 2001). The peak of the larval developmental life stage on Fort Drum was similar to other studies, peaking at the end of summer (August and September) (Wilson et al. 1985, Maupin

et al. 1991, Fish 1993, Ostfeld et al 1995). In contrast to other reports, we did not find a secondary peak of the nymph or larval developmental stage (Mannelli et al. 1994, Ostfeld et al. 1995, Brunner and Ostfeld 2008), which may be due to increased latitude. Because spirochetes are not passed from adult female to offspring efficiently (Shaw 2001), *B. burgdorferi* was not detected in collected larvae, which explains the low index of abundance of *B. burgdorferi*-positive ticks at the end of the summer. Our estimated indices of abundance are conservative because we were only able to collect questing ticks; unsampled ticks may not have been questing due to environmental conditions, movement, or they were questing on lower strata on vegetation. However, because we did not conduct a nested PCR to identify the specific *Borrelia burgdorferi* DNA sequences, specifically the 16S-23S rRNA IGS locus, we cannot confirm if this estimated apparent prevalence reflects the prevalence of *Borrelia burgdorferi* that cause infection in humans (Bunnikis et al. 2004). Similarly, approximately 1% and 4% of ticks were infected with *Borrelia miyamotoi* and *Anaplasma phagocytophilum* respectively (Table 2.13 and 2.14), although sequencing was not conducted to estimate prevalence that cause infection in humans.

We consistently found ticks at high indices of abundance in forested areas (Daniel et al. 1977, Eisen et al. 2010, Dobson et al. 2011) as the dense woody vegetation inhibits wind, which in turn reduces any saturation deficit (Gray 1991), thus increasing questing success and survivability (Randolph and Storey 1999, Perret et al. 2000). We observed the highest indices of abundance for all developmental stages in the coniferous and mixed forest cover types. This was likely due to the presence of high-quality food resources for hosts that are burdened by ticks (Ostfeld et al. 1995, Brunner and Ostfeld 2008), as well as higher tree density, canopy cover (both of which reduce sunlight penetration and wind), and leaf litter depth all of which provide refuge for the vector species. With tick index of abundance positively related to increasing leaf

litter depth and tree species richness (highly collinear with tree density and canopy cover), as well as negatively related to coarse woody debris decay, this suggests increased probability of tick-host interactions and elevated tick burdens with increased vegetation density at the lowest strata, including leaf litter and coarse woody debris (Carey and Johnson 1995, Loeb 1996, Davis et al. 2010). This microhabitat provides a stable microclimate with increased relative humidity as well as reduced predation risk for both black-legged ticks and hosts, all of which promote tick survival (Ginsberg and Ewing 1989, Adler et al. 1992, Goddard 1992, Stafford 1994, Lindsay et al. 1999, Schmidt et al. 1999, Lubelczyk et al. 2004, Prusiniski et al. 2006). Similar support was provided by Carey et al. (1980) and Anderson and Magnarelli (1984) who observed higher occurrences of black-legged ticks in deciduous forest habitats of New England and Godsey et al. (1987) who reported highest densities in transition zones between coniferous and deciduous forest communities in Wisconsin. The coniferous cover type, which had the highest tick indices of abundance, existed in the smallest patch sizes, explaining the negative relation patch size has on highest tick indices of abundance. We observed no questing ticks in the grassland cover type, likely due to higher air and soil temperature and lower relative humidity as a result of greater sun exposure which causes high tick mortality (Ostfeld et al. 1995, Bertrand and Wilson 1996). However, we do recognize that tick drags only push down the top of the vegetation without being able to sample ticks that may be questing on the lower strata of the vegetation.

Shrub cover types on Fort Drum have low tick indices of abundance. The shrub cover type had a significantly lower average tree dbh (diameter at breast height), potentially allowing for more sunlight and wind penetration, ultimately leading to more tick desiccation or ticks seeking refuge rather than questing. Increased light penetration promotes less complex stems causing a less suitable questing substrate, while less leaf debris at ground level causes a less

hospitable habitat due to an increased saturation deficit, all potentially causing desiccation (Lindsay et al. 1999, Schultze and Jordan 2005). Although stem density was high, potentially providing a greater amount of substrate for questing, there was significantly lower leaf litter depth in the shrub cover type, resulting in a lack of suitable microhabitat for refuge. While there were low adult tick indices of abundance in the deciduous cover type, there were higher relative indices of abundance for nymphs and larvae. The high index of abundance in larvae may indicate that deciduous forests have an ample amount of food resources for hosts such as deer, the primary host for adult ticks (Piesman et al. 1979, Anderson and Magnarelli 1980, Schulze et al. 1984, Spielman et al. 1985) in the winter, resulting in frequent egg masses. The high index of abundance in nymphs in the deciduous cover type may indicate that there are greater and higher quality food resources for small mammals, the primary hosts for nymphs (Maupin et al. 1991, Ostfeld et al 1995), in the summer when their developmental stage peak occurs. The high stem/sapling density and greater depth of leaf litter provides a greater amount of questing substrate and a more suitable microhabitat for winter dormancy, respectively, which explains why black-legged ticks are often abundant in deciduous forests (Curtis 1959, Guerra et al. 2002). The developed cover type, which is transitional areas between human developed areas (open areas) and forested edges, has moderate to low indices of abundance due to its composition of shared cover types with potentially harsh environmental conditions.

The high indices of *Ixodes scapularis* abundance and *Borelia burgdorferi* apparent prevalence in the Cantonment Area of Fort Drum is likely due to the lake-effect environmental conditions found in this part of the Northeast. With an average annual precipitation of 109.5 cm of rainfall and 289.6 cm of snowfall (U.S. Climate Data), Fort Drum has a consistent level of high humidity. Humidity below approximately 90% (Stafford 1994), results in slowed

developmental success and growth rates of all stages in the tick's life cycle (Needham and Teel 1991), which negatively affects oviposition and hatching success, and decreases overall survival due to desiccation (Bertrand and Wilson 1996, Brownstein et al. 2003). A weakness in our models was that we recorded environmental conditions from a local weather station; we would suggest future studies record environmental conditions at the ground level of each tick drag to observe differences in the environmental conditions of the microhabitat among cover types, as well as soil moisture content.

### **CHAPTER 3**

#### **INFLUENCE OF SMALL MAMMAL ABUNDANCE AND DIVERSITY ON BLACK- LEGGED TICK (*IXODES SCAPULARIS*) ABUNDANCE AND LYME AGENT (*BORRELIA BURGDORFERI*) PREVELANCE ON FORT DRUM MILITARY INSTALLATION, NEW YORK**

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**Influence of Small Mammal Abundance and Diversity on Black-legged Tick (*Ixodes scapularis*) Abundance and Lyme Agent (*Borrelia burgdorferi*) Apparent Prevalence on Fort Drum Military Installation, New York**

SAMANTHA R. FINO, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

JOHN W. EDWARDS, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

SHELDON F. OWEN, Division of Forestry and Natural Resources, West Virginia University,  
Morgantown, WV 26506, USA

JEFFERY WIMSATT, School of Medicine, West Virginia University, Morgantown, WV 26506,  
USA

RAYMOND E. RAINBOLT, Natural Resources Branch, US Army, Fort Drum, NY 13602, USA

MEAGAN MARSHALL, Public Health Command, US Army, Fort Meade, MD 20755, USA

**ABSTRACT**

Lyme disease (*Borrelia burgdorferi*) is the most common infectious vector-borne zoonotic disease spread by black-legged ticks (*Ixodes scapularis*) in the Northern hemisphere. The spatial distribution of black-legged ticks is dependent on the movements of their hosts. Tick abundance is dependent in large measure on host abundance, however prevalence of Lyme disease is

dependent on host specificity. The objective of our study was to determine the spatial distributions and index of abundance of the host populations as well as the vector-host interactions on Fort Drum Military Installation as they relate to *Borrelia burgdorferi* apparent prevalence. Small mammals were captured and marked during the summers of 2015–2016 using Sherman and Tomahawk traps in 2 6 × 6 grids per cover type (coniferous forest, deciduous forest, developed, grassland, mixed forest, shrub forest). Tick *Borrelia burgdorferi* burdens and ear punches were tested using a real-time PCR multiplex assay that detected *Borrelia burgdorferi*. The small mammal community was dominated by *Peromyscus* sp. and members of the family Sciuridae, effective reservoirs that adapt well to fragmented, human developed areas. We found a positive relation between both vector and host indices of abundance as well as between indices of host diversity and index of abundance of Lyme-positive ticks. Although there was significantly higher tick burden occurrences on individual *Peromyscus* sp., there were significantly greater Lyme-positive tick burden occurrences on chipmunks. Additionally, a greater proportion of chipmunks had ear punches that tested positive for Lyme disease. Cover types with high small mammal indices of abundance also had high small mammal diversity, as well as high indices of abundance of ticks and Lyme-positive ticks, supporting an amplification effect. Knowledge of the basic spatial patterns of the small mammal host community and the vector-host relationship will allow resource managers to better assess and communicate the potential risk of exposure to the human population, as well as develop habitat management strategies to decrease disease prevalence by reducing human exposures.

**KEYWORDS** black-legged tick, *Borrelia burgdorferi*, cover type, diversity, host species, *Ixodes scapularis*, Lyme disease, small mammal abundance



Lyme disease (*Borrelia burgdorferi*) is the most common infectious vector-borne zoonotic disease spread by black-legged ticks (*Ixodes scapularis*) in the Northern Hemisphere. Ticks require 3 successful blood meals, each from a separate vertebrate host to complete their life cycle (Hazler and Ostfeld 1995, Bertrand and Wilson 1996, Ostfeld et al. 1996a). There are over 60 vertebrate species (Shaw 2001), 29 recorded mammals, 49 birds, and even some reptile species, that can serve as hosts for *Ixodes scapularis*, suggesting they are indiscriminate in host selection (Oliver 1989, James and Oliver 1990, Schmidt 1999), although the successful feeding and molting of the tick may vary based on the host species. In the Northeast, the most important host of immature black-legged ticks relative to Lyme disease transmission is the white-footed mouse (*Peromyscus leucopus*) (Bosler et al. 1984, Levine et al. 1985, Anderson et al. 1987, Magnarelli et al. 1988, Mather et al. 1989, Anderson and Magnarelli 1993, Apperson 1993, Levin and Fish 1998). White-footed mice are not only disproportionately represented in the small mammal community (Ostfeld and Keesing 2000b), with a widespread distribution due to their adaptability to anthropogenic changes (LoGiudice et al. 2008) and frequency of tick parasitism, but they are also the most competent reservoir of the Lyme disease spirochete. Hence, black-legged ticks feeding on an infected host have a high probability of becoming infected with *Borrelia burgdorferi* (Shaw 2001). Schmidt and Ostfeld (2001) reported white-footed mouse reservoir competence at > 90%, based on the production of newly molted infected nymphs. In another study, Mather (1993) reported between 40–80% of larvae feeding on an infected *Peromyscus leucopus* obtain *Borrelia burgdorferi*.

Other small mammals abundant in eastern deciduous forests include eastern chipmunk, *Tamias striatus*, as well as the short-tailed shrew, *Blarina brevicauda*, and the masked shrew, *Sorex cinereus*, which also serve as hosts for *Ixodes scapularis* (Schmidt et al. 1999, Shaw 2001,

Brisson et al. 2008). These species, along with *Peromyscus* sp., transmit *Borrelia burgdorferi* to 80–90% of infected ticks (Brisson et al. 2008). Chipmunks and shrews, however, are slightly less competent reservoirs and are not as efficient as white-footed mice in transmitting *Borrelia burgdorferi* to uninfected black-legged ticks due to specific physiological immune responses by the host to the pathogen (Nupp and Swihart 2000, Ostfeld and Keesing 2000a, Anderson et al. 2003, Wilder and Meikle 2006). Additionally, Schmidt et al. (1999) and Shaw (2001) determined that larval tick burdens are about 3 times higher on white-footed mice than on chipmunks in the same environment. However, more mice on the landscape draw larvae away from chipmunks while more chipmunks on the landscape draw nymphs away from mice (Mannelli et al. 1993, Brunner and Ostfeld 2008). This then allows for the most efficient reservoir to influence the abundance of infected nymphs (Brisson et al. 2008).

The abundance of host-seeking as well as feeding black-legged ticks is influenced by population density and distribution of host species. The abundance of host-seeking ticks in the environment, as well as tick burdens on hosts, and their distributions are directly related to host densities (Ostfeld et al. 1995, Brunner and Ostfeld 2008). However, while tick density is a function of host density, spirochete prevalence is a function of each hosts' reservoir competencies as well (Van Buskirk and Ostfeld 1998). Ostfeld et al. (1995, 1996c) found that the probability of a black-legged tick encountering a host and the proportion of total black-legged ticks attached to an individual white-footed mouse increases dramatically at population densities above 10 mice per hectare. At such densities, mice will occupy a greater proportion of the landscape and therefore questing black-legged ticks have higher success rates (Wolff 1985, Ostfeld et al. 1996b, Brunner and Ostfeld 2008). A greater population of *Peromyscus leucopus* will provide increased opportunities for larvae and nymphs to successfully feed and acquire

*Borrelia burgdorferi*, resulting in a high abundance of infected nymphs the following year (Ostfeld et al. 2001).

The prevalence of Lyme disease is dependent on host abundance, host-tick encounter rates, and the ability of the preferred host to transmit disease to a feeding tick. While both poor groomers, mice were found to be more efficient groomers than chipmunks, although their higher tick burdens counteract this ability (Shaw 2001). Keesing et al. (2009) found that certain species such as opossums (*Didelphis virginiana*) and squirrels (*Sciurus* sp.) have a more effective immune response, allowing these individuals to kill between 83–96% of tick burdens because increased grooming reduces infestations. Only 3% and 15% of ticks that feed on opossums and squirrels, respectively, are successful (Keesing et al. 2009). Yet, squirrels receive 5 to 37 times as many infected tick bites compared to other host species (Randolph and Craine 1995).

Vertebrate species such as squirrels, deer, voles, raccoons, opossums and skunks are considered to be dilution hosts because they are poor reservoirs for *Borrelia burgdorferi* (Levi et al. 2016, LoGiudice et al. 2003, Brisson and Dykhuizen 2004). As a result, high host diversity on the landscape will divert tick-host interactions away from effective reservoirs. Due to the difficulty of discriminating *Peromyscus leucopus* and *Peromyscus maniculatus* in the field, there is a lack of research on reservoir competence differences (Oliver et al. 2006), although one study reports the effective reservoir competence for *Peromyscus maniculatus* to be about 33% (Peavey and Lane 1995). Black-legged ticks are opportunistic and will attach to the first host they encounter (Shaw 2001), thus, tick burdens will be more frequent on the most abundant host of the community.

The distributions of *Peromyscus* and *Tamias*, as well as species of *Sciurus*, are heavily dependent on the microhabitat characteristics and mast production. The population density and breeding season abundance of mice has been found to be directly related to the previous year's mast production, specifically acorn abundance (Wolff 1996, Ostfeld et al. 1996a, McCracken et al. 1999, McShea 2000, Elias et al. 2004). In fact, years with a high mast production allowed *Peromyscus* to breed over the winter in response to an excess of stored acorns (Pucek et al. 1993, Ostfeld 1996a). Maupin et al. (1991) and Adler et al. (1992) both found that tick burdens on white-footed mice increased with density of woody vegetation, where mast production is more likely, and decreased with herbaceous vegetation. Other studies have found that increased probability of tick-host interactions and elevated tick burdens occur in areas with increased vegetation density at ground level, due to its stable microclimate, increased relative humidity, and reduced predation risk for both black-legged ticks and hosts (Ginsberg and Ewing 1989, Adler et al. 1992, Goddard 1992, Stafford 1994, Lindsay et al. 1999, Schmidt et al. 1999, Lubelczyk et al. 2004, Prusiniski et al. 2006). Woody debris and brush piles, common in forested habitats, also provide the above benefits and have been found to increase overwinter survival in small mammals (Carey and Johnson 1995, Loeb 1996, Davis et al. 2010). Prusiniski et al. (2006) found that as density of woody vegetation and shrub coverage increased, small mammal diversity decreased. However, there was likely still a high occurrence of *Borrelia burgdorferi* infection because the density of *Peromyscus* increases with denser woody vegetation (Myton 1974, Adler and Wilson 1987). Regardless, because individual ticks can only move a few meters themselves (Falco and Fish 1989, Carroll and Schmidtman 1996), the abundance and dispersal of black-legged ticks across habitat types is heavily reliant on host distributions and

movements, which are determined by patch size and vegetative qualities (Ostfeld et al. 1995, Van Buskirk and Ostfeld 1998).

The high risk of Lyme disease to the human population calls for research that analyzes the relationship between vector and host populations' distributions and abundances in consideration of habitat differences. A primary goal of this project was to understand the distributions and abundances of the host populations on Fort Drum as a function of cover type, as well as to determine the estimated prevalence of Lyme disease within the small mammal community. Knowledge of the basic spatial patterns of various small mammal species will allow resource managers to better assess and communicate the likelihood of encountering a Lyme-positive tick.

## **METHODS**

Our study area was located on the Cantonment Area of Fort Drum Military Installation (Chapter 2). Off-host tick collection, *Borrelia burgdorferi* detection, and vegetation surveys followed the same methodology as described in Chapter 2.

### **Small mammal capture**

Small mammal trapping occurred from June – July 2015 and 2016 to target small mammal peak activity (O'Farrell 1975, Hanser et al. 2011). While mice are active all year (O'Farrell 1975), many small mammals (i.e., chipmunks) enter into torpor during winter months and only emerge when there are available food resources (MacMillen, 1964, O'Farrell 1975). Live-capture Sherman traps (H.B. Sherman Inc., Tallahassee, USA) 8.9 × 7.6 × 22.9 cm were used for animal capture. To improve the likelihood of capturing animals too large for Sherman

traps, 49.0×15.2×15.2-cm live-capture #202 Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI) were also used.

Small mammal trapping was conducted in each of the 6 cover types used in tick sampling (Fig. 1.2). Two Sherman traps and one tomahawk trap were placed at each trapping station with their rear corners touching one another and their openings facing outward. Each trap triad was placed at each point of a 6×6 grid (Appendix 29). Thus, each trapping grid contained 72 Sherman traps and 36 tomahawk traps. Each trapping station was 10 m apart from one another. Small mammal trapping grids were replicated (2) in each cover type to increase sample sizes and better survey host populations across the Cantonment Area landscape.

Traps were deployed between 0700–0900 on Monday of a trapping week. Each trap was baited with a peanut butter-honey-oats mixture on a ~2.5-cm<sup>2</sup> square of paper and also contained a palm-sized ball of polyester batting for nesting. Traps were not placed in excessively wet areas or in areas without shade. Traps were checked beginning at 0700 each morning and again at 1500 each afternoon for three consecutive days; 3 consecutive days of continuous trap placement in a trapping array was considered the minimum required to assess local species richness (Manley et al. 2002). Checked traps were rebaited and resupplied with polyester batting as necessary. All non-functioning traps, meaning the door was closed without a capture, the bait was missing without a capture, or a trap was missing or broken, were reset, rebaited or replaced (Nelson and Clark 1973). After each trapping session, traps were soaked in a mild bleach solution (CDC recommends 45 ml/3.8 liters) for 10 minutes to reduce the risk of Hantavirus (Mills et al. 1995).

During trap checks, trap outcomes, whether each trap was open, sprung, or sprung with a capture, were noted. Captured animals were released into a plastic or cloth bag depending on the animal's size and type of trap. Small mammals were grasped at the nape of the neck for examination (Manley et al. 2006). Captured individuals were identified to species, sexed, aged (juveniles or adults), examined for breeding status (pregnant, lactating, enlarged testes or nonbreeding), weighed and released (Kunz et al. 1996). Because *Peromyscus leucopus* and *Peromyscus maniculatus* are difficult to discriminate in the field, both were recorded as *Peromyscus* sp. All new captures were marked with numbered ear tags (Kent Scientific Cooperation). Captures of previously marked animals were recorded. Non-target animals were released without processing. Ticks were removed from captured animals with tweezers and placed in labeled individual vials per tick for diagnostic sampling of *Borrelia burgdorferi*. In 2016, ear punches were taken from captured animals and placed in labeled vials with 80% ethanol for diagnostic sampling for *Borrelia burgdorferi*.

### **Mast collection**

Hard and soft mast were surveyed in deciduous, coniferous, mixed, and shrub cover types from August 2015 through December 2015 and again from May 2016 through December 2016. One mast trap (Appendix 31) consisted of four 5-gallon plastic buckets each 28.9 cm in diameter. Five holes were drilled at the bottom of each bucket to allow for water drainage. Buckets were arranged in 2×2 array with a sample area of 0.26 m<sup>2</sup>. A fitted aluminum wire screen was placed in the bottom of the bucket to prevent any mast materials from escaping through the drilled holes. Bucket arrays were attached around a 1.82-m tall metal t-post with wire hooks. Buckets were covered with poultry wire secured with 16 gauge tie wire to deter animals from entering the buckets. Mast traps were placed 20.1 m apart along transects. There

were 39 mast traps placed within a one-hectare plot (Appendix 30). Transects were oriented on randomly chosen azimuth of 320 degrees in the deciduous plot, 50 degrees in the shrub plot, 100 degrees in the coniferous plot and 300 degrees in the mixed plot.

All mast traps were cleaned of debris and organic materials the week of 13 July 2015. Mast trap collections occurred biweekly, starting the first week of August, 2015, and ended the week of 7 December 2015. In 2016, all mast traps were cleaned of debris and organic material the week of 25 April. Mast trap collections occurred biweekly, starting the first week of May, 2016, and ended the week of 14 November 2016 due to snow. Seed and fruit material was removed from individual mast traps and placed into a paper bag. Ground-plot mast surveys were conducted at each mast trap site to survey mast production below the height of the mast traps. An azimuth in increments of 30 degrees was assigned randomly for each sample period, without repetition. A 1-m<sup>2</sup> PVC frame was placed 6.1 m from the mast trap “t-post” in the specified random azimuth direction. Seed and fruit material within the sample frame was removed and placed into a separate paper bag. All samples were stored in a freezer to prevent decay.

Hard and soft mast was separated by species and placed in individual containers made of noncorrosive metal or glass. The sample within the container was no more than 0.3 g per cm<sup>2</sup> and spread evenly within the container to allow for air circulation (Nitrate Elimination Co. 2012). To achieve a constant weight measurement, seeds and fruit were dried in an oven at 100° C for 72 hours to remove moisture, and then weighed to the nearest 0.0001 g (Braun 2005).

### **Statistical analysis**

Small mammal species composition was calculated across both years. Average Shannon (Shannon and Weaver 1949) and Simpson Diversity Indices (Simpson 1949), and Jaccard’s



index of similarity (Jaccard 1908), were calculated for all cover types to evaluate and compare small mammal diversity (Hamilton et al. 2015, Ostfeld and Keesing 2000a, Payne and Caire 1999, Hayslett 1992). Average trapping success was also calculated for each cover type as well as for each species. Pairwise comparisons were used to observe any statistically significant difference in diversity indices or trapping success. Index of abundance estimates for cover types and for each species were calculated using the minimum number of unique individuals of our limited recapture success. Apparent infection prevalence of attached ticks was estimated, as well as the proportion of rodents exposed to *Borrelia burgdorferi*. The rate of positive ear punches per rodent species was also calculated. Lastly, the relationship between positive tick burdens and positive ear punches was examined.

We used a Poisson distribution to model small mammal indices of abundances (*Peromyscus* sp., Eastern chipmunk; hereafter chipmunk, American red squirrel; hereafter red squirrel, Eastern gray squirrel; hereafter gray squirrel, all hosts) in different cover types.  $Y_i$  denoted estimated index of abundance, which we modeled as a Poisson random variable:  $y_i \sim \text{Poisson}(\lambda_i)$  because the data were formatted as count data. These resulting indices of abundances were used as predictor variables in the models for tick index of abundance and Lyme-positive tick index of abundance (Chapter 2). Model selection for total index of abundance was based on the Wald's test ( $p < 0.05$ ) and lowest relative AICc score (highest relative AICc weight). The predictor variable month, vegetative characteristics and environmental conditions were not included in evaluation of models for total index of abundance of ticks because our focus was the relationship it had with index of abundance of small mammal host species. Model selection for total Lyme-positive index of abundance of ticks included the predictor variables of year, cover type, and host species. Likewise, the model selection for index of abundance of various host

species included predictor variables year and cover type as our focus was on the spatial distribution of the host community. We conducted parametric bootstrapped pairwise comparisons with a 95% confidence interval to observe any statistical differences in estimated index of abundance among cover types. This was done for tick count data, positive-*Borrelia burgdorferi* tick count data, and small mammal count data discriminated by species.

We modeled estimated index of abundance (response variable) as a function of additive predictor variables year, cover type, and various vegetative measurements (Table 2.1). Because several of these vegetative characteristics had high collinearity  $r$  value  $> 0.70$  (Appendix 20), we ran each vegetative characteristic as an independent model and then selected the top models that did not have vegetative predictor variables that had high covariance with previously selected vegetative characteristics. Sum-to-zero coding was used for year effect (Yandell 1997). The count data of small mammal index of abundance was used as a predictive variable for black-legged tick index of abundance (Table 3.1). Additionally, small mammal host diversity indices were used as predictive variables for Lyme-positive tick index of abundance (Table 3.2). We developed the following models: (1) estimated index of abundance of *Peromyscus* sp. (Tables 3.3 and 3.4), (2) estimated index of abundance of chipmunk (Tables 3.5 and 3.6), (3) estimated index of abundance of red squirrel (Tables 3.7 and 3.8), (4) estimated index of abundance of gray squirrel (Tables 3.9 and 3.10), and (5) estimated index of abundance of all small mammal hosts (Tables 3.11 and 3.12). Within the estimated index of abundance of each small mammal host species, we evaluated predictive vegetative variables that help to explain index of abundance.

Additionally, we used a binomial distribution to model Lyme-positive tick burdens on small mammal hosts and Lyme-positive ear punches from small mammal hosts with the

predictor variables of host species or cover type.  $Y_i$  denoted whether a tick or ear punch was positive for *Borrelia burgdorferi*, which we modeled as a binomial random variable:  $y_i \sim \text{binomial}(\theta_i)$ . Model selection was based on the Wald's test ( $p < 0.05$ ) and lowest relative AICc score (highest relative AICc weight) (Table 3.18, Table 3.19 and Table 3.23).

## RESULTS

The species composition of the small mammal community was comprised of *Peromyscus* sp. ( $n = 79$ ; 38%), followed by chipmunk ( $n = 59$ ; 28%), red squirrel ( $n = 33$ ; 16%) and gray squirrel ( $n = 18$ ; 9%). The remaining species composition included: meadow vole (< 3%), meadow jumping mouse (< 1%), short-tailed shrew (< 2%), northern flying squirrel (< 1%), southern flying squirrel (< 2%), long-tailed weasel (< 2%), striped skunk (< 1%), and Virginia opossum (< 1%). Average trapping success was significantly greater (Table 3.15) in the developed cover type at 13.54 captures per 100 trapping events, followed by coniferous forest (Tables 3.14 and 3.15). There was a higher index of abundance of small mammal hosts in the developed cover type, followed by coniferous forest (Fig. 3.1, Table 3.21). More individual *Peromyscus* sp. were captured in the developed, deciduous and coniferous forests while more individual chipmunks were captured in the developed cover type (Table 3.21). There were significantly more individual *Peromyscus* sp. captured, followed by chipmunk, and there were significantly more small mammal captures in the developed cover type, followed by coniferous forest (Table 3.13). Vegetative characteristics did not predict index of abundance of *Peromyscus* sp. (Tables 3.3 and 3.4) and chipmunk (Tables 3.5 and 3.6). Index of abundance of red squirrel was negatively related to increasing ground stem density (Fig. 3.2). Index of abundance for gray squirrels was positively related to increasing tree species richness and snag decay (Figs. 3.3 and 3.4), and was

negatively related to increasing midstory cover (Fig. 3.5). The index of abundance of all small mammal host species was negatively related to increasing snag decay, or the degradation of suitable snags (Fig. 3.6).

Estimated index of abundance of black-legged ticks and Lyme-positive ticks was greatest in the coniferous cover type (Figs. 2.2–2.6). Estimated index of abundance of black-legged ticks was positively related to increasing estimated index of abundance of all small mammal host species (Fig. 3.7). Jaccard's index of similarity and dissimilarity indicated that the grassland cover type was significantly different (Wald test  $p < 0.001$ ) than other cover types while mixed and coniferous cover types were the most similar in regards to species composition (Table 3.16). Average indices of diversity were greatest in the developed and coniferous forest cover types (Table 3.14). Estimated index of abundance of Lyme-positive ticks was positively related to increasing average small mammal host Simpson's index of diversity (Fig. 3.9) as well as average small mammal host Shannon's index of diversity (Fig. 3.8).

Of the 209 individual small mammals captured, 95 (45%) had one or more ticks attached to their head at the time of capture, hereafter referred to as tick burden. This is half of the individuals captured in areas with observed tick burdens (Table 3.17). There was a greater number of *Peromyscus* sp. individuals with tick burdens compared to other small mammal host species. In addition, a greater number of individuals captured in the developed cover type had tick burdens compared to individuals captured in other cover types (Table 3.17). From our models (Table 3.18 and 3.19), *Peromyscus* sp. and gray squirrel had significantly greater tick burdens than chipmunk (Fig. 3.10), and the developed and mixed-forest cover types had small mammal individuals with significantly greater tick burdens than in the shrub cover type (Table 3.20).

Of the 95 individuals with tick burdens, 42 (44%) individuals had an attached tick that tested positive for *Borrelia burgdorferi*. The apparent infection prevalence of tick burdens on small mammals was 32% (56/174). There was a significantly greater estimated index of abundance of Lyme-positive tick burdens on chipmunks (Fig. 3.11, Table 3.20) compared to *Peromyscus* sp. and gray squirrels based on our model (Table 3.19). Likewise, there was a greater estimated index of abundance of Lyme-positive tick burdens in the developed cover type (Table 3.17), although it was not significant (Table 3.20). Of the 115 ear punches collected in 2016, 41 (35.65%) were positive for *Borrelia burgdorferi*. A greater number of individuals tested positive for Lyme disease in the developed cover type (n = 22) compared to the other cover types (Table 3.22). There were 15 individual *Peromyscus* sp. and chipmunks that tested positive for *Borrelia burgdorferi*, however, there was a greater proportion of sampled chipmunks (57.69%) than sampled *Peromyscus* sp. (30.61%) that were positive for Lyme disease (Table 3.22). The proportion of red squirrels positive for *Borrelia burgdorferi* was comparable to that of *Peromyscus* sp. at 35.29% (Table 3.22). Based on the model (Table 3.23), there were no significant differences in *Borrelia burgdorferi* apparent prevalence among species and cover types (Table 3.24). There were 10 individuals with an attached tick as well as an ear punch that tested positive for *Borrelia burgdorferi*: 4 *Peromyscus* sp., 4 chipmunk, and 2 red squirrel; 7 were captured in the developed, 1 in the mixed, 1 in the coniferous, and 1 in the deciduous cover types. There were 15 individuals with an attached tick that tested positive for *Borrelia burgdorferi* but had ear punch that tested negative: 8 *Peromyscus* sp., 2 red squirrel, and 5 gray squirrel; 5 were captured in the developed, 2 in the mixed, 5 in the coniferous, and 3 in the deciduous cover types. There were no individuals that had an ear punch that tested positive for *Borrelia burgdorferi* but attached ticks that tested negative.

## DISCUSSION

The small mammal community within the heavily fragmented Cantonment Area of Fort Drum Military Installation was dominated by *Peromyscus* sp. and chipmunks (66% together), known effective reservoirs of Lyme disease (Brisson et al. 2008). Red (16%) and gray (9%) squirrels also had a large presence in the small mammal community, indicating that these species may be more competent reservoirs than previously thought. Because *Peromyscus* sp., chipmunks, red and gray squirrels can all better adapt to anthropogenic changes and forest fragmentation (LoGiudice et al. 2008), their disproportionate, abundant population densities in the community allow for more frequent and higher tick burdens on effective reservoirs (Ostfeld and Keesing 2000b). The high indices of abundance of effective reservoirs may also be due to the decline or lack of competitor and predator species, such as raccoon, opossum, red and gray fox, in such a fragmented landscape, and as a result, more resources become available for small mammal host populations and their reproductive success, survival and abundance increase (Ostfeld and Keesing 2000a, Schmidt and Ostfeld 2001, Keesling et al. 2009). However, there was no significant difference between indices of abundance of small mammal species, suggesting that any or all of these species may be contributing to the Lyme disease system on Fort Drum. While our methodology did include both Sherman and Tomahawk traps in hopes of detecting the mammal community's diversity, these traps target the species we captured most often and provide only a preliminary estimate of the index of abundance. Despite the selectiveness of our trapping methodology, we captured 12 different mammalian species.

The coniferous and deciduous cover types had high small mammal and tick indices of abundance, likely due to the favorable microhabitat characteristics. They also had the lowest

most production in comparison to the shrub and mixed forest cover types. Because the distribution of black-legged ticks across various cover types is dependent on host species' movements, which are largely influenced by mast production (Ostfeld et al. 1995, Wolff 1996, Jones et al. 1998), the abundances of the vector and hosts on Fort Drum was expected to be as high if not higher in the deciduous cover type compared to the mixed and coniferous cover types. Although the limited length of this study impedes the ability to model a time series of mast production and small mammal host index of abundance, this information suggests that properties of the specific cover type other than mast production may be driving the distribution of small mammal hosts. Furthermore, the lifespan of small mammals may differ by cover type, therefore implying a more aggressive transmission dynamic to maintain high prevalence of *Borrelia burgdorferi* in the vector and host populations if survival was low. Models for index of abundance of red squirrels and gray squirrels indicate that ground stem density, tree species richness, snag decay and midstory cover, all of which may serve as refuge habitat (Carey and Johnson 1995, Loeb 1996, Davis et al. 2010), are significant predictors of their distributions on the landscape. Models for index of abundance of *Peromyscus* sp. and chipmunk, however, indicated that vegetative characteristics were not significant predictors of their distributions. This also suggests the successful ability of these competent reservoir hosts to adapt to developed and fragmented areas (Ostfeld and Keesing 2000b, LoGiudice et al. 2008).

The developed and coniferous cover types both had a high index of abundance of small mammal hosts, with comparatively high chipmunk and squirrel captures, a high index of abundance of Lyme-positive questing ticks, and a high average diversity index, as index of diversity was positively related to increasing index of abundance of Lyme-positive ticks in the model. In contrast, the deciduous cover type had a relatively high index of abundance of small

mammal hosts, consisting of primarily *Peromyscus* sp., a low index of abundance of Lyme-positive questing ticks, and a low average diversity index. This was the opposite trend we were expecting and unlike other documented Lyme disease systems it does not indicate a dilution effect but rather an amplification effect (Levi et al. 2016, Keesing et al. 2006). Areas with high diversity often exhibit low *Borrelia burgdorferi* apparent prevalence on the landscape as poor reservoirs will serve as dilution hosts (LoGiudice et al. 2003, Brisson and Dykhuizen 2004, Keesing et al. 2009). It has been hypothesized that an increase in diversity of hosts, many of which are less competent reservoirs, will reduce the risk of human exposure to Lyme disease (Van Buskirk and Ostfeld 1995, Rosenblatt et al. 1999, Ostfeld and Keesing 2000a, Ostfeld and Keesing 2000b). Albeit, the presence of certain diversifying hosts may be more important than the diversity index of a cover type. However, our results indicated that increased diversity was positively related to increasing Lyme-positive ticks. For example, coniferous forests and developed areas had species compositions with a large chipmunk and squirrel presence and a higher prevalence of Lyme-positive tick counts. It is important to note that because it is difficult to discriminate *Peromyscus* species in the field as species hybridization has been reported in the northeastern United States due to their overlapping distributions (Tessier et al. 2004); in any case, we identified *Peromyscus* only to the genus level. As a result, the apparent prevalence estimates for *Peromyscus* sp. are likely influenced if they include samples taken from *Peromyscus* sp. hybrids or from the less competent reservoir represented by *Peromyscus maniculatus* (Peavey and Lane 1995).

Although we found a greater number of individual *Peromyscus* sp. with a tick burden and a Lyme-positive tick burden (n = 46, 58% and n = 18, 39%, respectfully), chipmunks had a significantly greater proportion of individuals with Lyme-positive tick burdens (n = 15, 79%)



compared to *Peromyscus* sp. and gray squirrel. The proportions of individuals with tick and Lyme-positive tick burdens indicated that red squirrels (52% and 29%, respectively), which was not statistically significant from Lyme-positive tick burdens on chipmunks, and gray squirrels (72% and 30%, respectively) may also serve as important hosts and potential reservoirs. This may be related to the fact that gray and red squirrels are more frequent in cover types with high tick and Lyme-positive tick counts (Table 3.21 and 2.11). All cover types except shrub forest had a high proportion (> 50%) of individuals with tick burdens, however, the greatest number of individuals with Lyme-positive tick burdens occurred in the developed cover type (n = 21), although there was no significant difference of individuals with Lyme-positive tick burdens between cover types. Although the same number of individual *Peromyscus* sp. and chipmunk had ear punches that tested positive for Lyme disease, there was a greater proportion of positive chipmunks (58%) compared to *Peromyscus* sp. (31%) that had the capability of transmitting Lyme disease to an uninfected tick. Additionally, there was a greater proportion of red squirrels with positive ear punches (35%) compared to *Peromyscus* sp., suggesting that other small mammal hosts may be acting as effective reservoirs for Lyme disease due to observation that these species are more frequent in cover types with high tick and Lyme-positive tick counts (Table 3.21 and 2.11). Furthermore, of the 10 individuals with an attached tick as well as an ear punch that tested positive for *Borrelia burgdorferi*, 4 were *Peromyscus* sp., 4 were chipmunk and 2 were red squirrel while of the 15 individuals with an attached tick that tested positive for *Borrelia burgdorferi* but had ear punch that tested negative, 8 were *Peromyscus* sp., 2 were red squirrel, and 5 were gray squirrel. Not only were there more negative *Peromyscus* sp. ear punches for *Borrelia burgdorferi* when there was a Lyme-positive attached tick on that individual, but there were also no chipmunks that had an attached tick that tested positive for

*Borrelia burgdorferi* but had ear punch that tested negative, suggesting chipmunks may play a greater role than previously thought in Lyme disease prevalence on the landscape. Additionally, the same number of red squirrels with an attached tick that tested positive for *Borrelia burgdorferi* had ear punches that tested positive and negative, further supporting their potential effective reservoir competence. Surprisingly, meadow voles, only captured in the grassland cover type where no ticks were detected, had a very high infection apparent prevalence of 75%, which may indicate that tick drags are an ineffective method for observing the presence of ticks. The developed cover type, with the highest small mammal indices of abundance, had the greatest number of individuals positive for *Borrelia burgdorferi* ( $n = 22$ ). It is important to note that this is not a measure of reservoir competence, which involves both the successful feeding of a tick and transmission of the spirochete.

Our results suggest that the Lyme-disease system on Fort Drum is different than those previously documented and described. This may be due to unique qualities of Fort Drum, such as the lake-effect environmental conditions found in this part of the Northeast resulting in high humidity and harsh winters, the heavily fragmented and developed nature of the Cantonment Areas, and or that the deciduous forests lack oak trees forcing rodents to seek food resources elsewhere. These qualities may encourage unexpected competent reservoirs in the Lyme-disease system on Fort Drum. Although we did not have sufficient recaptures for a proper spatially explicit mark-recapture analysis and sample sizes were small, our indices of small mammal abundance are conservative as they are the minimum number of individuals within that area. Furthermore, this information provides a basis to help understand the vector-host relationships and distributions on the Cantonment Area of Fort Drum Military Installation. Because black-legged ticks do not move large distances on their own, host distributions and movements, which

are determined by patch size and juxtaposition, need to be researched in order to determine concentrated areas with higher Lyme disease prevalence (Ostfeld et al. 1995, Van Buskirk and Ostfeld 1998). We would suggest future studies discriminate the genus *Peromyscus* to species and focus on the reservoir competence of and Lyme disease prevalence in other small mammal host species that exist in the community to better understand the vector-host relationships in the Cantonment Area.

## **CHAPTER 4**

### **MANAGEMENT RECOMMENDATIONS FOR LYME DISEASE (BORRELIA BURGDOFFERI) ON FORT DRUM MILITARY INSTALLATION, NEW YORK**

## **Management Recommendations for Lyme Disease (*Borrelia burgdorferi*) on Fort Drum Military Installation, New York**

SAMANTHA R. FINO, Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506, USA

### **INTRODUCTION**

There are 22 military installations in the Northeast (above the Mason-Dixon Line and Pennsylvania as the western boundary) collectively within the range of *Ixodes scapularis* that can carry Lyme disease. Installations range in size from Fort Drum at 433 km<sup>2</sup> to Fort Devens at less than 20 km<sup>2</sup> and most contain diverse habitat types suitable for *Ixodes scapularis*. Although the branch of military and specific mission may differ among installations, the potential for exposure of active duty personnel and their families to Lyme disease is a growing concern for the Department of Defense (Piacentino and Schwartz 2002). Fort Drum Military Installation near Watertown, New York is the largest military installation (433 km<sup>2</sup>) in the Northeast and home to approximately 19,500 active duty soldiers and their families.

The U.S. Army Public Health Command Human Tick Test Kit Program reported a mean annual Lyme disease incidence of  $52.2 \pm 7.6$  per 100,000 person-years in soldiers between January 1, 2006 and December 31, 2012. Of 14 military treatment facility locations, Fort Drum had the highest proportion of *Ixodes scapularis*, as opposed to other tick species, found attached to service members at 92%. The U.S. Army Public Health Command Human Tick Test Kit Program also reported an increase in Lyme disease incidences of 5.7% from 2006–2012 (Rossi et al. 2015). Of recorded Lyme diagnoses, Fort Drum, NY had 38 incident cases of Lyme disease during 2004–2013, making it one of the highest in the nation (Hurt and Dorsey 2014). Despite

this status, no previous intensive survey of *Ixodes scapularis* and its hosts relative to season and habitat has taken place on Fort Drum Military Installation. With rising prevalence rates, temporal- and spatial-specific recommendations and management efforts are necessary.

Our study (Chapters 2 and 3) and the following management recommendations are specific to the Cantonment Area. The Cantonment Area is approximately 4,000 ha and consists of 30% developed landscape, 30% grassland, 9% mixed forest, 5% coniferous forest, 8% shrub, and 18% deciduous forest (Figure 1.2). The Cantonment Area includes buildings, residential homes, barracks, motor pools, land navigation courses, local training areas, and recreation areas, such as parks, sports fields, green spaces and trails.

The potential risk for Fort Drum personnel and their family members to be exposed to Lyme disease via encounters with infected ticks warrants research to better manage the level of risk. Knowledge of the basic spatial and temporal patterns of *Ixodes scapularis* will allow resource managers to assess and communicate the likelihood of encountering a Lyme-positive tick and to take necessary actions to minimize that risk. Specifically, our objective was to develop management recommendations based on the distributions, densities, and Lyme disease apparent prevalence of the vector and host populations on Fort Drum. The following management recommendations are for the Cantonment Area of Fort Drum Military Installation.

## **MANAGEMENT RECOMMENDATIONS**

With a *Borrelia burgdorferi* apparent prevalence of 35% (Table 2.11), and other pathogens such as *Borrelia miyamotoi* with a apparent prevalence of < 1% (Table 2.13) and *Anaplasma phagocytophilum* with a apparent prevalence of 4% (Table 2.14), as well as co- (n = 29) and tri-infected (n = 2) ticks, there is a need to implement management practices that decrease the

risk of human exposure to tick-borne illnesses on the Cantonment Area of Fort Drum.

However, such practices can be costly in both equipment and personnel. The following habitat and wildlife management recommendations should, at minimum, be executed on areas in contact with or in close proximity to human developed areas as well as in areas of high use by soldiers and family members. More intensive practices should be confined to areas of high human use. There are several options and alternatives of habitat and wildlife management that can be done individually or in conjunction with one another. Possible options include, but are not limited to: (1) educational and outreach practices, (2) residential landscape alteration/modification, (3) leaf litter and questing substrate removal, (4) a selective cut, (5) grassland restoration and invasive species removal, (6) mowing surroundings of high human use areas, (7) the use of fungi as a biological control, and (8) the distribution of bait boxes.

#### *Education and outreach*

Whenever outside, it is important to practice personal preventative measures against Lyme disease, such as wearing light colored clothing, tucking pants into socks, wearing repellent, promptly inspecting oneself to remove ticks, exposing untreated clothing under high dryer heat for 10 minutes, and getting pets treated or vaccinated (Ginsberg 1994). Lyme disease-positive black-legged tick abundance was found greatest in the coniferous and mixed forest cover types in spring and fall months (due to the adult developmental stage peaks) (Fig. 2.5). This is due in part to the fact that adults have the highest infection apparent prevalence compared to other developmental stages at 48% (Table 2.11). Furthermore, coniferous and mixed cover types provide ticks a more suitable microhabitat. Although these cover types are only 5% and 9% of the Cantonment Area respectively, they have the highest Lyme disease apparent prevalence

(Table 2.11) and probability of encountering a Lyme-positive tick (Table 2.12). The percentage of positive-*Borrelia burgdorferi* tick declines significantly during summer months and in cover types that are less hospitable for ticks, such as shrub and deciduous forests (Table 2.12). Ideally, humans would refrain from activity in coniferous and mixed forest patches during the spring (once the snow melts through May) and fall months (starting in October until there is snow cover); whereas activity in grassland, shrub or deciduous areas could continue through the year with minimal exposure to *Borrelia burgdorferi*. Furthermore, because index of abundance of questing ticks are positively related to increasing humidity (Fig. 2.8) and temperature (Fig. 2.7), human activity could be decreased on relatively humid and hot days. Additionally, the Army could utilize information available from the CDC or NYSDOH to educate the public on tick-borne diseases and/or develop public education seminars regarding black-legged tick spatial and temporal distributions specific to Fort Drum, as well as preventative personal protective measures, and symptom reviews should they acquire a Lyme disease infection in the future.

#### *Habitat management*

Entities responsible for landscaping (e.g., Directorate of Public Works, Directorate of Family, Morale, Welfare & Recreation, Fort Drum Mountain Community Homes) should remove leaf litter piles (Fig. 2.10), coarse woody debris (Fig. 2.9), and stone walls (Stafford 2004) from residential yards and other areas with high levels of human use. These landscape features provide suitable microhabitat for both vector and host species. The CDC (2017) also recommends planting deer resistant crops in gardens to prevent attracting deer carrying tick burdens from entering the yard. If additional children's playsets are constructed, the CDC



(2017) suggests that their location be in direct sunlight where ticks will likely desiccate (Ostfeld et al. 1995, Bertrand and Wilson 1996).

In regards to habitat management outside of residential developments in the Cantonment Area, I would suggest a removal (raking or burning) of leaf litter and coarse woody debris that serve as refuge microhabitat, as well as ground-cover vegetation that may be used as questing substrate, in areas with high tick and Lyme-positive tick counts. The positive relationship tick index of abundance has with leaf litter depth (Figure 2.10) as well as the negative relationship with coarse woody debris decay (Figure 2.9), suggest increased probability of tick-host interactions and elevated tick burdens with increased vegetation density at the lowest strata closest to the ground, including leaf litter and coarse woody debris (Carey and Johnson 1995, Loeb 1996, Davis et al. 2010). The stable microclimate under leaf litter and coarse woody debris, with increased relative humidity and reduced predation risk for both black-legged ticks and hosts, promotes tick survival (Ginsberg and Ewing 1989, Adler et al. 1992, Goddard 1992, Stafford 1994, Lindsay et al. 1999, Schmidt et al. 1999, Lubelczyk et al. 2004, Prusiniski et al. 2006). Therefore, the duff and leaf litter layer should be raked monthly throughout the fall when needles begin to drop in the coniferous and mixed forest cover types. Furthermore, this should be done annually as different tree species hold their leaves for different periods of time.

Additionally, because estimated index of abundance of ticks was positively related to increasing tree species richness (Fig. 2.11), which is highly collinear with tree density and canopy cover (Appendix 20), I would suggest a selective cut of large, mast producing, dominant or co-dominant pine and hemlock trees in the coniferous and mixed-forest cover types. A selective cut would not only remove food resources from host species (Yamasaki et

al. 2000), but also to increase sunlight penetration and allow for wind movement through the forest. This management effort would also decrease pine needle depth and therefore microhabitat suitability for black-legged ticks, resulting in increased desiccation. Thinning based on basal area of coniferous and mixed stands with high canopy cover and basal area (Appendix 19) would likely decrease tick index of abundance due to their higher risk of desiccation (Ostfeld et al. 1995, Bertrand and Wilson 1996). Conifer thinning or pruning should occur in the spring before mast and needles drop and every 5 years to compete with regeneration (LandOwner Resource Centre, American Forest Foundation 2014). While I understand that these may interfere with the success of other wildlife species, such as interfering with thermal cover for deer (MNDNR 2009), in a fragmented landscape that is heavily developed such as the Cantonment Area, the decrease of Lyme disease on the landscape is of the greatest importance for the residents of Fort Drum. Hardwood trees, such as oak trees, which are primarily present in the coniferous and mixed cover types and serve as roosting habitat for endangered bat species (Jachowski et al. 2016), should not be removed.

As part of the invasive species management effort on Fort Drum, I would recommend converting the shrub cover type, dominated by common buckthorn (*Rhamnus cathartica*) and honeysuckle (*Lonicera sp.*), into restored grassland fields. Although the shrub cover type had low tick and Lyme-positive tick indices of abundance (Fig. 2.2-2.6), we did not detect any ticks in the grassland cover type (Chapter 2) most likely due to sunlight and wind causing desiccation. Early successional fields composed of native grass and wildflower species vegetation serve as great habitat for migratory birds, bees, butterflies, as well as other insects, pollinators, and species of conservation concern (NRCS 2013). By converting the shrub cover type into

grassland cover type, invasive species are removed and native habitat for pollinators and migratory birds is promoted without encouraging the presence and success of black-legged ticks.

Additionally, areas of high human use, such as hiking trails, playgrounds, and recreational fields, should be surrounded by a 3 meter buffer of mowed grasses followed by a 1 meter barrier of dark colored wood chips (CDC 2017a). Mowed and woodchip areas should act as a barrier with high sunlight exposure between human-developed areas and forested areas to prevent human-tick interactions. Additionally, trees that provide cover over these areas of high human-use should be removed. Instead, gazebos and pavilions can provide localized shade.

#### *Tick management*

*Metarhizium brunneum/anisopliae* and *Beauveria bassiana*, fungi that act as a parasitoid, can also be used to reduce risk of exposure of Lyme disease (Hornbostel et al. 2005). Nest boxes or tubes can be constructed with batting treated with the fungus. As the *Peromyscus* sp. use these nest boxes or tubes, fungus will get on their fur, as well as current or subsequent tick burdens. The fungus penetrates the cuticle and penetrates into the tick body where it proliferates. The substances produced by the fungus inside the tick are toxic and lethal (Bioforsk 2013). Furthermore, the fungus can cause ticks to feed on host blood more poorly, as well as reduce their success in molting into the next developmental stage or laying eggs (Hornbostel et al. 2004). The fungus can also grow in the soil where it can come into contact with other hosts with tick burdens or off-host ticks. I would suggest dusting the leaf/needle litter annually in coniferous and mixed forests, as well as developed areas, in spring as the small mammals emerge from hibernation or torpor. This would allow efficient transfer of the fungi from host to tick during the nymphal peak as the fungi is temperature sensitive (Bharadwaj and Stafford

2012). Three treatments are recommended per year throughout the spring and early summer in conjunction with the nymphal peak (Allabouttrees.com). I would also supplement dusting with the annual distribution of nesting boxes and tubes on trees. I would suggest 5 constructed and treated nests per 50 m<sup>2</sup>, and they should be monitored weekly for replenishment, repair or replacement. *Metarhizium burnneum/anisopliae* is an EPA-approved biological control which can be purchased online and is competitive to chemical treatments, such as pesticides that prevent or kill ticks and herbicides that kill herbaceous cover which serve as questing substrate.

### *Small mammal management*

Bait box stations that apply Fipronil to small mammals that enter the bait box station (CDC 2015a) or tick tubes treated with acaricide permethrin (Ticksinmaine.com) would be encouraged for developed areas, as well as areas in close proximity to trails and recreational areas that run through coniferous, mixed and deciduous cover types. The bait box and tick tube treatment reduce infestation prevalence on hosts and risk of exposure to an infected tick by 97% (Schulze et al. 2017, Ticktubes.com). Bait boxes or tick tubes should be deployed at the start of spring and Fipronil/permethrin should be replenished in July. Weekly monitoring of bait boxes is necessary to replenish bait accordingly. This would need to be done annually due to likely immigration/emigration and increased reproductive rates. Furthermore, these treatments should be executed at a higher magnitude of 1 bait box or tick tube per 50 m<sup>2</sup> in cover types with greater indices of abundances (Fig. 3.1). Bait boxes cost approximately \$50 per box and tick tubes cost approximately \$25 for a 6-count pack. Alternatively, vaccinated bait, such as with doxycycline which reduced Lyme disease by 94.3% (Dolan et al. 2011), could be distributed in a similar manner, although it is important to note that this method may

encourage antibiotic resistance. With *Peromyscus* sp. and chipmunks having the greatest black-legged tick burdens and Lyme-positive tick burdens, respectively (Table 3.17), as well as an observed positive relationship between index of abundance of vector and hosts (Fig. 3.7), wildlife management practices that negatively impact these species is vital in order to decrease Lyme disease prevalence on the landscape and human risk of exposure.

### *Monitoring*

If Fort Drum decides to move forward with these habitat and wildlife management recommendations, I would suggest developing 1-ha plots (based on the constraints of some of the forest fragments) evenly spaced throughout the Cantonment Area. There would be a plot for each habitat/wildlife management recommendation individually, a plot for each various combination of habitat/wildlife management recommendation, and a control plot where no habitat/wildlife management occurred. In the following year after the habitat/wildlife management was executed, tick densities and Lyme disease prevalence should be monitored biweekly after snow melt through June and again starting in October until the first snow fall in order to capture the adult and nymph peaks (Figs. 2.2 and 2.3), and as described in the methods of Chapter 2 because samples collected from tick drags are a better representation of potential human-tick interactions and human risk of exposure. Based on the results, a particular management plan can be developed, established, and modified with annual black-legged tick monitoring via tick drags.

### *Future research*

It is evident that the Fort Drum Lyme disease system may be different than that of previously studied systems. With one nymphal peak (Fig. 2.3) and low indices of host

abundance (Fig. 3.1), there may be other components of the ecosystem that are contributing to the high Lyme disease apparent prevalence in the Cantonment Area. Because Fort Drum has primarily well-drained sandy soils (Web Soil Survey 2015) that provide high quality habitat (Kitron et al. 1992, Glass et al. 1994), future research should investigate the relationship of soil and moisture content with tick distributions and prevalence. Additionally, other potential hosts, such as large rodents and mesocarnivores (e.g., groundhogs, fox, skunks, raccoons), should be explored in regards to their reservoir competence and distributions. Similarly, the relationship between the distributions of white-tailed deer, the primary hosts for adult *Ixodes scapularis* (Piesman et al. 1979, Anderson and Magnarelli 1980, Schulze et al. 1984, Spielman et al. 1985), and tick distributions should be observed. Lastly, an investigation of the predator community (raptors, carnivores) within the Cantonment Area should be conducted to gain a better understanding of what may be controlling the small mammal populations. All in all, this study provides a baseline for the tick and small mammal distributions on Fort Drum and clearly indicates that there are likely other components that are contributing to the Lyme disease prevalence.

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Table 2.1. Explanatory variables used in candidate Poisson models to evaluate variation in estimated index of abundance of black-legged ticks on Fort Drum Military Installation, New York, during April–November, 2015–2016.

Variable Type	Variable	Description
Temporal	m	Month of study
	y	Year of study (2015 or 2016)
Spatial	ct	Cover type
	patch	Patch size (square meters)
Environmental	h	Humidity (%)
	p	Pressure (mmHg)
	t	Temperature (C)
	w	Wind speed (mph)
Vegetative	cwd	Coarse woody debris decay (scale 1–5)
	l	Leaf litter depth (cm)
	spp	Tree species richness
	dbh	Tree dbh (cm)
	c	Canopy cover (%)
	sd	Snag decay (scale 1-9)
	sdbh	Snag dbh (cm)
	cwdc	Coarse woody debris density
mid	Midstory cover (scale 1-6)	

	sh	Snag height (m)
	sspp	Stem species richness
	stem	Stem count
	cwddbh	Coarse woody debris dbh (cm)
	cwdl	Coarse woody debris length (m)
	tree	Tree density
Other	sm	Small mammal index of abundance
	shan	Shannon's index of diversity
	simp	Simpson's index of diversity

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Table 2.2. Relative support for 5 candidate Poisson models of estimated index of abundance of total questing ticks (A) on Fort Drum Military Installation, New York, during April–November, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, and  $w$  is the model weight. See Table 2.1 for description of model variables.

Model	$K$	AICc	$\Delta\text{AICc}$	$w$
A(~h+t+cwd+l+spp+dbh+patch)	8	2649.12	0.00	0.66
A(~t+cwd+l+spp+dbh+patch)	7	2650.69	1.55	0.31
A(~h+t+cwd+spp+dbh+patch)	7	2656.41	7.24	0.02
A(~t+cwd+spp+dbh+patch)	6	2657.55	8.33	0.01
A(~h+t+cwd+l+spp+patch)	7	2661.39	12.29	0.01

Table 2.3. Model parameter estimates for Poisson models of estimated index of abundance of total questing ticks (A) on Fort Drum Military Installation, New York, during April–November, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
A(~h+t+cwd+l+spp					
+dbh+patch)	Intercept	-3.86	0.28	-13.61	<0.001
	t	0.03	0.01	10.47	<0.001
	h	0.25	0.13	1.91	0.01
	spp	0.24	0.03	7.19	<0.001
	cwd	-0.41	0.08	-4.86	<0.001
	l	0.10	0.03	3.02	<0.001
	dbh	0.01	0.01	3.79	<0.001
	patch	-0.01	0.01	-6.59	<0.001

Table 2.4. Model parameter estimates for Poisson models of estimated index of abundance of adult questing ticks (Aa) on Fort Drum Military Installation, New York, during April–November, 2015–2016 Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
Aa(~y*m+ct)	Intercept	-3.44	0.11	-30.86	<0.001
	August	19.61	970.00	-0.02	0.98
	July	19.54	929.87	-0.02	0.98
	June	-1.96	0.27	-7.24	0.00
	May	-0.35	0.13	-2.72	0.01
	November	0.69	0.12	5.81	0.00
	October	0.07	0.13	0.55	0.58
	September	-3.03	0.42	-7.21	0.00
	y	0.05	0.10	0.46	0.64
	Deciduous	-1.10	0.15	-7.34	0.00
	Developed	-0.30	0.12	-2.49	0.01
	Mix	-0.08	0.09	-0.96	0.34
	Shrub	-1.09	0.18	-5.98	0.00
	August:y	-0.06	970.00	0.00	1.00
	July:y	-0.07	929.87	0.00	1.00
	June:y	-0.44	0.27	-1.64	0.10
	May:y	-0.16	0.13	-1.20	0.23
	November:y	-0.25	0.12	-2.13	0.03

October:y	-0.27	0.13	-2.06	0.04
September:y	-0.08	0.42	-0.20	0.85

---

Table 2.5. Model parameter estimates for Poisson models of estimated index of abundance of nymphal questing ticks (An) on Fort Drum Military Installation, New York, during April–November, 2015–2016. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
An(~y*m+ct)	Intercept	-22.72	1057.25	-0.02	0.98
	August	18.75	1057.25	0.02	0.99
	July	19.45	1057.25	0.02	0.99
	June	20.05	1057.25	0.02	0.99
	May	18.85	1057.25	0.02	0.99
	November	0.02	1365.06	0.00	1.00
	October	8.33	1284.60	0.01	1.00
	September	17.61	1057.25	0.02	0.99
	y	-0.03	1057.25	0.00	1.00
	Deciduous	-0.98	0.14	-6.78	<0.001
	Developed	-1.08	0.17	-6.43	<0.001
	Mix	-0.44	0.10	-4.33	<0.001
	Shrub	-1.40	0.23	-6.14	<0.001
	August:y	-0.12	1057.25	0.00	1.00
	July:y	0.07	1057.25	0.00	1.00
	June:y	-0.11	1057.25	0.00	1.00
	May:y	-0.43	1057.25	0.00	1.00
	November:y	-0.02	1365.06	0.00	1.00

October:y	-8.48	1284.60	-0.01	1.00
September:y	0.04	1057.25	0.00	1.00

---



Table 2.6. Model parameter estimates for Poisson models of estimated index of abundance of larval questing ticks (Al) on Fort Drum Military Installation, New York, during April–November, 2015–2016. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
Al(~y*m+ct)	Intercept	-22.11	647.65	-0.03	0.97
	August	19.09	647.65	0.03	0.98
	July	16.97	647.65	0.03	0.98
	June	18.45	647.65	0.03	0.98
	May	16.97	647.65	0.03	0.98
	November	0.04	836.43	0.00	1.00
	October	16.77	647.65	0.03	0.98
	September	19.38	647.65	0.03	0.98
	y	0.00	647.65	0.00	1.00
	Deciduous	-0.04	0.11	-0.34	0.74
	Developed	-0.38	0.12	-3.25	0.00
	Mix	0.06	0.08	0.81	0.42
	Shrub	-1.77	0.30	-5.99	<0.001
	August:y	1.06	647.65	0.00	1.00
	July:y	-0.27	647.65	0.00	1.00
	June:y	0.18	647.65	0.00	1.00
	May:y	-0.58	647.65	0.00	1.00
	November:y	-0.05	836.43	0.00	1.00

October:y	0.43	647.65	0.00	1.00
September:y	-0.17	647.65	0.00	1.00

---

Table 2.7. Model parameter estimates for Poisson models of estimated index of abundance of Lyme-positive adult questing ticks (Pa) on Fort Drum Military Installation, New York, during April–November, 2015–2016. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
Pa(~y*m+ct)	Intercept	-3.92	0.15	-26.96	<0.001
	August	-20.15	1601.46	-0.01	0.99
	July	-20.10	1552.24	-0.01	0.99
	June	-3.01	0.59	-5.10	<0.001
	May	-0.59	0.17	-3.40	<0.001
	November	0.36	0.16	2.31	0.02
	October	-0.45	0.20	-2.26	0.02
	September	-20.19	1660.77	-0.01	0.99
	y	0.04	0.13	0.29	0.77
	Deciduous	-1.23	0.23	-5.32	<0.001
	Developed	-0.21	0.17	-1.26	0.21
	Mix	-0.06	0.13	-0.43	0.66
	Shrub	-1.01	0.26	-3.89	<0.001
	August:y	-0.06	1601.46	0.00	1.00
	July:y	-0.06	1552.24	0.00	1.00
	June:y	-0.85	0.59	-1.44	0.15
	May:y	-0.10	0.17	-0.60	0.55
November:y	-0.28	0.16	-1.76	0.08	

October:y	-0.57	0.20	-2.84	<0.001
September:y	-0.12	1660.77	0.00	1.00

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Table 2.8. Model parameter estimates for Poisson models of estimated index of abundance of Lyme-positive nymphal questing ticks (Pn) on Fort Drum Military Installation, New York, during April–November, 2015–2016. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
Pn(~y*m+ct)	Intercept	-23.67	1695.00	-0.01	0.99
	August	17.15	1695.00	0.01	0.99
	July	18.92	1695.00	0.01	0.99
	June	19.23	1695.00	0.01	0.99
	May	17.93	1695.00	0.01	0.99
	November	-0.08	2222.00	0.00	1.00
	October	7.93	2098.00	0.00	1.00
	September	17.33	1695.00	0.01	0.99
	y	<0.001	1695.00	0.00	1.00
	Deciduous	-0.86	0.34	-2.54	0.01
	Developed	-2.32	0.72	-3.21	<0.001
	Mix	-0.30	0.23	-1.30	0.19
	Shrub	-1.24	0.47	-2.63	0.01
	August:y	0.83	1695.00	0.00	1.00
	July:y	-0.56	1695.00	0.00	1.00
	June:y	-0.22	1695.00	0.00	1.00
	May:y	0.45	1695.00	0.00	1.00
	November:y	-0.09	2222.00	0.00	1.00

October:y	-8.28	2098.00	0.00	1.00
September:y	0.31	1695.00	0.00	1.00

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Table 2.9. Parametric bootstrapped estimates of index of abundance of ticks from a generalized linear Poisson model on Fort Drum Military Installation, New York, during April–November, 2015–2016 spatially and temporally. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left. NAs represent that no ticks of that developmental stage were collected during that month.

<b>Comparison 1</b>	<b>Comparison 2</b>	<b>Adult index of abundance confidence intervals of bootstrap estimates</b>	<b>Nymph index of abundance confidence intervals of bootstrap estimates</b>
<i>Cover type</i>			
Coniferous	Deciduous	(0.016,0.029)*>	(0.008,0.016)*>
Coniferous	Developed	(0.002,0.015)*>	(0.008,0.017)*>
Coniferous	Mixed	(-0.002,0.008)	(0.004,0.010)*>
Coniferous	Shrub	(0.015,0.029)*>	(0.010,0.019)*>
Deciduous	Developed	(-0.021,-0.007)*<	(-0.002,0.003)
Deciduous	Mixed	(-0.026,-0.014)*<	(-0.008,-0.002)*<
Deciduous	Shrub	(-0.005,0.005)	(-0.001,0.005)

Developed	Mixed	(-0.012,0.001)	(-0.009,-0.003)*<
Developed	Shrub	(0.007,0.020)*>	(-0.001,0.005)
Mixed	Shrub	(0.013,0.026)*>	(0.004,0.011)*>
<i>Month</i>			
April	May	(0.002,0.018)*>	NA
April	June	(0.021,0.036)*>	NA
April	July	NA	NA
April	August	NA	NA
April	September	(0.024,0.039)*>	NA
April	October	(-0.012,0.007)	NA
April	November	(-0.042,-0.022)*<	NA
May	June	(0.014,0.023)*>	(-5.506,-1.542)*<
May	July	NA	(-2.542,-0.444)*<
May	August	NA	(0.788,1.490)*>
May	September	(0.017,0.026)*>	(0.495,1.015)*>
May	October	(-0.020,-0.005)*<	(-1.699,1.439)
May	November	(-0.051,-0.033)*<	NA



June	July	NA	(0.934,3.326)*>
June	August	NA	(2.370,6.999)*>
June	September	(0.001,0.006)*>	(2.142,6.463)*>
June	October	(-0.038,-0.024)*<	(-1.699,6.383)
June	November	(-0.070,-0.050)*<	NA
July	August	NA	(1.275,3.954)*>
July	September	NA	(1.045,3.356)*>
July	October	NA	(-1.699,3.698)
July	November	NA	NA
August	September	NA	(-0.717,-0.162)*<
August	October	NA	(-1.699,2.477)
August	November	NA	NA
September	October	(-0.041,-0.027)*<	(-0.717,-0.162)*<
September	November	(-0.073,-0.054)*<	NA
October	November	(-0.040,-0.019)*<	NA

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Table 2.10. Parametric bootstrapped estimates of index of abundance of Lyme-positive ticks from a generalized linear Poisson model on Fort Drum Military Installation, New York, during April–November, 2015–2016 spatially and temporally. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol  $>$  indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol  $<$  indicates the item in the column on the right is significantly greater than the item in the column on the left. NAs represent that no ticks of that developmental stage were collected during that month.

<b>Comparison 1</b>	<b>Comparison 2</b>	<b>Adult index of abundance confidence intervals of bootstrap estimates</b>	<b>Nymph index of abundance confidence intervals of bootstrap estimates</b>
<i>Cover type</i>			
Coniferous	Deciduous	(0.014,0.026)* $>$	(0.006,0.011)* $>$
Coniferous	Developed	(0.002,0.014)* $>$	(0.006,0.012)* $>$
Coniferous	Mixed	(-0.002,0.007)	(0.003,0.008)* $>$
Coniferous	Shrub	(0.013,0.026)* $>$	(0.007,0.014)* $>$
Deciduous	Developed	(-0.018,-0.006)* $<$	(-0.001,0.003)
Deciduous	Mixed	(-0.024,-0.012)* $<$	(-0.005,-0.001)* $<$
Deciduous	Shrub	(-0.005,0.004)	(-0.001,0.004)

Developed	Mixed	(-0.011,0.001)	(-0.006,-0.002)*<
Developed	Shrub	(0.005,0.020)*>	(-0.001,0.003)
Mixed	Shrub	(0.011,0.024)*>	(0.003,0.007)*>
<i>Month</i>			
April	May	(0.002,0.015)*>	NA
April	June	(0.017,0.033)*>	NA
April	July	NA	NA
April	August	NA	NA
April	September	(0.020,0.036)*>	NA
April	October	(-0.012,0.007)	NA
April	November	(-0.037,-0.016)*<	NA
May	June	(0.014,0.023)*>	(-5.863,-1.340)*<
May	July	NA	(-1.998,-0.127)*<
May	August	NA	(1.065,2.112)*>
May	September	(0.017,0.027)*>	(0.583,1.306)*>
May	October	(-0.017,-0.002)*<	(-1.699,2.016)
May	November	(-0.045,-0.022)*<	NA

June	July	NA	(1.014,4.341)*>
June	August	NA	(2.414,7.970)*>
June	September	(0.001,0.006)*>	(2.094,7.034)*>
June	October	(-0.035,-0.020)*<	(-1.699,7.123)
June	November	(-0.063,-0.039)*<	NA
July	August	NA	(1.272,4.053)*>
July	September	NA	(0.914,3.060)*>
July	October	NA	(-1.699,3.564)
July	November	NA	NA
August	September	NA	(-1.187,-0.259)*<
August	October	NA	(-1.699,0.023)
August	November	NA	NA
September	October	(-0.038,-0.024)*<	(-1.699,1.045)*<
September	November	(-0.066,-0.043)*<	NA
October	November	(-0.035,-0.012)*<	NA

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Table 2.11. Apparent prevalence of *Borrelia burgdorferi* on a spatial and temporal scale on Fort Drum Military Installation, New York during 2015–2016.

<b>Categorical variable</b>	<b>No. individuals</b>	<b>No. total individuals</b>	<b>% infection rate</b>
<b>positive for <i>B. burgdorferi</i></b>			
<hr/>			
<i>Developmental stage</i>			
Adult	340	711	47.82%
Nymph	97	535	17.57%
<i>Cover type</i>			
Coniferous	177	540	32.78%
Deciduous	34	113	30.09%
Developed	52	135	38.51%
Mixed	152	403	37.72%
Shrub	22	55	40.00%
<i>Month</i>			
April	68	108	62.96%
May	90	314	28.66%
June	39	342	11.40%
July	29	154	18.83%
August	7	451	1.55%
September	6	310	1.94%
October	65	174	37.36%
November	133	299	44.48%

**Total**

437

1246

35.07%

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Table 2.12. Percentage of positive-*Borrelia burgdorferi* tick per 100 square meters on Fort Drum Military Installation, New York, during April–November 2015–2016.

<b>Month</b>	<b>Cover type</b>	<b>Adult</b>	<b>Nymph</b>
<i>April</i>			
	Coniferous	86.20%	0.00%
	Deciduous	43.92%	0.00%
	Developed	79.86%	0.00%
	Mixed	84.65%	0.00%
	Shrub	51.40%	0.00%
<i>May</i>			
	Coniferous	70.46%	18.54%
	Deciduous	29.95%	8.30%
	Developed	62.71%	10.99%
	Mixed	68.47%	14.11%
	Shrub	35.86%	5.75%
<i>June</i>			
	Coniferous	20.47%	77.14%
	Deciduous	6.47%	46.41%
	Developed	16.91%	13.51%
	Mixed	19.48%	66.53%
	Shrub	8.00%	34.73%
<i>July</i>			
	Coniferous	0.00%	60.00%

Deciduous	0.00%	32.15%
Developed	0.00%	8.62%
Mixed	0.00%	49.32%
Shrub	0.00%	23.27%

*August*

Coniferous	0.00%	6.23%
Deciduous	0.00%	6.23%
Developed	0.00%	2.68%
Mixed	0.00%	0.63%
Shrub	0.00%	1.84%

*September*

Coniferous	0.00%	12.17%
Deciduous	0.00%	5.34%
Developed	0.00%	1.27%
Mixed	0.00%	9.18%
Shrub	0.00%	3.68%

*October*

Coniferous	89.23%	0.00%
Deciduous	47.85%	0.00%
Developed	83.52%	0.00%
Mixed	87.87%	0.00%
Shrub	55.61%	0.00%

*November*



Coniferous	97.66%	0.00%
Deciduous	66.62%	0.00%
Developed	95.21%	0.00%
Mixed	97.14%	0.00%
Shrub	74.60%	0.00%

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Table 2.13. Apparent prevalence of *Borrelia miyamotoi* on a spatial and temporal scale on Fort Drum Military Installation, New York during 2015–2016.

<b>Categorical variable</b>	<b>No. individuals</b>	<b>No. total individuals</b>	<b>% infection rate</b>
<b>positive for <i>B. miyamotoi</i></b>			
<hr/>			
<i>Developmental stage</i>			
Adult	9	711	1.27%
Nymph	3	535	0.56%
<i>Cover type</i>			
Coniferous	8	540	1.48%
Deciduous	2	113	1.77%
Developed	1	135	0.74%
Mixed	1	403	0.25%
Shrub	0	55	0.00%
<i>Month</i>			
April	4	108	3.70%
May	2	314	0.64%
June	2	342	0.58%
July	0	154	0.00%
August	0	451	0.00%
September	0	310	0.00%
October	0	174	0.00%
November	4	299	1.34%

**Total**

12

1246

0.96%

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Table 2.14. Apparent prevalence of *Anaplasma phagocytophilum* on a spatial and temporal scale on Fort Drum Military Installation, New York during 2015–2016.

<b>Categorical variable</b>	<b>No. individuals</b>	<b>No. total individuals</b>	<b>% infection rate</b>
<b>positive for <i>A. phagocytophilum</i></b>			
<i>Developmental stage</i>			
Adult	46	711	6.47%
Nymph	4	535	0.75%
<i>Cover type</i>			
Coniferous	25	540	4.63%
Deciduous	4	113	3.54%
Developed	10	135	7.41%
Mixed	10	403	2.48%
Shrub	1	55	1.82%
<i>Month</i>			
April	9	108	8.33%
May	16	314	5.10%
June	4	342	1.17%
July	1	154	0.65%
August	0	451	0.00%
September	0	310	0.00%
October	10	174	5.75%
November	10	299	3.34%

**Total**

50

1246

4.01%

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Table 3.1. Model parameter estimates for Poisson models of estimated index of abundance of total questing ticks (A) on Fort Drum Military Installation, New York, during April–November, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
A(~y+ct+sm)	Intercept	1.92	0.23	8.19	<0.001
	y	0.03	0.03	1.02	0.31
	sm	0.03	0.02	1.35	0.18
	Deciduous	-0.44	0.12	-3.57	<0.001
	Developed	-0.75	0.24	-3.07	<0.001
	Mixed	0.13	0.17	0.78	0.44
	Shrub	-1.17	0.17	-6.76	<0.001

Table 3.2. Model parameter estimates for Poisson models of estimated index of abundance of total questing ticks (P) on Fort Drum Military Installation, New York, during April–November, 2015–2016. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
P(~y+ct+shan+simp)	Intercept	-3.59	0.31	-11.60	<0.001
	y	-0.30	0.06	-4.85	<0.001
	Deciduous	-1.03	0.23	-4.47	<0.001
	Developed	-0.35	0.16	-2.15	0.03
	Mix	-0.12	0.21	-0.56	0.58
	Shrub	-0.88	0.27	-3.20	<0.001
	shan	0.02	0.34	0.05	0.96
	simp	0.04	0.58	0.07	0.95

Table 3.3. Relative support for 5 candidate Poisson models of estimated index of abundance of *Peromyscus* sp. (D) on Fort Drum Military Installation, New York, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, while  $w$  is the model weight. See Table 2.1 for description of model variables.

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w</math></b>
D(~ct)	6	101.50	0.00	0.34
D(~ct+c)	7	102.19	0.69	0.24
D(~ct+sd)	7	103.96	2.46	0.10
D(~ct+sdbh)	7	105.27	3.77	0.05
D(~ct+l)	7	105.53	4.04	0.05



Table 3.4. Model parameter estimates for Poisson models of estimated index of abundance of *Peromyscus* sp. (D) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta AIC_c$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
D(~)	Intercept	3.91	1.86	2.10	0.04
	Deciduous	0.04	0.31	0.14	0.89
	Developed	-0.59	0.74	-0.80	0.43
	Grassland	-22.21	2858.77	-0.01	0.99
	Mix	-1.26	0.47	-2.70	0.01
	Shrub	-1.06	0.44	-2.41	0.02
	c	-0.02	0.02	-1.24	0.21

Table 3.5. Relative support for 5 candidate Poisson models of estimated index of abundance of chipmunk (C) on Fort Drum Military Installation, New York, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, while  $w$  is the model weight. See Table 2.1 for description of model variables.

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w</math></b>
C(~ct+cwdc+mid+sh)	9	83.68	0.00	0.24
C(~ct+mid)	7	83.97	0.29	0.21
C(~ct+cwdc)	7	84.46	0.78	0.16
C(~ct+mid+cwdc)	8	85.03	1.35	0.12
C(~ct+cwdc+sspp)	8	85.35	1.67	0.10

Table 3.6. Model parameter estimates for Poisson models of estimated index of abundance of chipmunk (C) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
C(~ct+cwdc+mid+sh)	Intercept	-12.51	1916.40	-0.01	1.00
	Deciduous	15.75	2524.26	0.01	1.00
	Developed	-296.37	39177.38	-0.01	0.99
	Grassland	-32.75	3984.23	-0.01	0.99
	Mix	47.90	6313.86	0.01	0.99
	Shrub	277.92	38428.99	0.01	0.99
	cwdc	21.15	3320.08	0.01	1.00
	mid	-139.68	19264.73	-0.01	0.99
	sh	-69.77	10147.11	-0.01	1.00

Table 3.7. Relative support for 5 candidate Poisson models of estimated index of abundance of red squirrel (R) on Fort Drum Military Installation, New York, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, while  $w$  is the model weight. See Table 2.1 for description of model variables.

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w</math></b>
R(~ct+stem)	7	65.27	0.00	0.30
R(~ct+stem+dbh)	8	65.36	0.09	0.29
R(~ct+stem+l)	8	66.44	1.17	0.17
R(~ct+cwddbh+stem)	8	69.77	4.51	0.03
R(~ct+sh+stem)	8	70.04	4.78	0.03

Table 3.8. Model parameter estimates for Poisson models of estimated index of abundance of red squirrel (R) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta\text{AICc}$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
R(~ct+stem)	Intercept	-0.28	0.52	-0.54	0.59
	Deciduous	-19.83	4921.30	-0.004	1.00
	Developed	1.98	0.49	4.07	<0.001
	Grassland	-17.00	4713.31	-0.004	1.00
	Mix	-1.51	0.78	-1.93	0.05
	Shrub	-0.96	0.67	-1.44	0.15
	stem	-1.56	0.57	-2.74	<0.001

Table 3.9. Relative support for 5 candidate Poisson models of estimated index of abundance of gray squirrel (G) on Fort Drum Military Installation, New York, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, while  $w$  is the model weight. See Table 2.1 for description of model variables.

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w</math></b>
G(~mid+spp+sd)	4	40.92	0.00	0.60
G(~cwdl+mid+spp+sd)	5	43.59	2.67	0.16
G(~dbh+mid+spp+sd)	5	44.22	3.29	0.12
G(~cwdl+mid+spp)	4	45.13	4.21	0.07
G(~cwdl+dbh+mid+spp+sd)	6	45.76	4.83	0.05

Table 3.10. Model parameter estimates for Poisson models of estimated index of abundance of gray squirrel (G) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta\text{AICc}$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
G(~mid+spp+sd)	Intercept	-7.27	2.79	-2.61	<0.001
	spp	3.69	1.05	3.52	<0.001
	sd	8.16	3.17	2.57	0.01
	mid	-4.45	1.68	-2.65	<0.001

Table 3.11. Relative support for 5 candidate Poisson models of estimated index of abundance of all host species (H) on Fort Drum Military Installation, New York, 2015–2016.  $K$  indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size,  $\Delta\text{AICc}$  is the difference in AICc units from the best approximating model, while  $w$  is the model weight. See Table 2.1 for description of model variables.

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w</math></b>
H(~ct+sd)	7	142.55	0.00	0.50
H(~ct+sd+dbh)	8	145.16	2.62	0.13
H(~ct+sd+cwdl)	8	146.09	3.54	0.08
H(~ct+sd+sdbh)	8	146.51	3.96	0.07
H(~ct+spp)	8	146.53	3.98	0.07



Table 3.12. Model parameter estimates for Poisson models of estimated index of abundance of all host species (H) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
H(~ct+sd)	Intercept	3.62	0.24	15.11	<0.001
	Deciduous	-1.34	0.30	-4.54	<0.001
	Developed	0.78	0.18	4.27	<0.001
	Grassland	-7.32	1.07	-6.77	<0.001
	Mix	-1.76	0.32	-5.58	<0.001
	Shrub	-1.26	0.27	-4.70	<0.001
	sd	-2.08	0.39	-5.33	<0.001

Table 3.13. Parametric bootstrapped estimates of index of abundance of small mammal hosts from a generalized linear Poisson model on Fort Drum Military Installation, New York, 2015–2016. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

<b>Category 1</b>	<b>Category 2</b>	<b>Index of abundance confidence intervals of bootstrap estimates</b>
<i>Cover type</i>		
Coniferous	Deciduous	(2.37,8.72)*>
Coniferous	Grassland	(8.19,13.90)*>
Coniferous	Developed	(-16.63,-7.42)*<
Coniferous	Mixed	(5.85,11.72)*>
Coniferous	Shrub	(3.40,9.73)*>
Deciduous	Grassland	(3.62,7.72)*>
Deciduous	Developed	(-21.54,-13.28)*<
Deciduous	Mixed	(0.97,5.53)*>
Deciduous	Shrub	(-1.54,3.52)
Grassland	Developed	(-26.94,-18.83)*<
Grassland	Mixed	(-4.01,-0.98)*<
Grassland	Shrub	(-6.46,-2.74)*<
Developed	Mixed	(16.49,24.52)*>
Developed	Shrub	(14.23,22.81)*>

Mixed	Shrub	(-4.32,-0.02)*<
<i>Species</i>		
<i>Peromyscus</i> sp.	Gray squirrel	(0.27,0.44)*>
<i>Peromyscus</i> sp.	Red squirrel	(0.25,0.41)*>
<i>Peromyscus</i> sp.	Chipmunk	(0.21,0.34)*>
Gray squirrel	Red squirrel	(-0.06,-0.01)*<
Gray squirrel	Chipmunk	(-0.13,-0.04)*<
Red squirrel	Chipmunk	(-0.09,-0.01)*<

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Table 3.14. Average trapping success per 100 capture events, Simpson’s diversity index and Shannon’s diversity index on Fort Drum Military Installation, New York, 2015–2016.

	<b>Developed</b>	<b>Grassland</b>	<b>Coniferous</b>	<b>Mixed</b>	<b>Deciduous</b>	<b>Shrub</b>
Trapping	13.54	0.70	4.82	1.58	2.29	2.61
Success						
Simpson’s	0.57	0.12	0.53	0.26	0.23	0.38
Diversity						
Index						
Shannon’s	0.96	0.17	0.97	0.44	0.35	0.70
Diversity						
Index						

Table 3.15. Parametric bootstrapped estimates of average trapping success, Simpson’s diversity index and Shannon’s diversity index from a generalized linear Poisson model on Fort Drum Military Installation, New York, 2015–2016. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

<b>Cover type 1</b>	<b>Cover type 2</b>	<b>Trapping Success CI of bootstrap estimates</b>	<b>Simpson’s diversity index CI of bootstrap estimates</b>	<b>Shannon’s diversity index CI of bootstrap estimates</b>
Coniferous	Deciduous	(-2.51,52.35)	(0.21,0.66)*>	(0.70,1.78)*>
Coniferous	Developed	(-1569.31,-93.21)*<	(-0.30,0.17)	(-0.66,0.67)
Coniferous	Grassland	(0.71,53.67)*>	(0.19,0.63)	(0.57,1.66)*>
Coniferous	Mixed	(-1.87,51.16)	(0.01,0.48)*>	(0.05,1.24)*>
Coniferous	Shrub	(2.21,54.51)*>	(0.37,0.81)*>	(0.97,2.02)*>
Deciduous	Developed	(-1602.33,-110.11)*<	(-0.73,-0.28)*<	(-1.77,-0.68)*<
Deciduous	Grassland	(-4.36,9.01)	(-0.22,0.15)	(-0.53,0.23)
Deciduous	Mixed	(-8.25,7.91)	(-0.40,-.01)*<	(-1.03,-0.15)*<
Deciduous	Shrub	(-2.04,9.28)	(-0.04,0.31)	(-0.09,0.54)
Developed	Grassland	(109.61,1602.05)*>	(0.26,0.70)*>	(0.51,1.68)*>
Developed	Mixed	(109.96,1597.19)*>	(0.06,0.54)*>	(0.03,1.25)*>

Developed	Shrub	(111.10,1601.74)*>	(0.44,0.86)*>	(0.90,2.02)*>
Mixed	Grassland	(-9.52,4.38)	(-0.38,0.02)	(-0.90,0.02)
Mixed	Shrub	(-3.12,5.45)	(-0.01,0.34)	(0.04,0.73)*>
Shrub	Grassland	(-2.21,9.95)	(0.16,0.51)*>	(0.44,1.27)*>

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Table 3.16. Jaccard's index of similarity between cover types on Fort Drum Military Installation, New York, 2015–2016.

<b>Cover type</b>	<b>Jaccard's</b>	<b>% similarity</b>	<b>% dissimilar</b>
Developed - Grassland	0.00	0.00	100.00
Developed - Mixed	0.38	37.50	62.50
Developed - Shrub	0.67	66.67	33.33
Developed - Deciduous	0.67	66.67	33.33
Developed - Coniferous	0.57	57.14	42.86
Mixed - Grassland	0.00	0.00	100.00
Mixed - Shrub	0.57	57.14	42.86
Mixed - Deciduous	0.38	37.50	62.50
Mixed - Coniferous	0.71	71.43	28.57
Shrub - Grassland	0.00	0.00	100.00
Shrub - Deciduous	0.43	42.86	57.14
Shrub - Coniferous	0.38	37.50	62.50
Deciduous - Grassland	0.00	0.00	100.00
Deciduous - Coniferous	0.57	57.14	42.86
Grassland - Coniferous	0.00	0.00	100.00

Table 3.17. Individuals with tick burdens and individuals exposed to *Borrelia burgdorferi* via Lyme-positive tick burdens on Fort Drum Military Installation, New York, during 2015–2016.

Categorical variable	# Individuals with tick burdens	# Individuals captured in cover types with observed tick burdens		# Individuals with a positive tick burdens	Total individuals captured with tick burden that is positive
		% of total individuals captured with tick burden	% of total individuals captured with a positive tick burdens		
<i>Species</i>					
<i>Peromyscus</i>					
sp.	46	79	58%	18	39.13%
Chipmunk	19	59	32%	15	78.95%
Red					
squirrel	17	33	52%	5	29.41%
Gray					
squirrel	13	18	72%	4	30.77%
<i>Cover Type</i>					
Coniferous	23	45	51%	8	34.78%
Deciduous	13	24	54%	8	61.54%
Developed	47	90	52%	21	44.68%



Mixed	8	11	73%	4	50.00%
Shrub	4	19	21%	1	25.00%
<b>Total</b>	<b>95</b>	<b>189</b>	<b>50%</b>	<b>42</b>	<b>44.21%</b>

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Table 3.18. Model parameter estimates for binomial models of estimated index of abundance of individuals with tick burdens (T) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
T(~host+ct)	Intercept	0.02	0.37	0.07	0.95
	gray squirrel	0.58	0.58	1.00	0.32
	red squirrel	-0.44	0.45	-0.99	0.32
	chipmunk	-0.97	0.42	-2.32	0.02
	Deciduous	0.20	0.55	0.36	0.72
	Developed	0.56	0.42	1.31	0.19
	Mixed	1.69	0.88	1.93	0.05
	Shrub	-0.87	0.68	-1.30	0.20

Table 3.19. Model parameter estimates for binomial models of estimated index of abundance of individuals with Lyme-positive tick burdens (*B.burg*) on Fort Drum Military Installation, New York, 2015–2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
B.burg(~host+ct)	Intercept	-1.42	0.84	-1.69	0.09
	gray squirrel	-16.15	1769.26	-0.01	0.99
	red squirrel	0.24	1.05	0.23	0.82
	chipmunk	1.03	0.88	1.16	0.24
	Deciduous	1.17	1.09	1.07	0.28
	Developed	1.02	1.01	1.01	0.31
	Mixed	1.49	1.57	0.95	0.34
	Shrub	17.96	3956.18	0.01	0.10

Table 3.20. Parametric bootstrapped estimates of number of tick burdens and Lyme-positive tick burdens off host species from a generalized linear Poisson and binomial model respectively on Fort Drum Military Installation, New York, 2015–2016. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

<b>Category 1</b>	<b>Category 2</b>	<b>Tick burden count confidence intervals of bootstrap estimates</b>	<b>Lyme-positive tick burden count confidence intervals of bootstrap estimates</b>
<i>Cover type</i>			
Coniferous	Deciduous	(-1.70,0.10)	(-1.18,0.18)
Coniferous	Developed	(-2.37,0.37)	(-0.22,0.38)
Coniferous	Mixed	(-24.99,0.18)	(-0.51,0.38)
Coniferous	Shrub	(-0.43,1.68)	(-0.75,0.52)
Deciduous	Developed	(-2.20,1.11)	(-0.03,1.20)
Deciduous	Mixed	(-25.20,0.69)	(-0.22,1.12)
Deciduous	Shrub	(-0.30,2.33)	(-0.50,1.25)
Developed	Mixed	(-23.36,0.92)	(-0.49,0.22)
Developed	Shrub	(0.24,2.96)*>	(-0.77,0.37)
Mixed	Shrub	(0.35,25.69)*>	(-0.75,0.62)

*Species*

<i>Peromyscus</i> sp.	Gray squirrel	(-3.53,0.64)	(-0.49,0.40)
<i>Peromyscus</i> sp.	Red squirrel	(-0.46,1.38)	(-1.51,0.01)
<i>Peromyscus</i> sp.	Chipmunk	(0.06,1.50)*>	(-3.81,-0.28)*<
Gray squirrel	Red squirrel	(-0.18,3.81)	(-1.72,0.18)
Gray squirrel	Chipmunk	(0.20,4.19)*>	(-3.98,-0.13)*<
Red squirrel	Chipmunk	(-0.23,1.02)	(-3.10,0.20)

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Table 3.21. Summary statistics of small mammal captured individuals on Fort Drum Military Installation, New York, during 2015–2016.

	<b>Deciduous forest</b>	<b>Developed</b>	<b>Coniferous forest</b>	<b>Grassland</b>	<b>Mixed forest</b>	<b>Shrub</b>	<b>Total</b>
<i>Peromyscus</i>							
sp.	21	25	20	0	6	7	79
Chipmunk	2	42	3	0	3	9	59
Red							
squirrel	0	18	10	0	2	3	33
Gray							
squirrel	1	5	12	0	0	0	18
Meadow							
vole	0	0	0	6	0	0	6
Short-tailed							
shrew	0	0	1	0	1	1	3
Long-tailed							
weasel	0	0	0	0	1	2	3
S. flying							
squirrel	1	0	2	0	0	0	3
Striped							
skunk	1	1	0	0	0	1	3
Meadow							
jumping							

mouse	0	0	0	2	0	0	2
<b>Total</b>	26	91	48	8	13	23	209

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Table 3.22. Summary statistics of Lyme-disease apparent prevalence from ear punch samples on Fort Drum Military Installation, New York, during 2016.

<b>Categorical variable</b>	<b>No. individuals</b>	<b>No. total individuals</b>	<b>Infection rate</b>
<b>positive for <i>B. burgdorferi</i></b>			
<i>Cover type</i>			
Coniferous	5	27	18.52%
Deciduous	4	13	30.77%
Developed	22	52	42.31%
Grassland	3	6	50.00%
Mixed	2	8	25.00%
Shrub	5	9	55.56%
<i>Species</i>			
<i>Peromyscus</i> sp.	15	49	30.61%
Chipmunk	15	26	57.69%
Red squirrel	6	17	35.29%
Gray squirrel	2	15	13.33%
Meadow vole	3	4	75.00%
Flying squirrel	0	2	0.00%
Meadow jumping mouse	0	2	0.00%
<b>Total</b>	<b>41</b>	<b>115</b>	<b>35.65%</b>



Table 3.23. Model parameter estimates for binomial models of estimated index of abundance of individuals with Lyme-positive ear punches (EP) on Fort Drum Military Installation, New York, 2016 within  $\Delta AICc$  of 2 used in model averaging to determine the final model. Parameter estimates ( $\beta$ ) are presented with standard errors (SE) as well as Z and p (Pr) values.

<b>Model</b>	<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Z value</b>	<b>Pr(&gt; z )</b>
EP(~host+ct)	Intercept	-1.15	0.60	-1.92	0.06
	gray squirrel	-0.85	0.88	-0.97	0.33
	red squirrel	0.23	0.63	0.36	0.72
	chipmunk	1.04	0.61	1.71	0.09
	Deciduous	0.34	0.85	0.40	0.69
	Developed	0.37	0.66	0.57	0.57
	Mixed	-0.01	0.99	-0.01	1.00
	Shrub	1.11	0.88	1.26	0.21

Table 3.24. Parametric bootstrapped estimates of Lyme-positive ear punches of host species from a generalized linear binomial model on Fort Drum Military Installation, New York, 2016.

Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk ( $\alpha=0.05$ ). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

<b>Category 1</b>	<b>Category 2</b>	<b>Ear punch confidence intervals of bootstrap estimates</b>
<i>Cover type</i>		
Coniferous	Deciduous	(-1.25,0.59)
Coniferous	Developed	(-0.80,0.47)
Coniferous	Mixed	(-1.22,0.73)
Coniferous	Shrub	(-3.61,0.32)
Deciduous	Developed	(-0.77,1.11)
Deciduous	Mixed	(-1.16,1.18)
Deciduous	Shrub	(-3.59,0.80)
Developed	Mixed	(-1.18,0.83)
Developed	Shrub	(-3.51,0.36)
Mixed	Shrub	(-3.81,0.70)
<i>Species</i>		
<i>Peromyscus</i> sp.	Gray squirrel	(-0.31,0.81)
<i>Peromyscus</i> sp.	Red squirrel	(-1.09,0.43)

<i>Peromyscus</i> sp.	Chipmunk	(-3.15,0.06)
Gray squirrel	Red squirrel	(-1.54,0.34)
Gray squirrel	Chipmunk	(-3.63,0.03)
Red squirrel	Chipmunk	(-2.91,0.32)

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Figure 1.1. Fort Drum Military Installation located in Jefferson County in northwestern New York.

## Cover types of Fort Drum Military Installation, New York

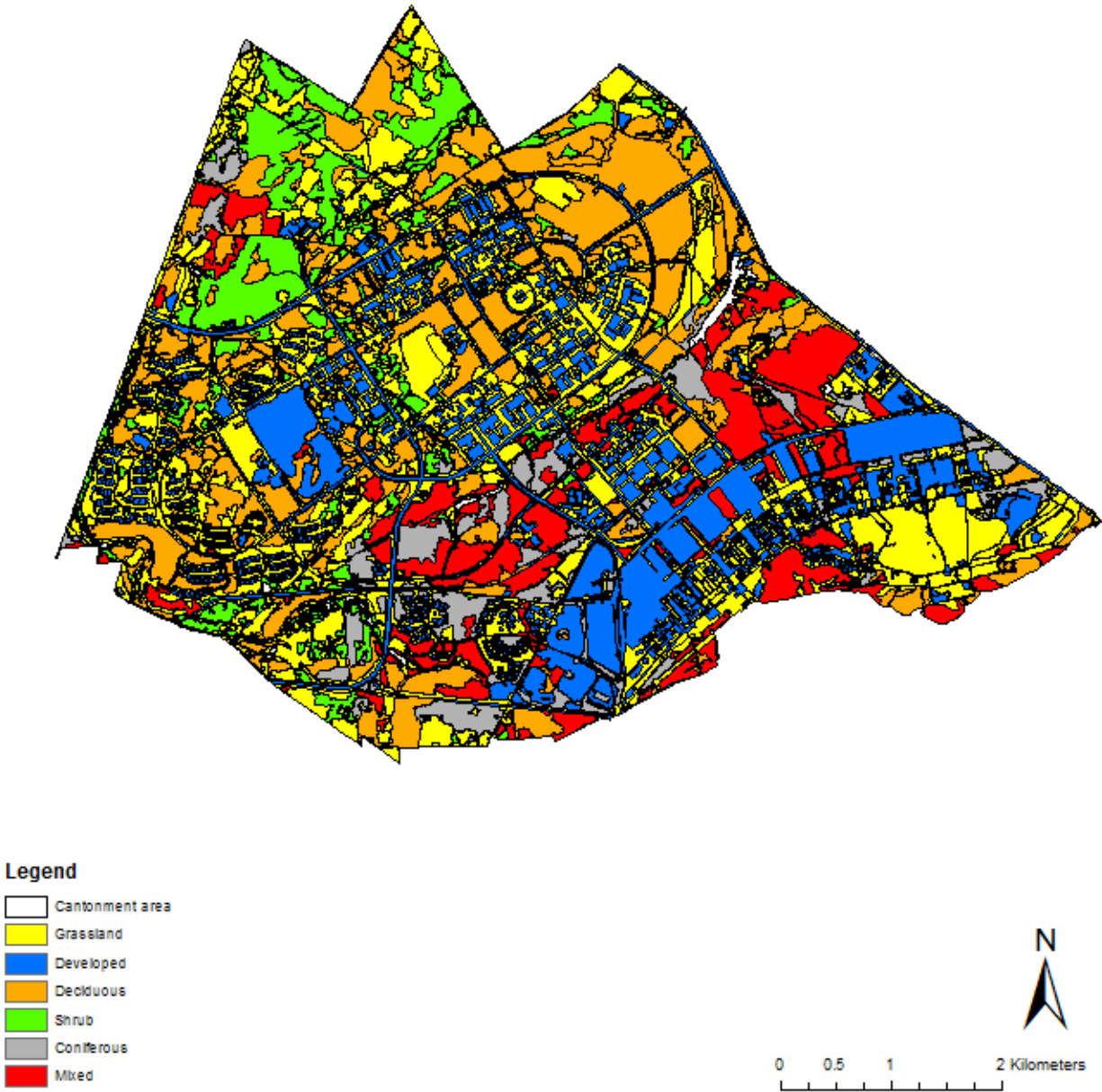


Figure 1.2. Cover types within the Cantonment Area of Fort Drum Military Installation, New York. Approximations of area are as follows: Deciduous = 752 ha, Developed = 1277 ha, Coniferous = 200 ha, Grassland = 1221 ha, Mixed = 364 ha, Shrub = 312 ha.

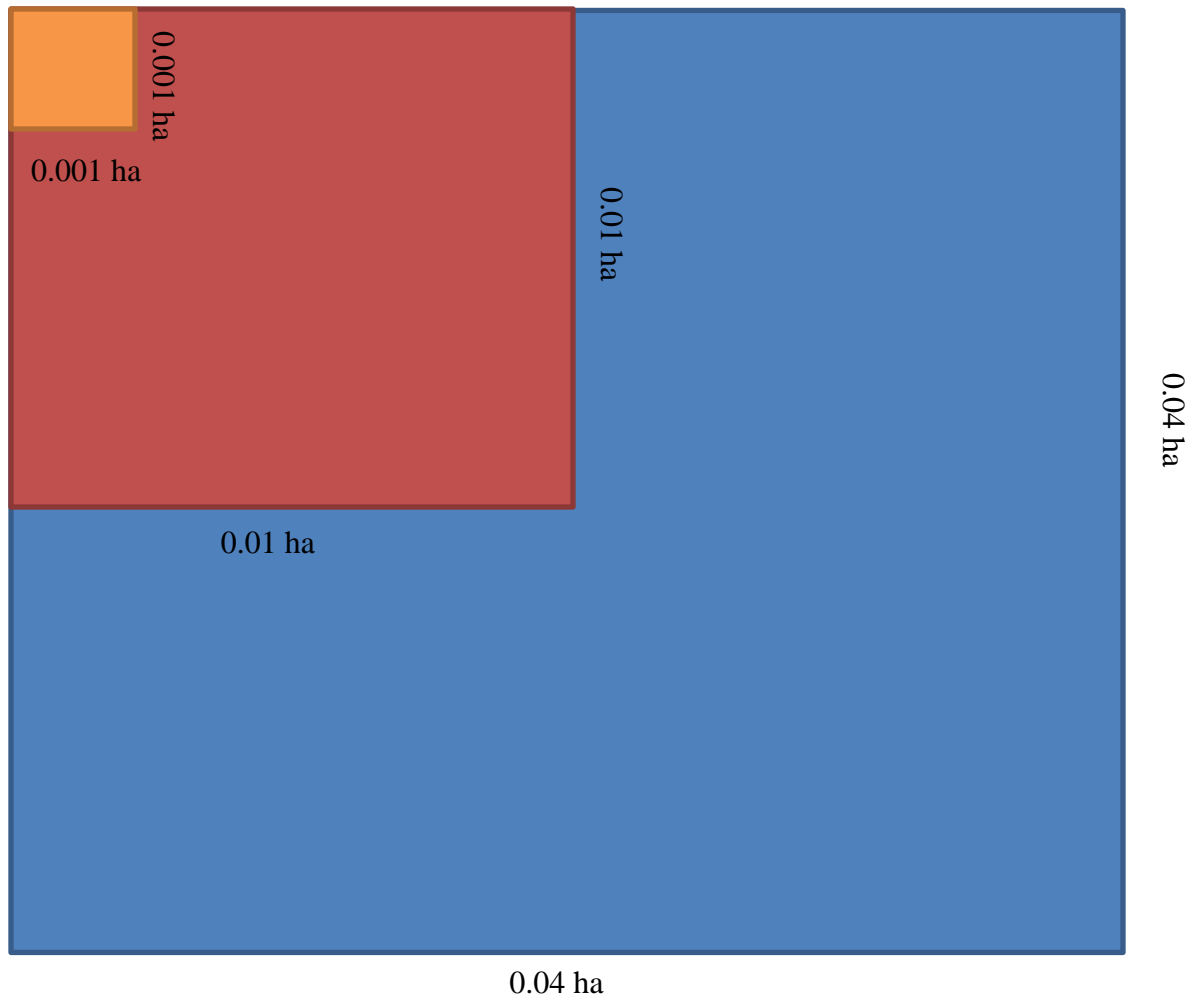


Figure 2.1. A vegetation survey plot on Fort Drum Military Installation, New York.

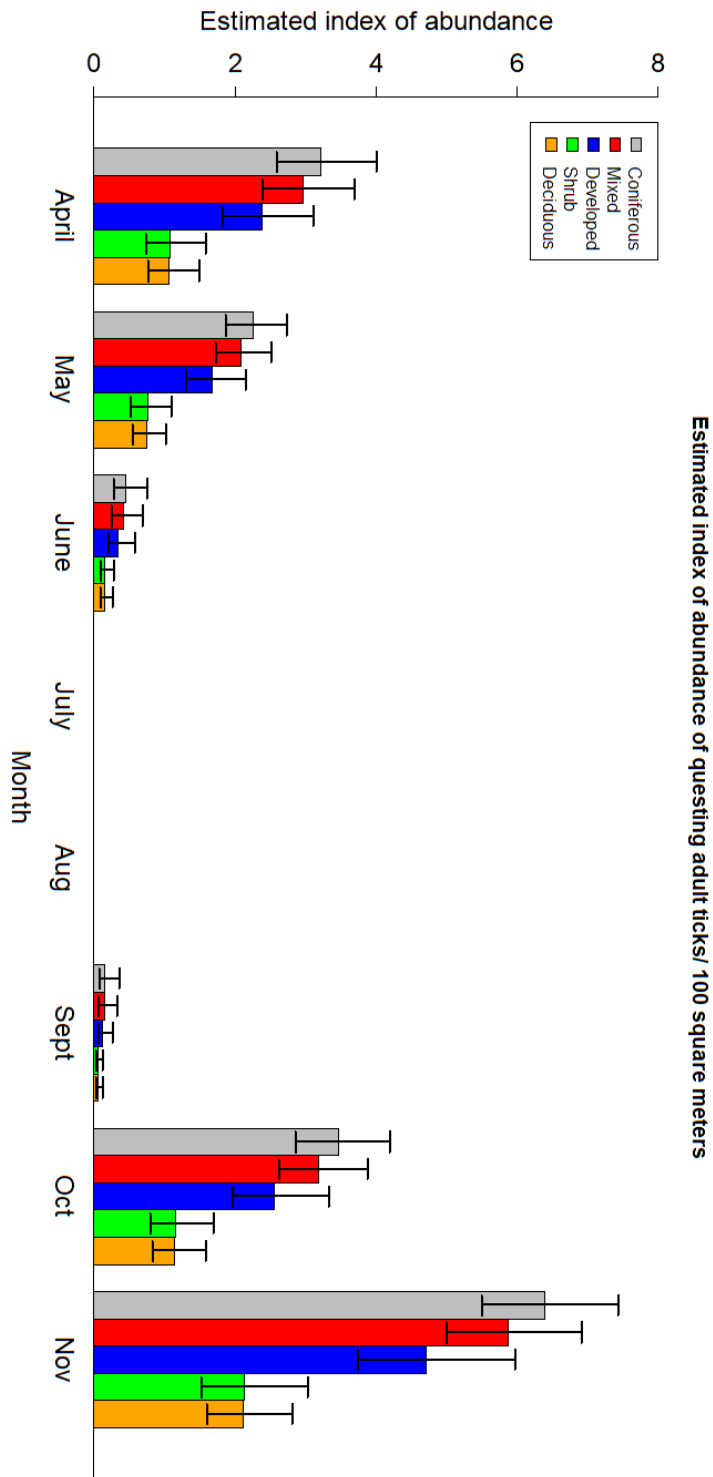


Figure 2.2. Estimated index of abundance of questing adult ticks with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

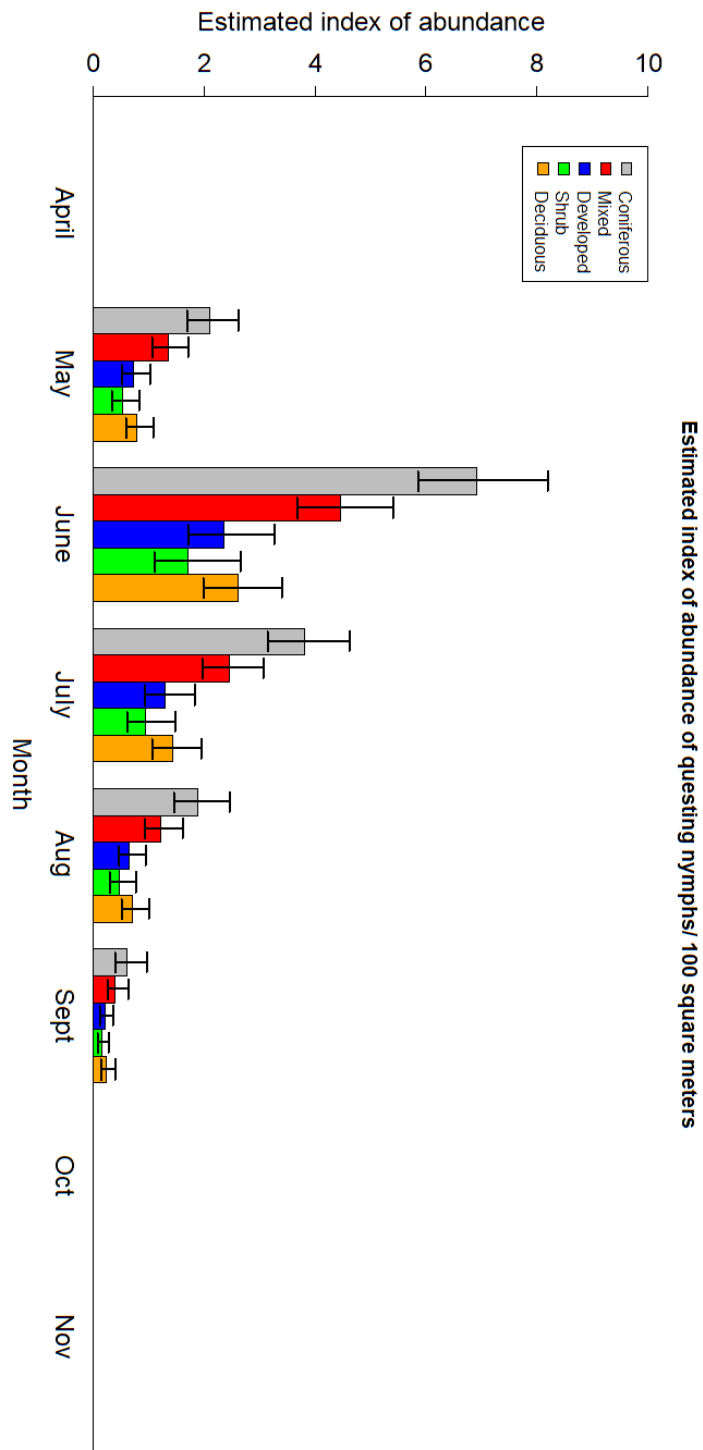


Figure 2.3. Estimated index of abundance of questing nymphal ticks with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.



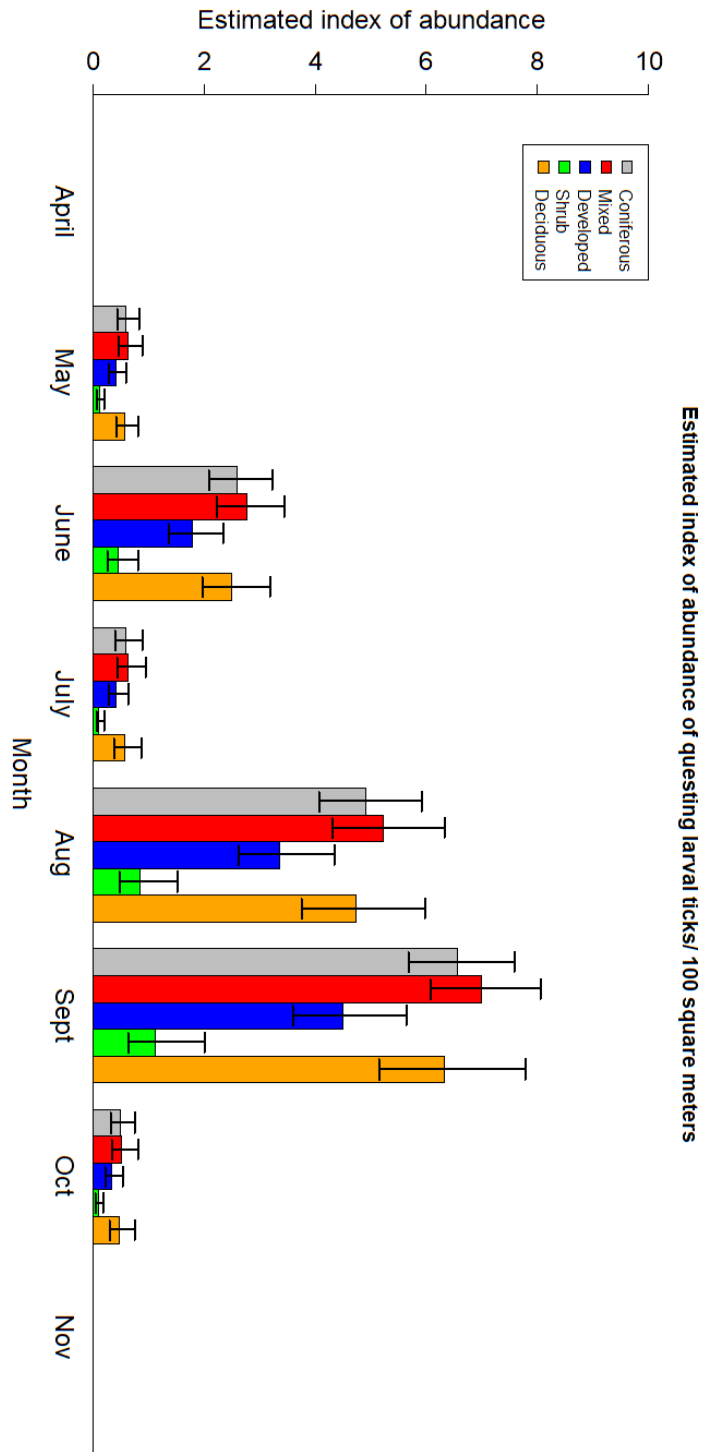


Figure 2.4. Estimated index of abundance of questing larval ticks with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

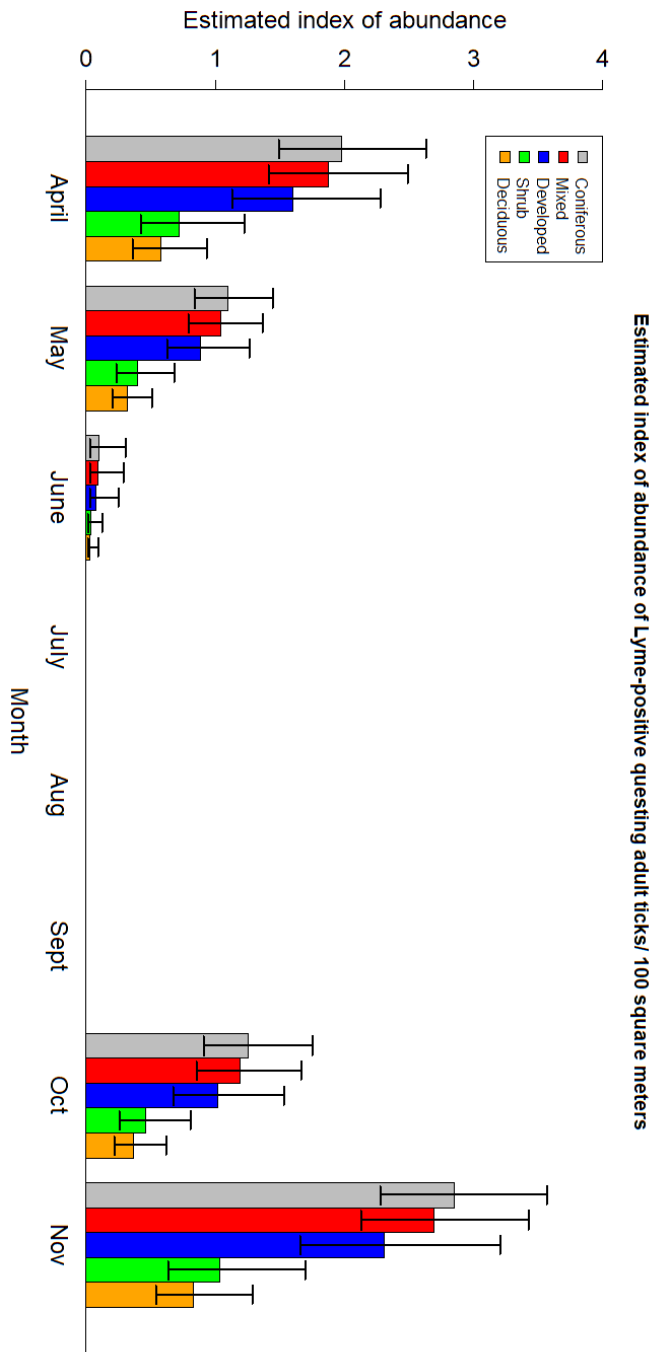


Figure 2.5. Estimated index of abundance of *B. burgdorferi*-positive questing adult ticks with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

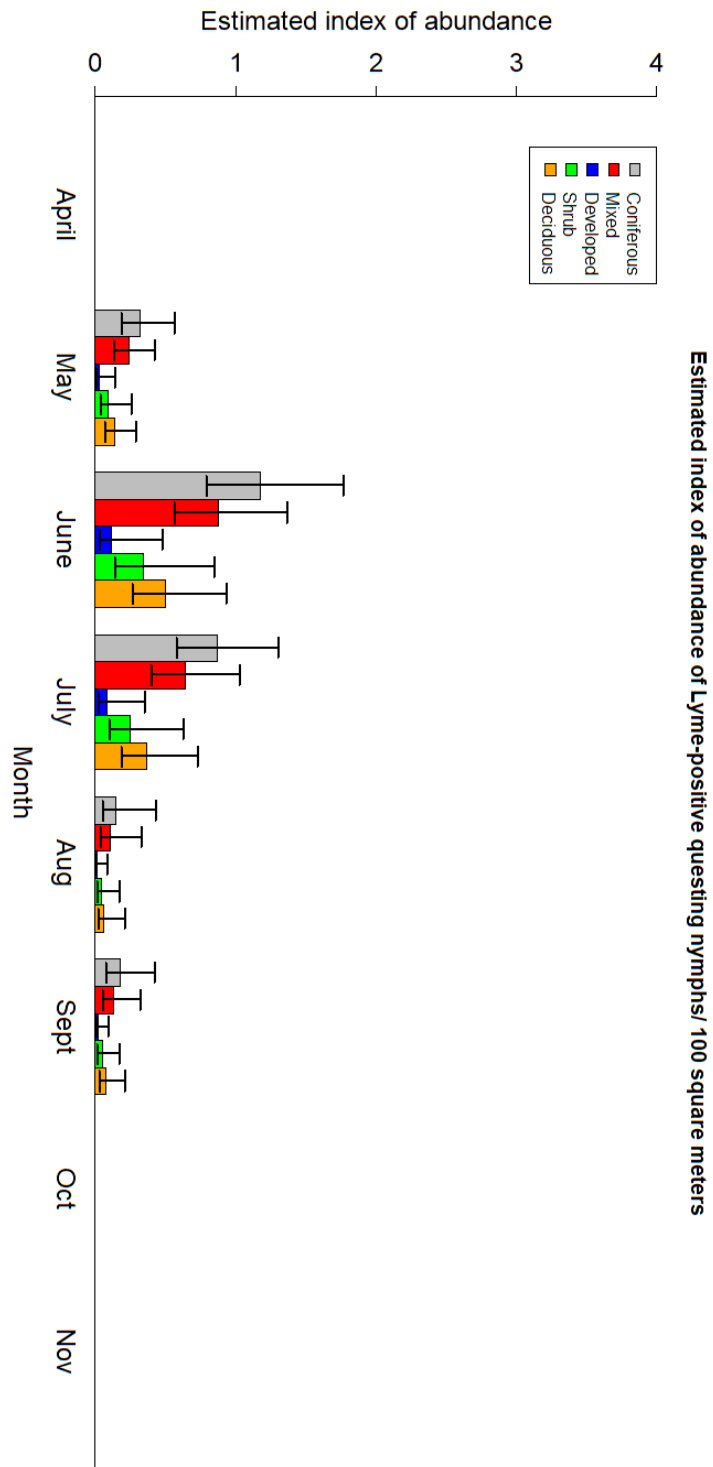


Figure 2.6. Estimated index of abundance of *B. burgdorferi*-positive questing nymphal ticks with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

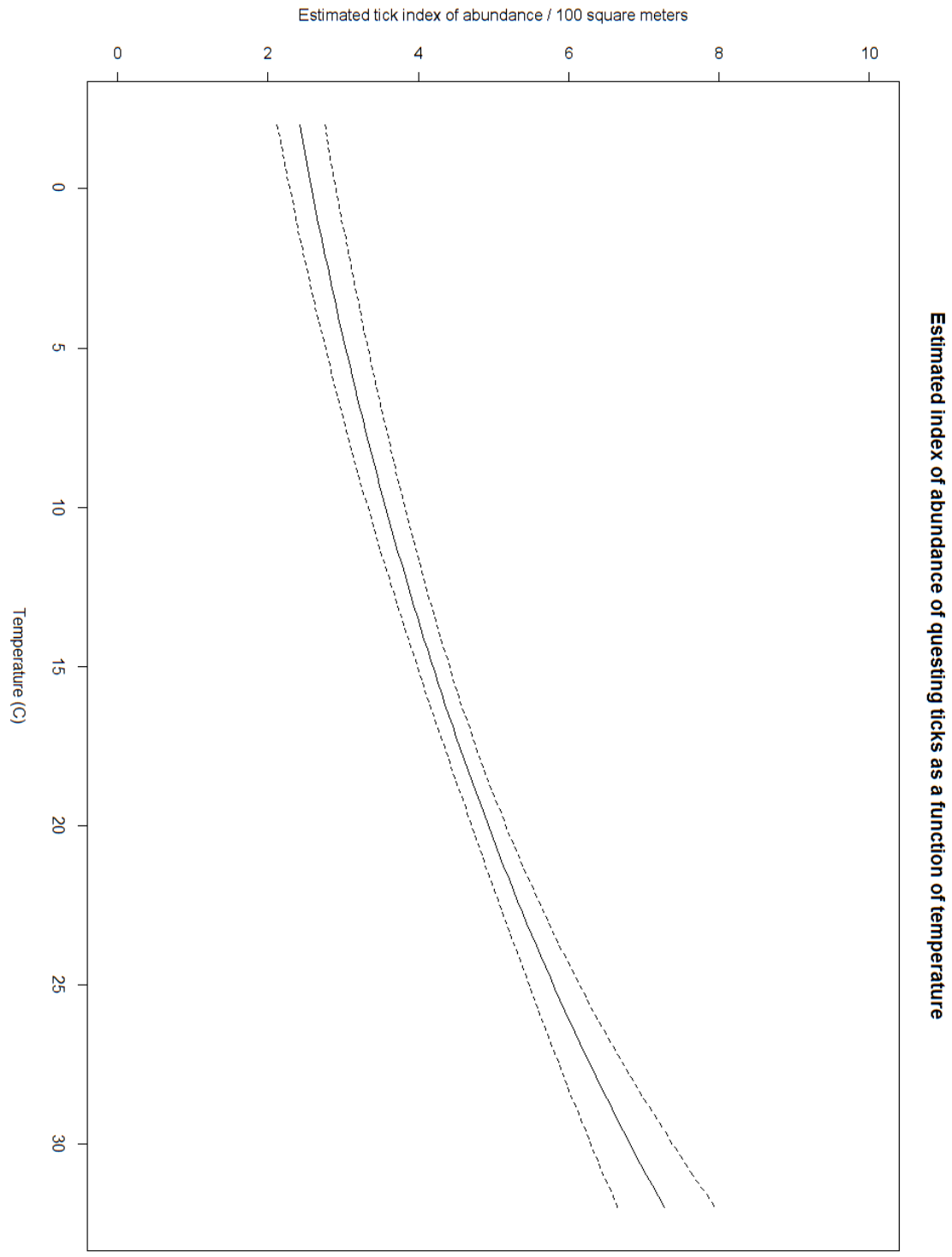


Figure 2.7. Estimated index of abundance of ticks related to temperature with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

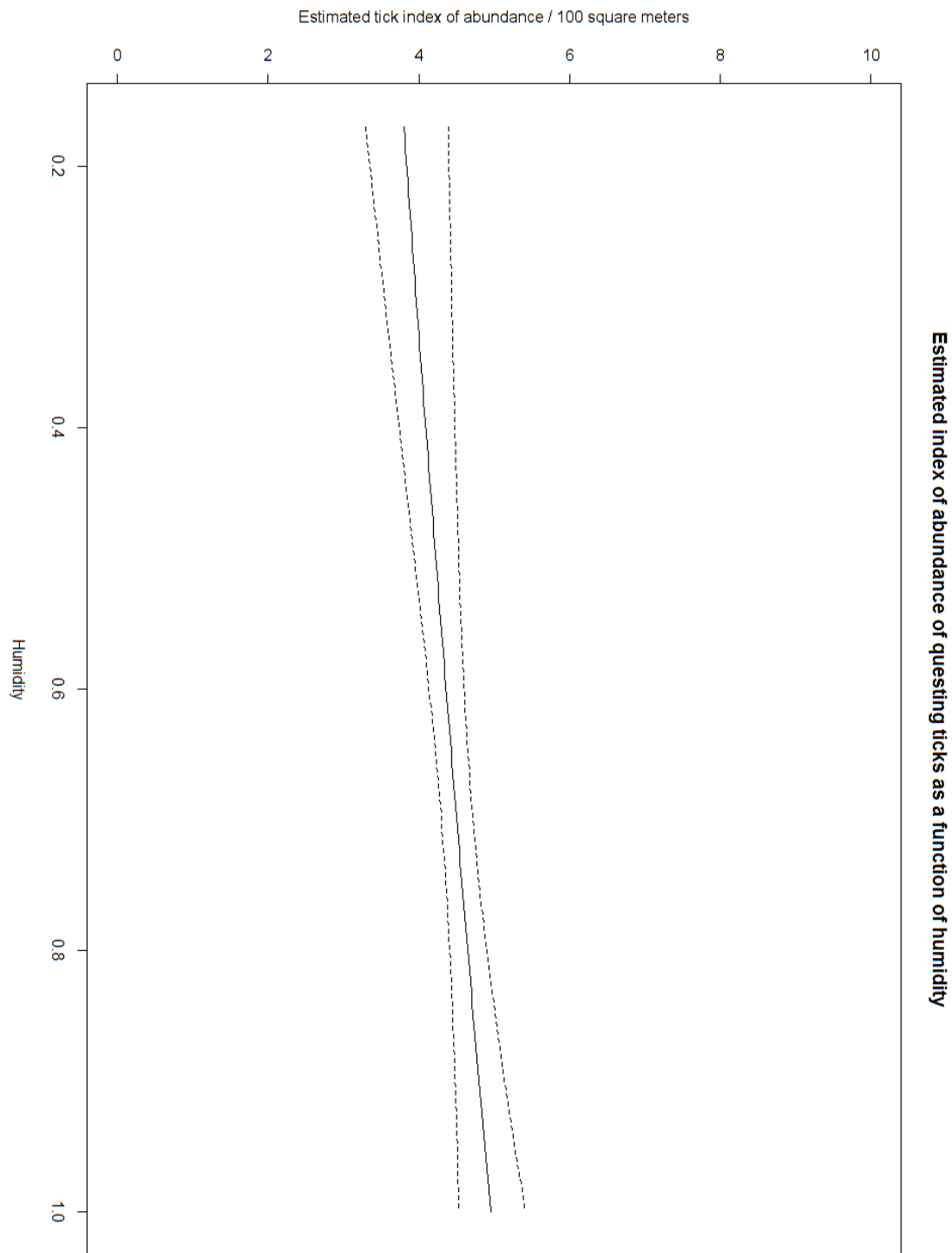


Figure 2.8. Estimated index of abundance of ticks related to relative humidity with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

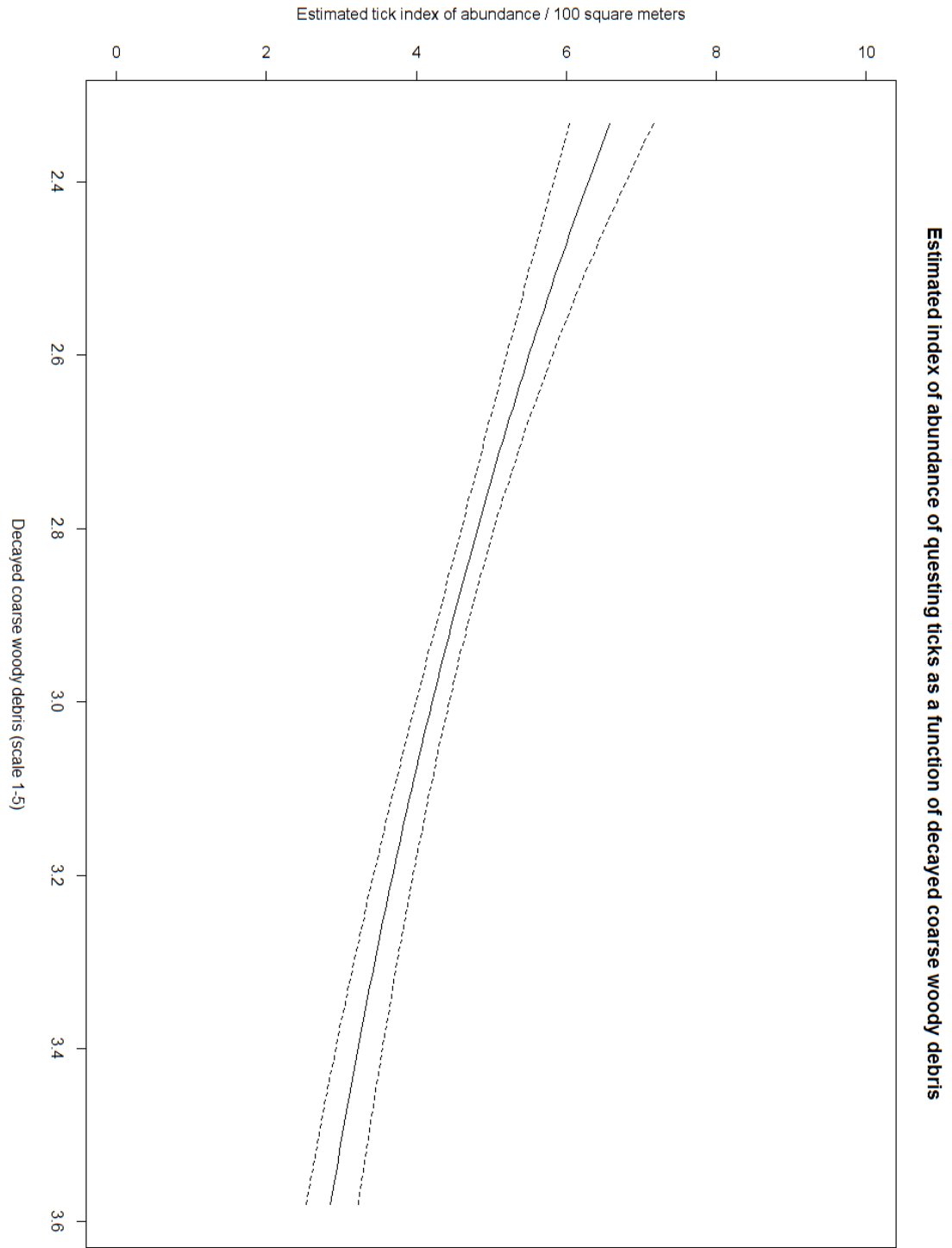


Figure 2.9. Estimated index of abundance of ticks related to coarse woody debris decay with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

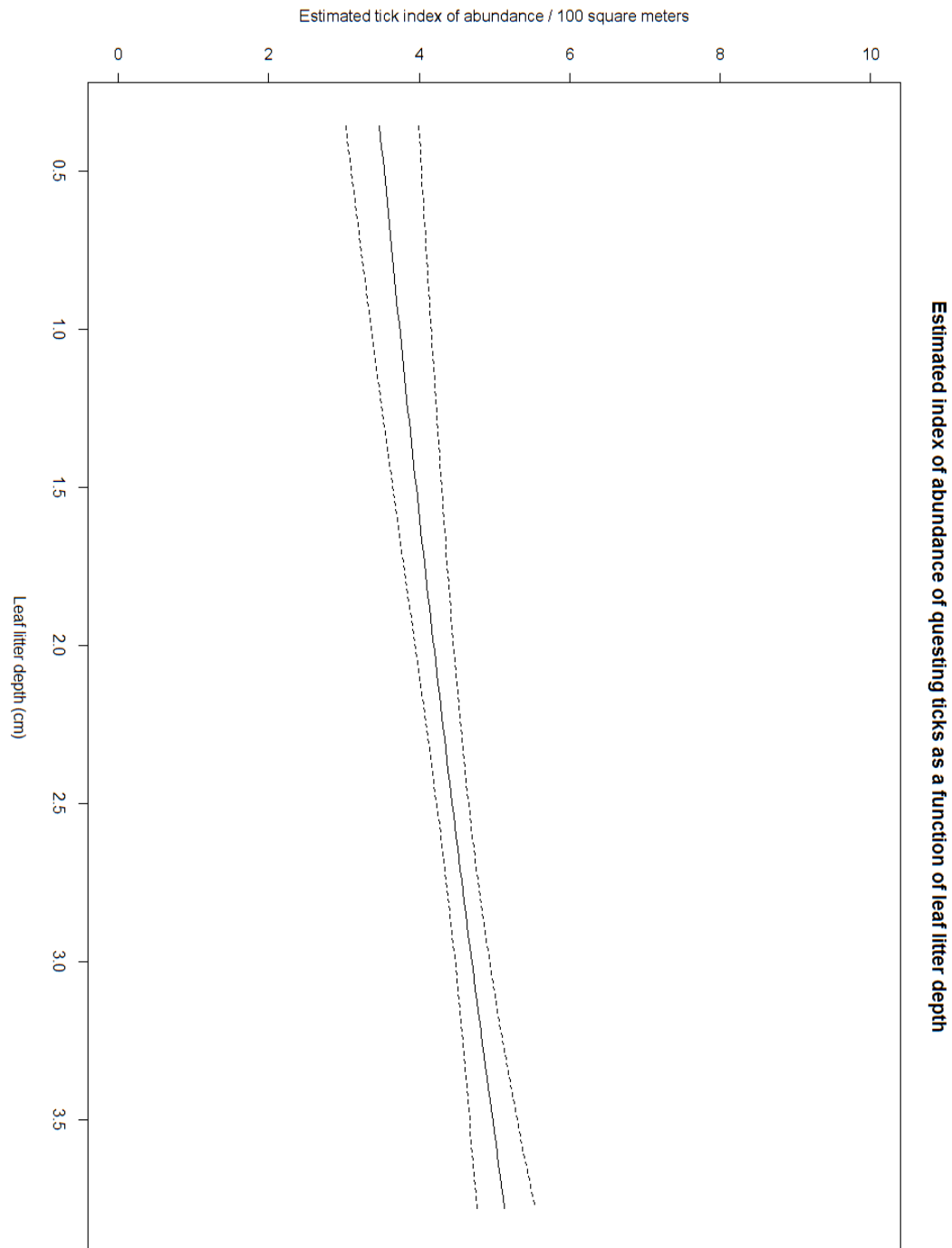


Figure 2.10. Estimated index of abundance of ticks related to leaf litter depth with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

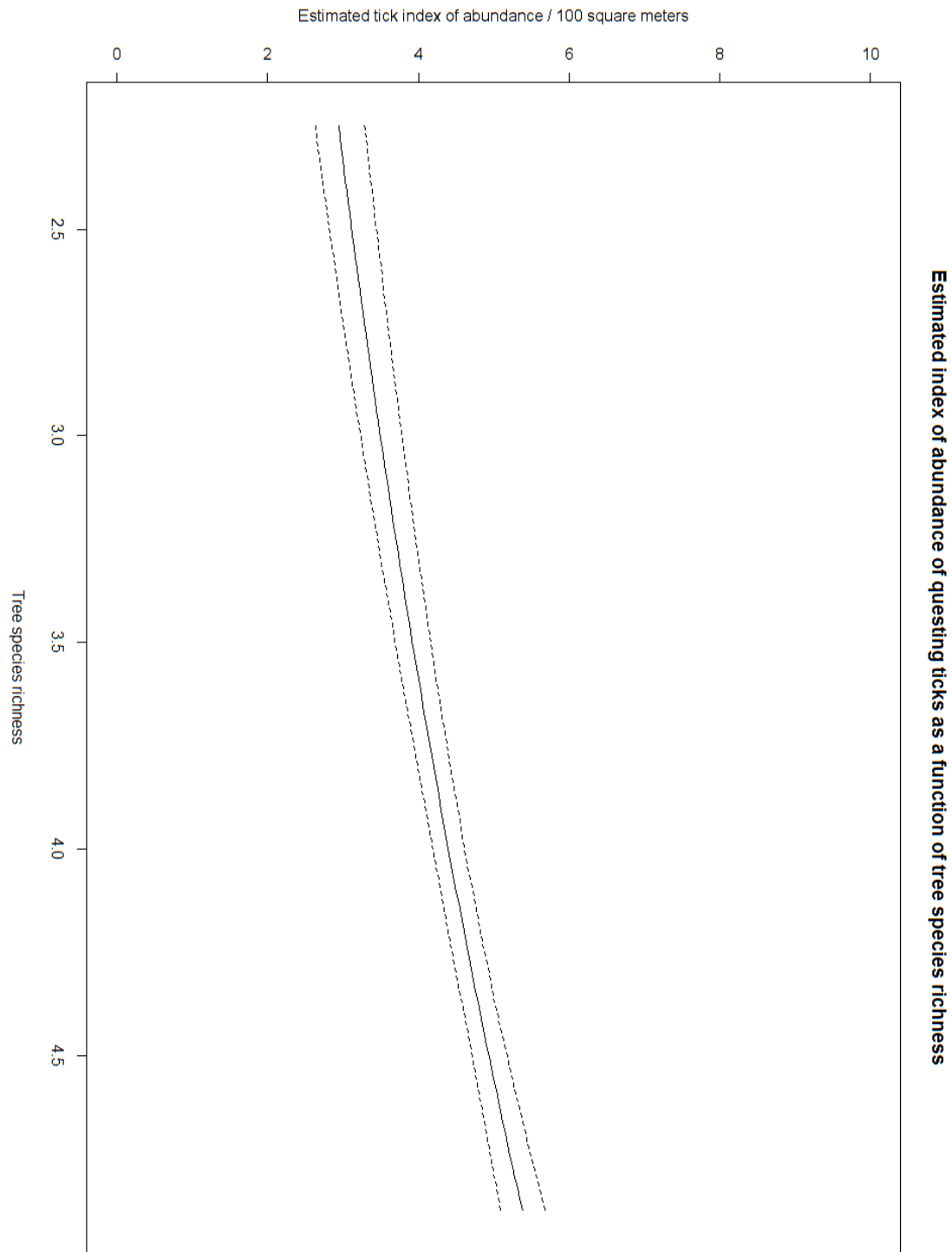


Figure 2.11. Estimated index of abundance of ticks related to tree species richness with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.



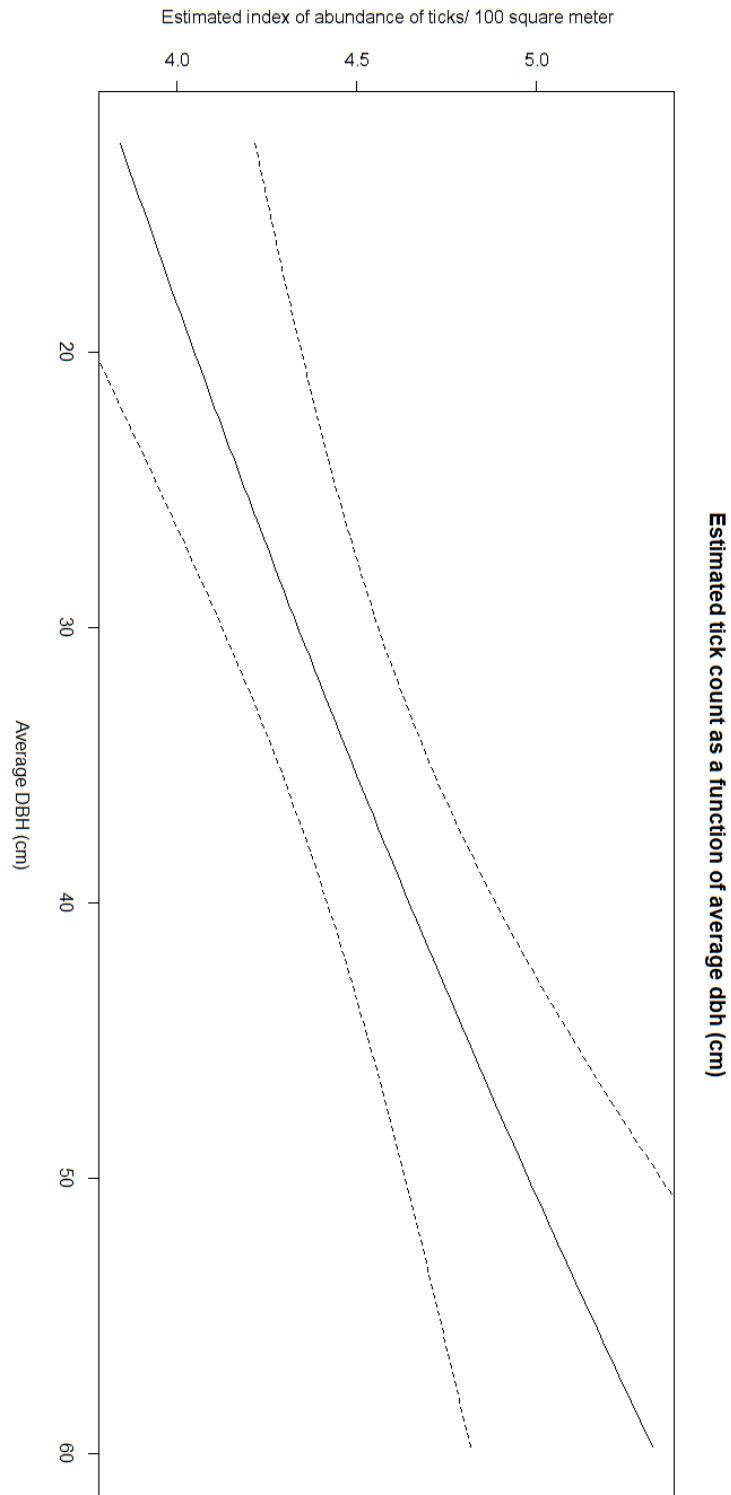


Figure 2.12. Estimated index of abundance of ticks related to dbh (cm) with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

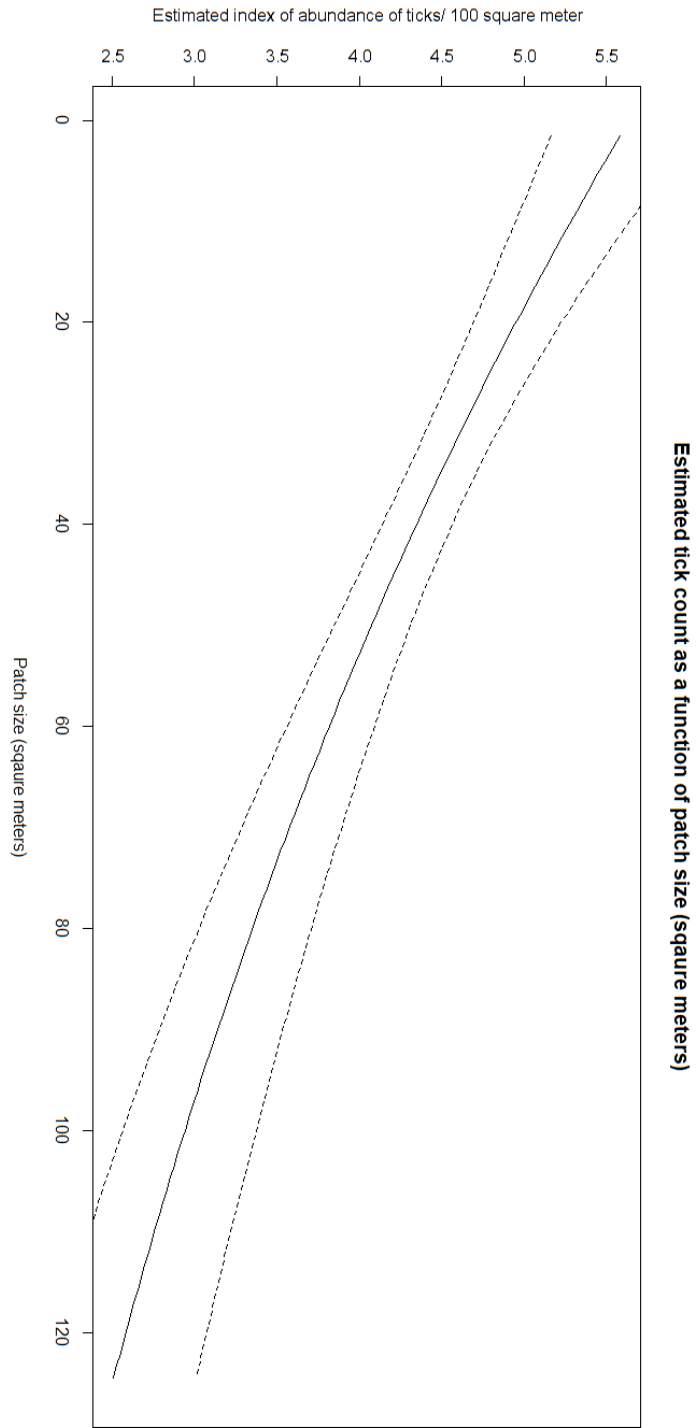


Figure 2.13. Estimated index of abundance of ticks related to patch size ( $m^2$ ) with a 95% confidence interval on Fort Drum Military Installation, New York, during April–November, 2015–2016.

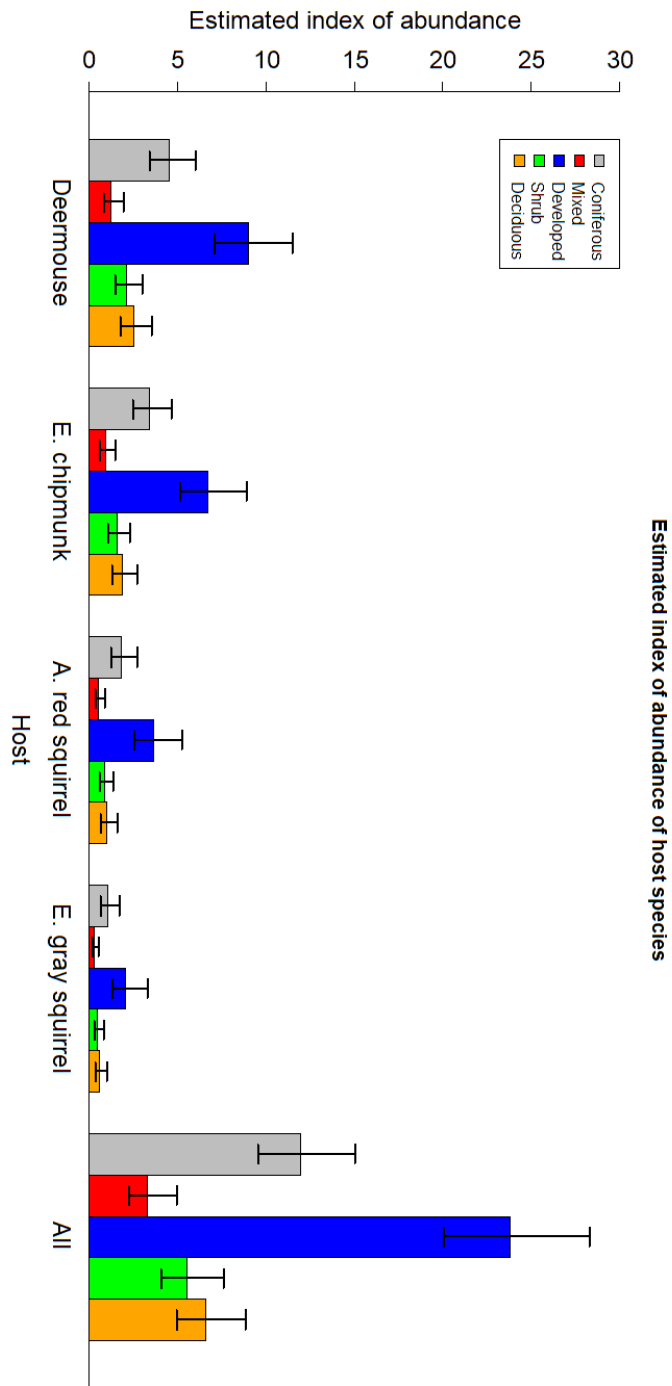


Figure 3.1. Species composition of dominate hosts in the small mammal community with a 95% confidence interval within the Cantonment Area of Fort Drum Military Installation, New York during 2015–2016.

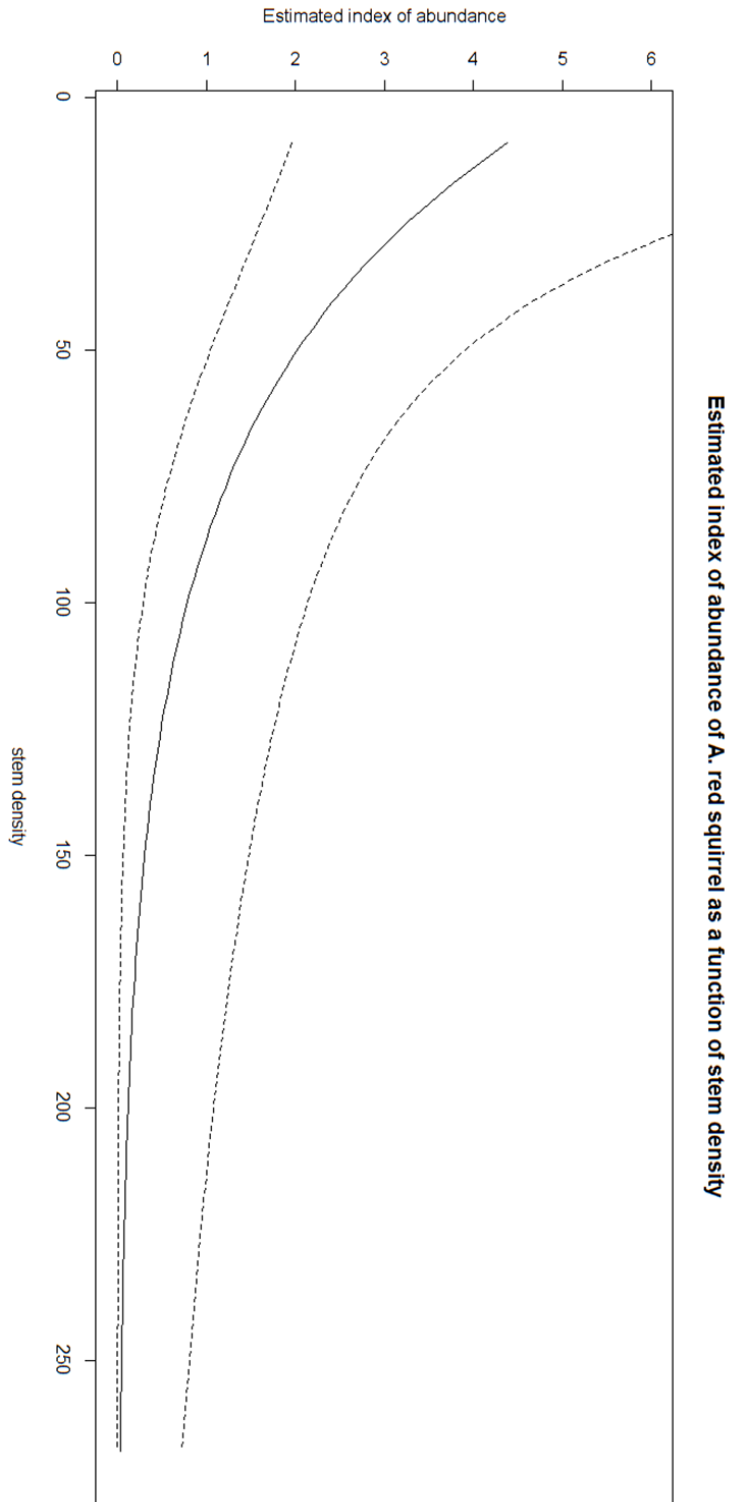


Figure 3.2. Estimated index of abundance of red squirrel related to stem density with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

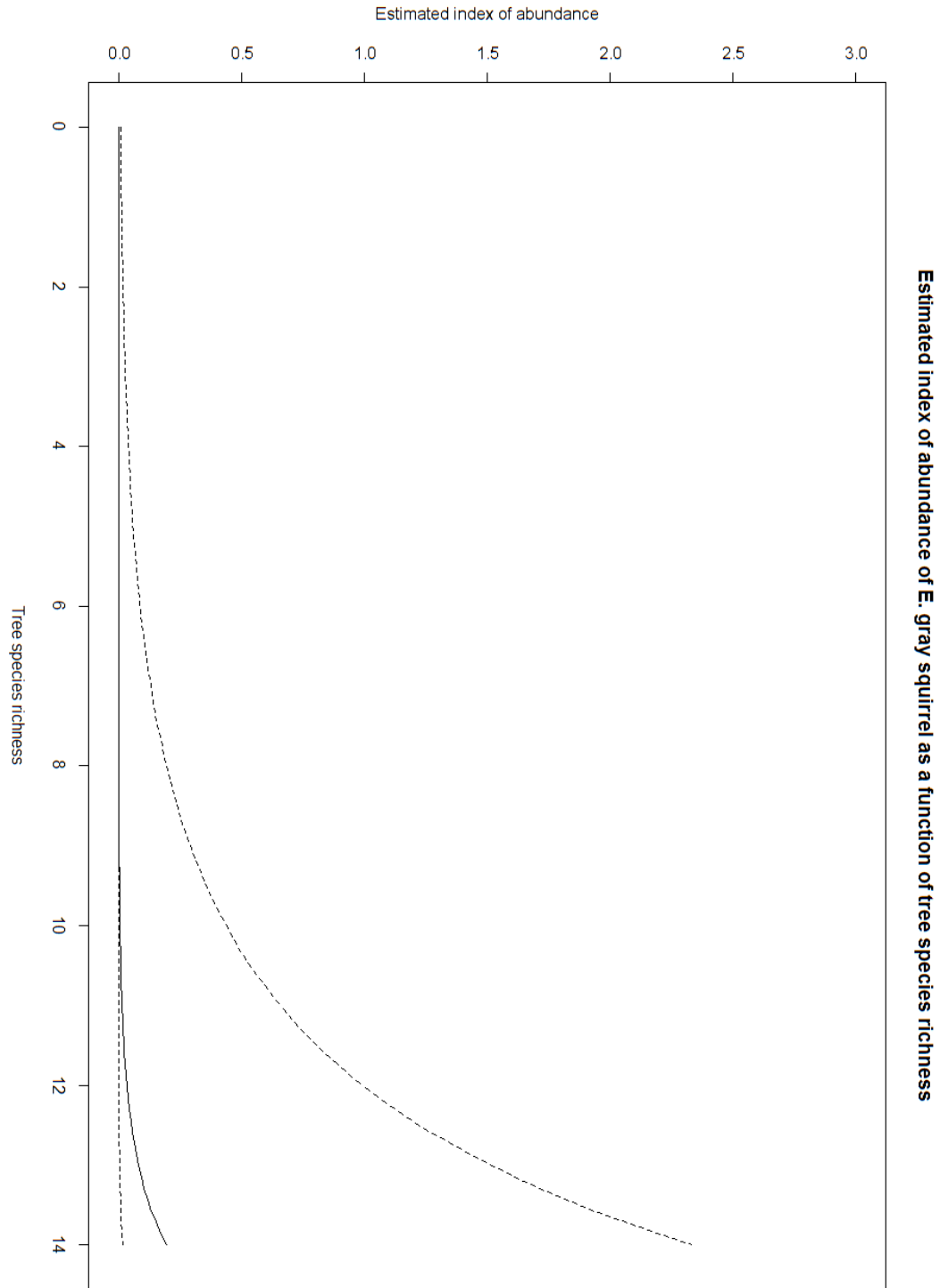


Figure 3.3. Estimated index of abundance of gray squirrel related to tree species richness with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

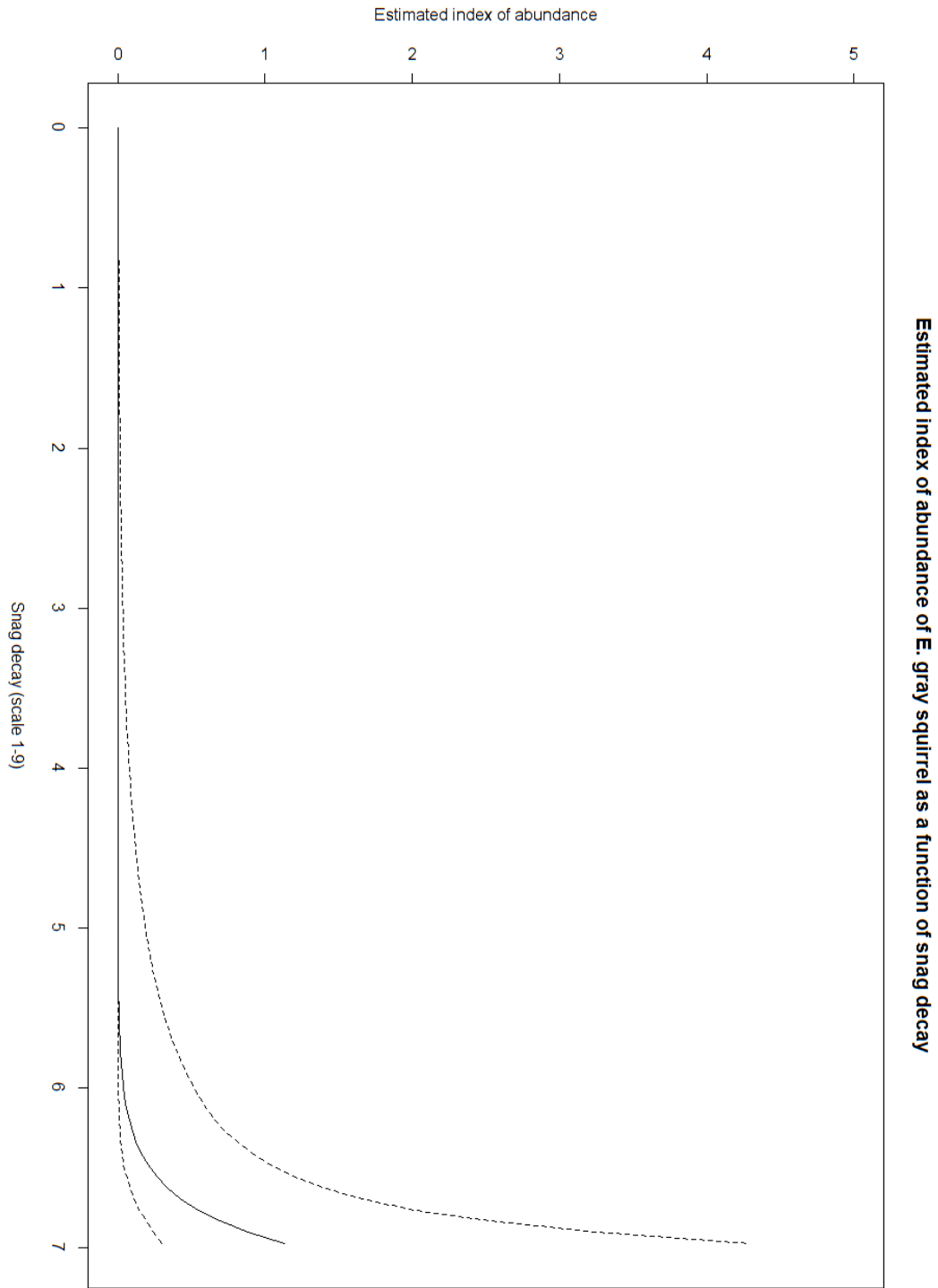


Figure 3.4. Estimated index of abundance of gray squirrel related to snag decay with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

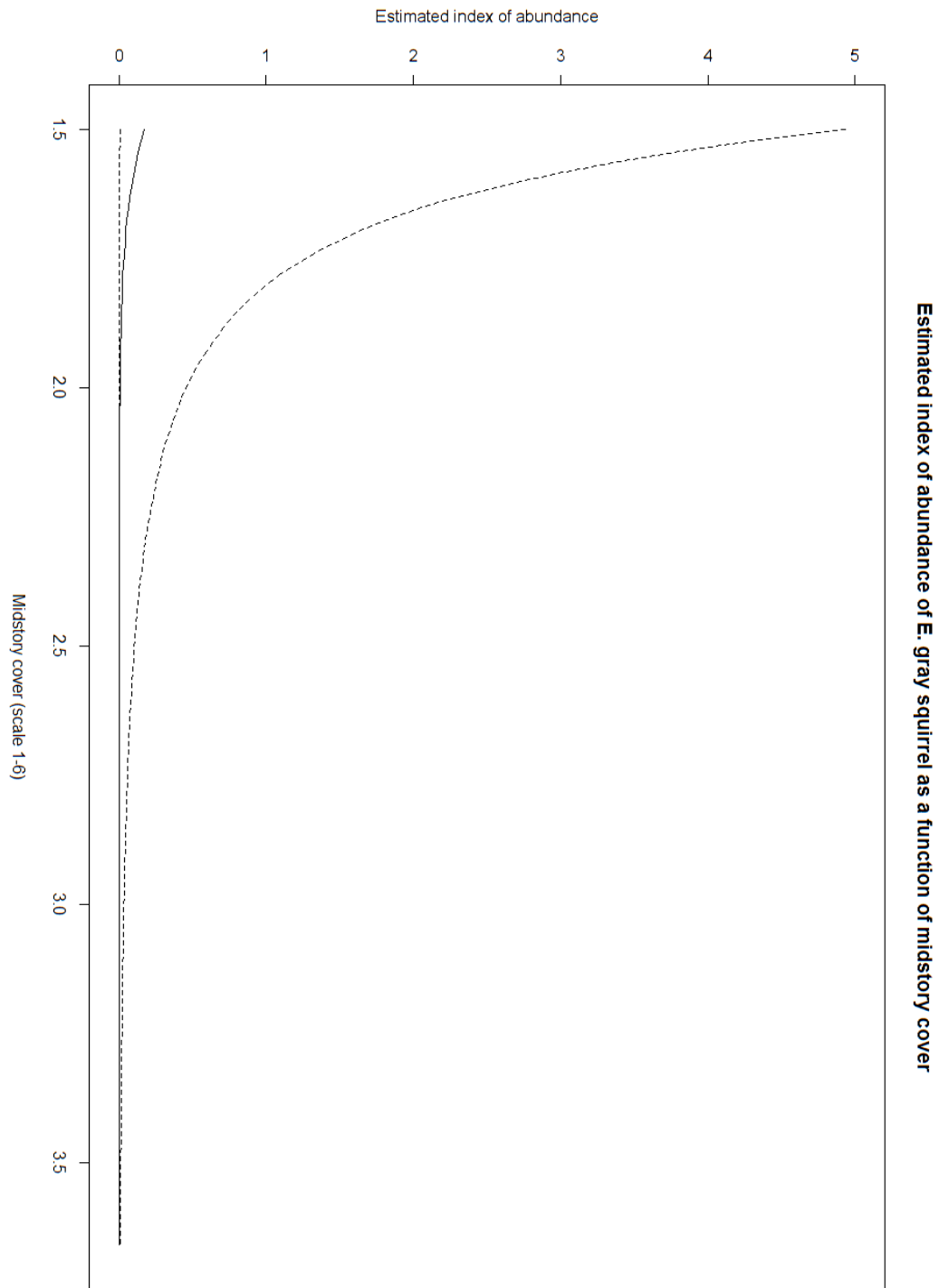


Figure 3.5. Estimated index of abundance of gray squirrel related to midstory cover with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

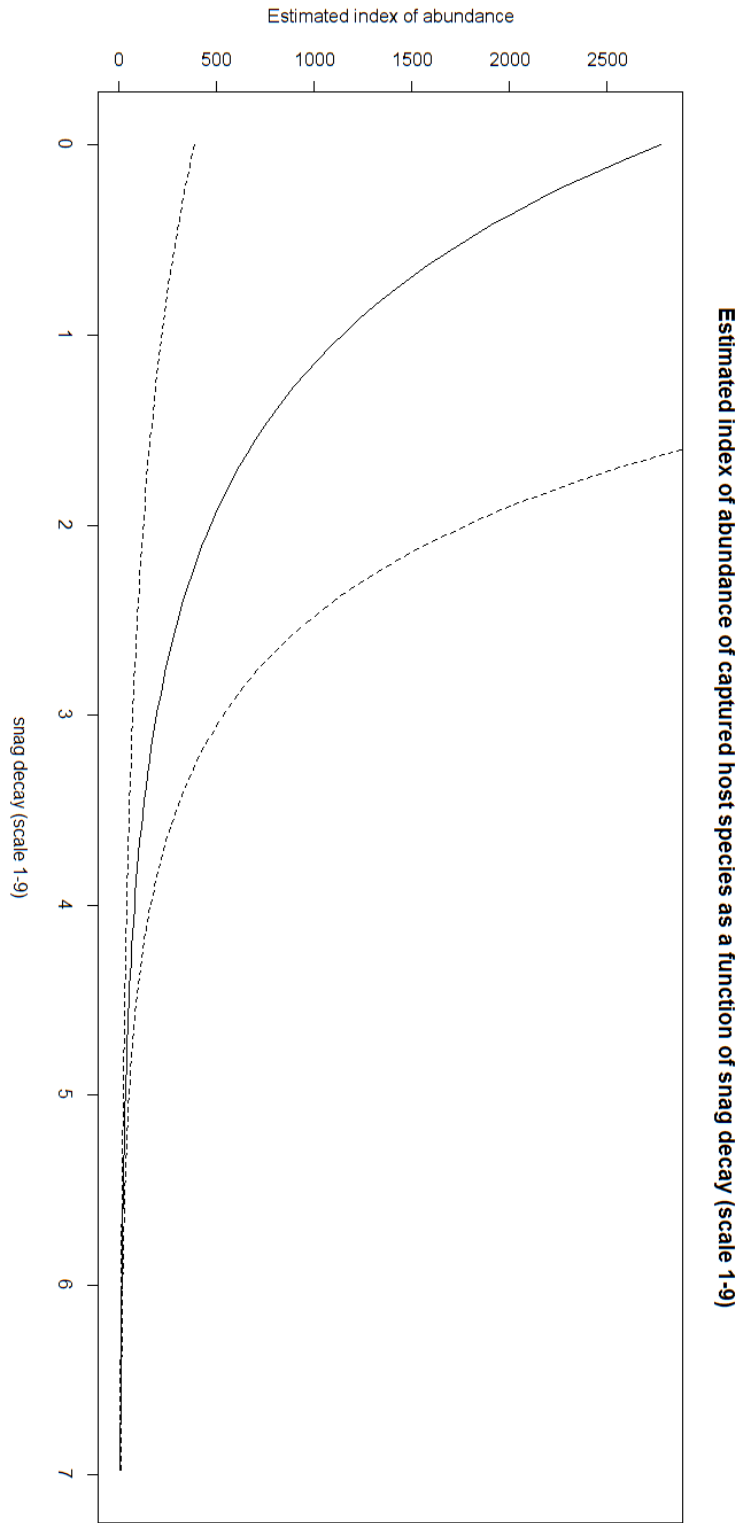


Figure 3.6. Estimated index of abundance of small mammal hosts related to snag decay with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.



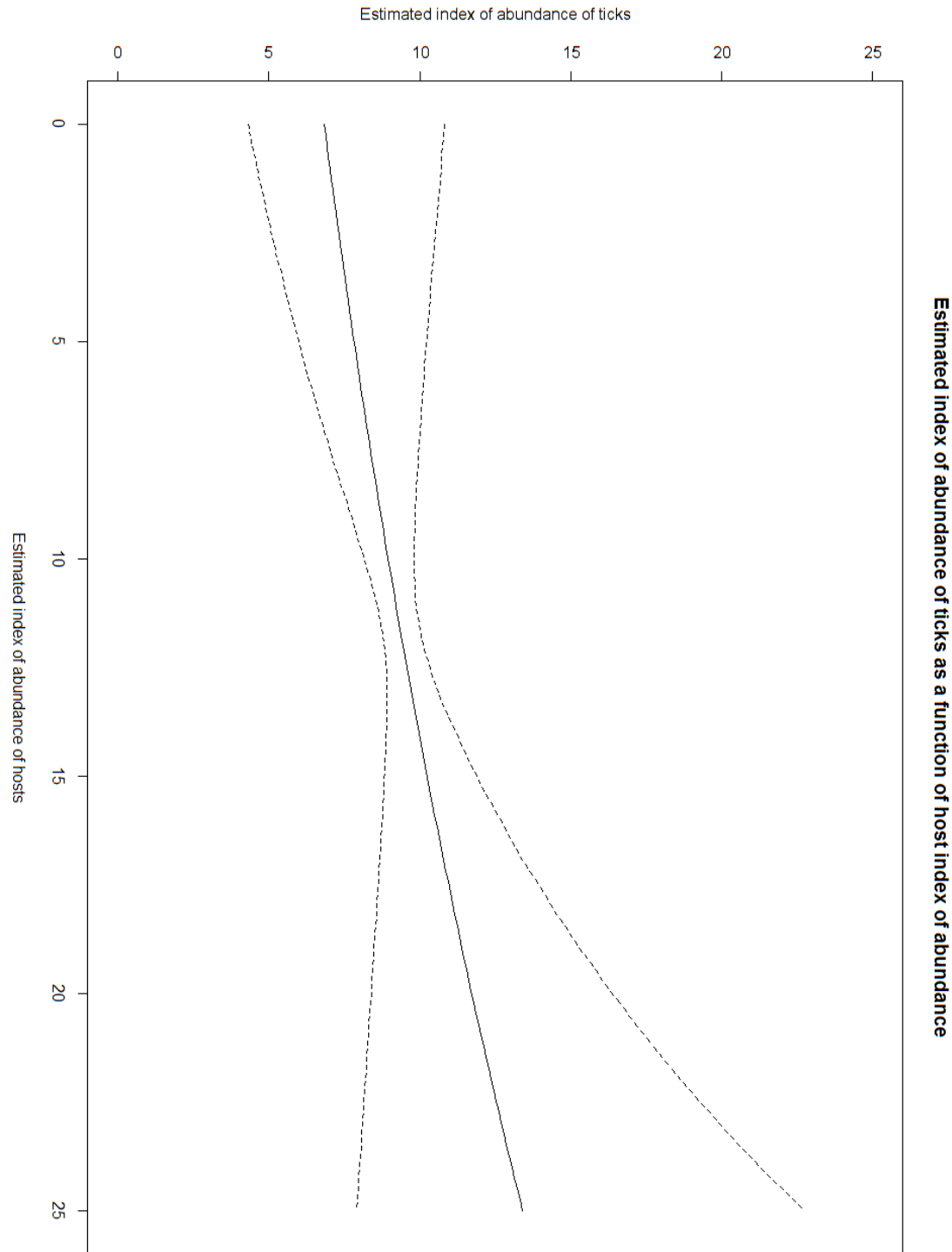


Figure 3.7. Estimated index of abundance of ticks related to estimated index of abundance of all small mammal host species with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

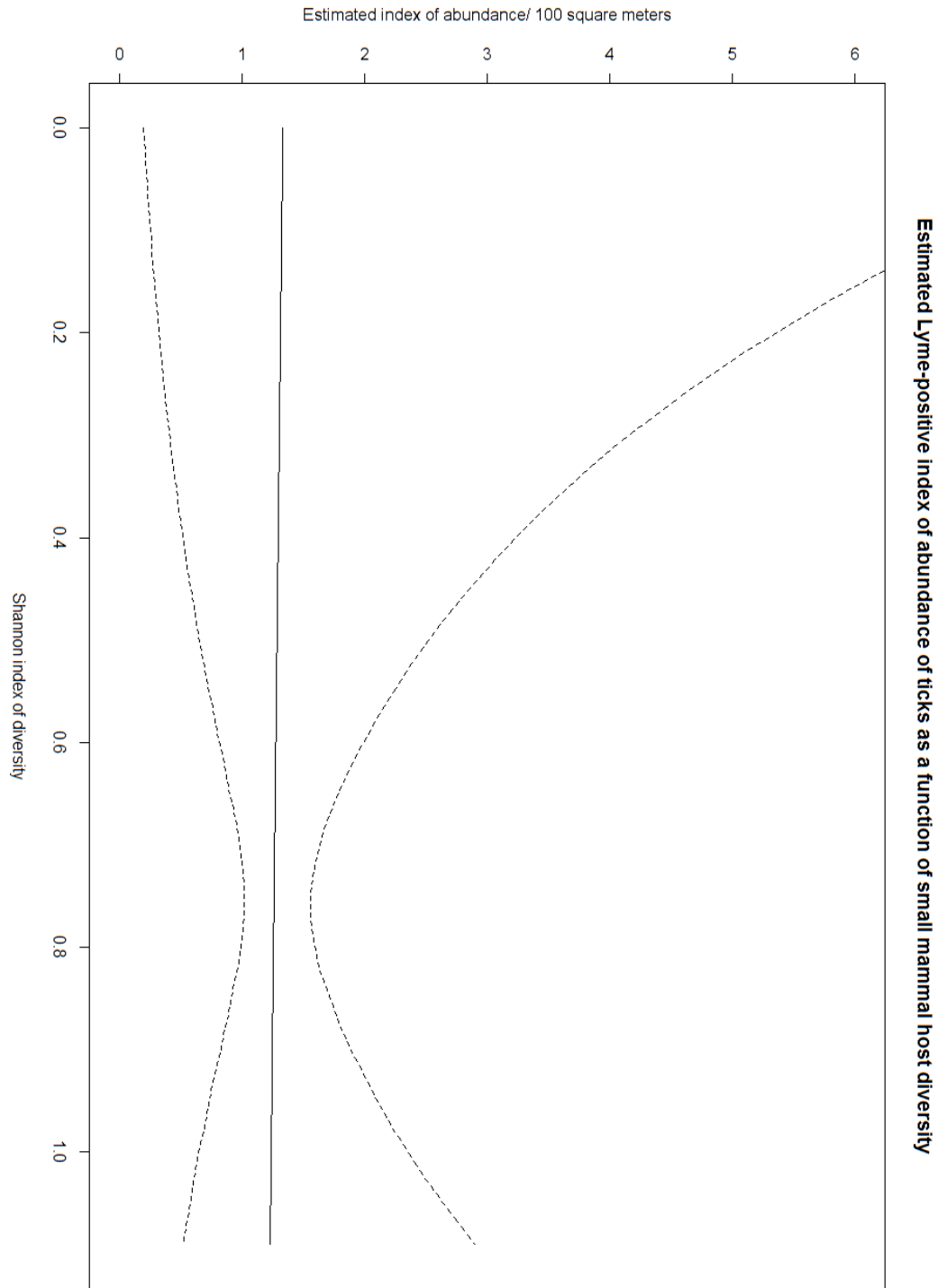


Figure 3.8. Estimated index of abundance of Lyme-positive ticks related to small mammal host Shannon’s index of diversity with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

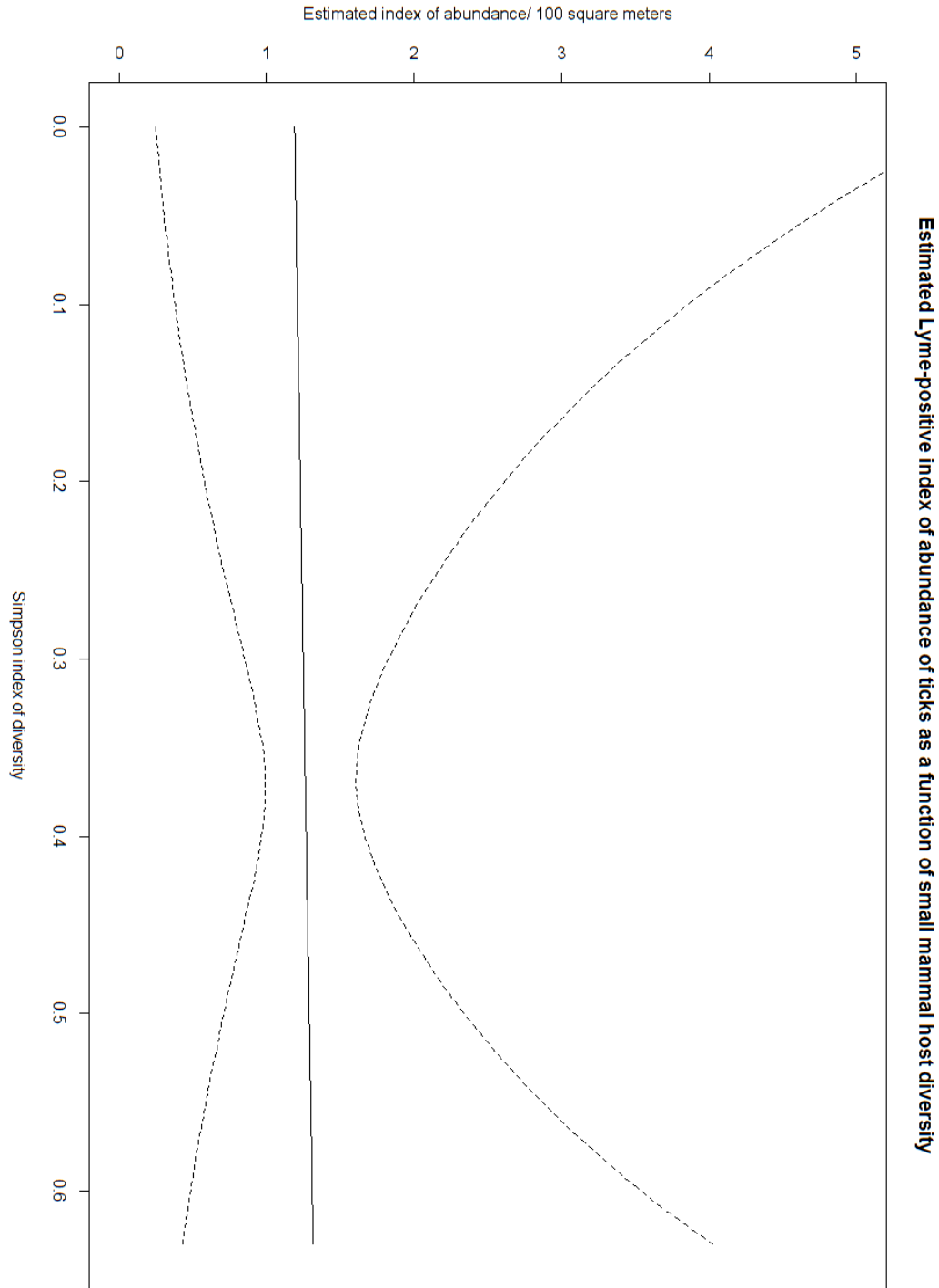


Figure 3.9. Estimated index of abundance of Lyme-positive ticks related to small mammal host Simpson's index of diversity with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

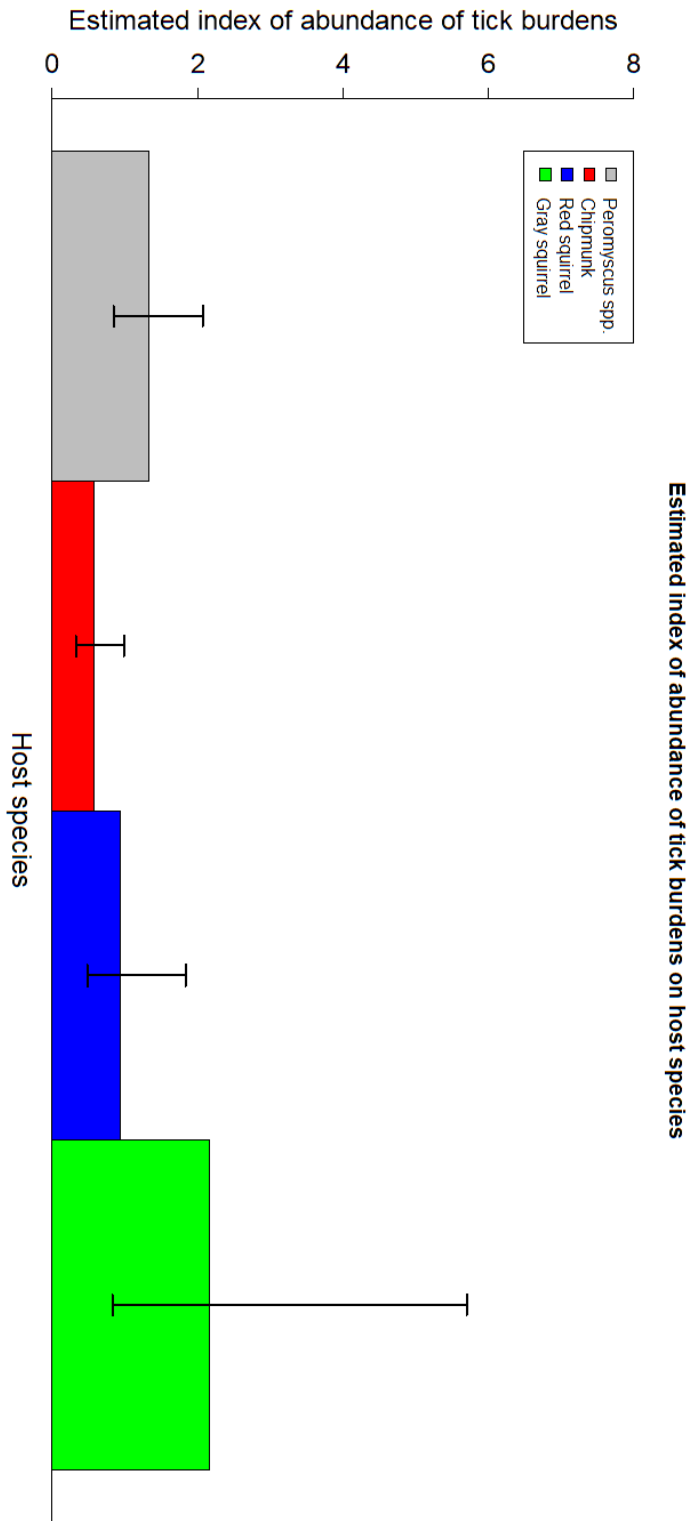


Figure 3.10. Estimated index of abundance of small mammal hosts with a tick burden with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

Estimated index of abundance of Lyme-positive tick burdens

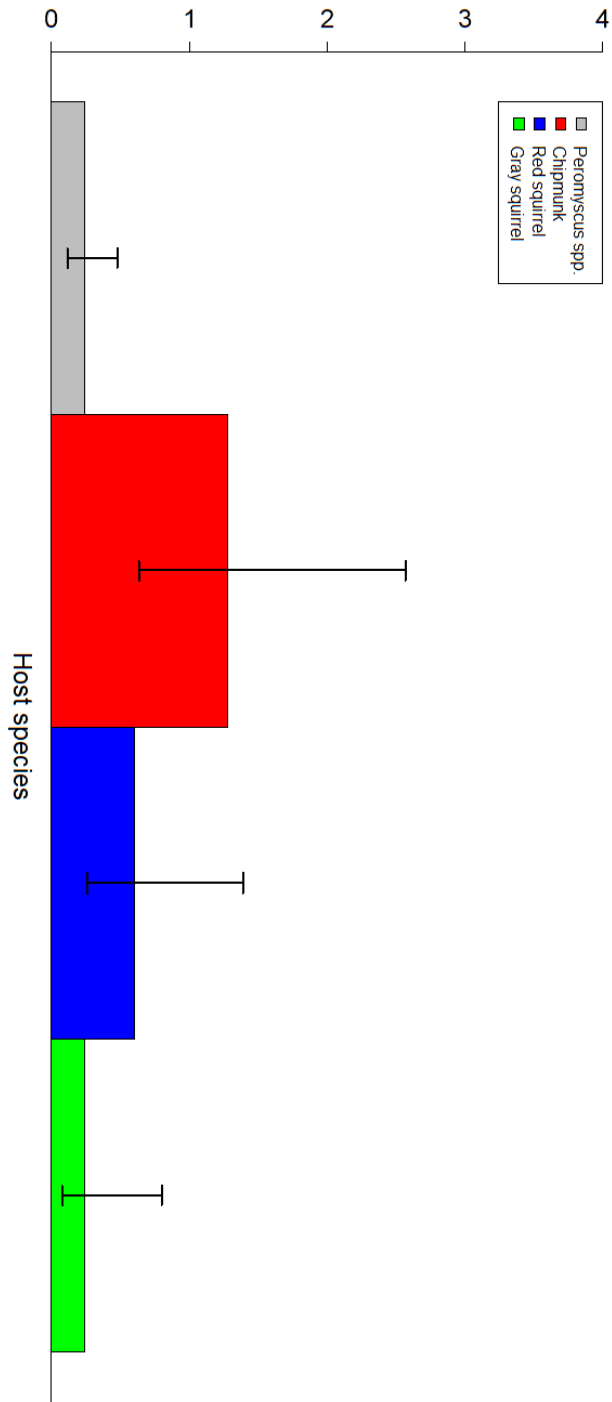
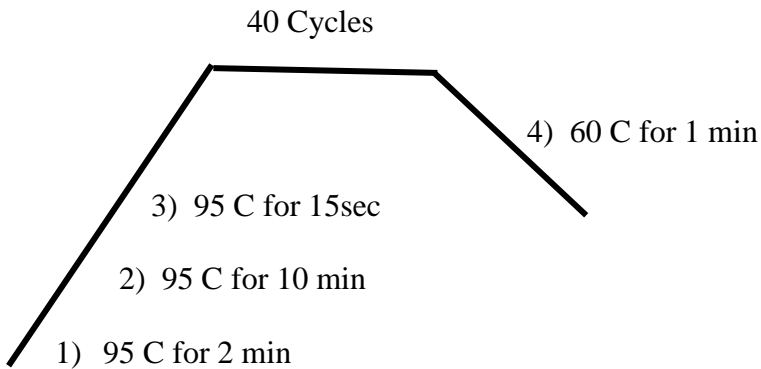


Figure 3.11. Estimated index of abundance of small mammal hosts exposed to a Lyme-positive tick burden with a 95% confidence interval on Fort Drum Military Installation, New York, 2015–2016.

**Appendix 1. Quantitative PCR - Prime Time *Borrelia* Assay (Courtney et al. 2004).**

Day 1

- a. Make an excel file which contains the identification of each sample being tested and their location in reference to the wells on the PCR plate
- b. Make the Master Mix (# of samples + error)\* volume of reagent
  - Rox Dye 0.4ul per sample
  - Assay Mix 1.0ul per sample (Primers and Probe)
  - Nuclease Free H<sub>2</sub>O 6.6ul per sample
  - Master Mix 10.0ul per sample
- c. Make sure to keep the master mix produced in this step on ice until use!!!
- d. Load 20ul of master mix in each well of the PCR plate for every well which will have a sample. Important to make sure you include some wells which will act as negative controls and wells which have the positive control!! Always do at least 2 Controls per plate
- e. Add 2ul of Sample DNA template to each well changing tips between each well to prevent contamination
- f. Cover the PCR plate with an optical slip mad especially for qPCR reactions and make sure it sealed by ruling the comb over the plate. Do not write on the slip cover!!
- g. Centrifuge the plate with a proper balance for about 20 sec at 8,000rpm
- h. Now you are ready to put the plate in the qPCR machine at the following conditions:



- i. After the qPCR has completed the run take the plate out and label it with the organism, primer name, todays date, and the samples ran. Place in the -20 or -80 freezer

**Appendix 2.** Summary statistics for ticks found in coniferous forests (per square meter) on Fort Drum Military Installation, New York, during April–November, 2015–2016.

Month	Larval		Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0278	0.0049	0.0278	0.0049
May	0.0119	0.0089	0.0348	0.0082	0.0230	0.0043	0.0696	0.0094
June	0.0489	0.0090	0.0778	0.0088	0.0067	0.0038	0.1333	0.0113
July	0.0189	0.0085	0.0233	0.0042	0.0000	0.0000	0.0422	0.0059
August	0.0056	0.0040	0.0156	0.0015	0.0000	0.0000	0.0211	0.0030
September	0.0833	0.0070	0.0033	0.0021	0.0011	0.0027	0.0878	0.0067
October	0.0000	0.0000	0.0011	0.0027	0.0444	0.0034	0.0456	0.0030
November	0.0000	0.0000	0.0000	0.0000	0.1033	0.0060	0.1033	0.0060
<b>2016</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0267	0.0051	0.0267	0.0051
May	0.0000	0.0000	0.0141	0.0041	0.0156	0.0031	0.0296	0.0039
June	0.0089	0.0066	0.0700	0.0048	0.0033	0.0032	0.0822	0.0055
July	0.0111	0.0047	0.0400	0.0045	0.0000	0.0000	0.0511	0.0046
August	0.1144	0.0078	0.0133	0.0032	0.0000	0.0000	0.1278	0.0081
September	0.0600	0.0018	0.0078	0.0019	0.0000	0.0000	0.0678	0.0022
October	0.0156	0.0079	0.0000	0.0000	0.0067	0.0030	0.0289	0.0053
November	0.0000	0.0000	0.0000	0.0000	0.0556	0.0056	0.0556	0.0056

**Appendix 3.** Summary statistics for *B. burgdorferi*-positive ticks found in coniferous forests (per square meter) on Fort Drum Military Installation, New York, during April–November, 2015–2016.

Month	Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>						
April	0.0000	0.0000	0.0156	0.0042	0.0156	0.0042
May	0.0030	0.0024	0.0111	0.0030	0.0141	0.0026
June	0.0133	0.0000	0.0000	0.0000	0.0133	0.0000
July	0.0067	0.0024	0.0000	0.0000	0.0067	0.0024
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0233	0.0038	0.0233	0.0038
November	0.0000	0.0000	0.0389	0.0058	0.0389	0.0058
<b>2016</b>						
April	0.0000	0.0000	0.0111	0.0034	0.0111	0.0034
May	0.0052	0.0028	0.0104	0.0031	0.0156	0.0027
June	0.0133	0.0021	0.0011	0.0027	0.0144	0.0018
July	0.0067	0.0024	0.0000	0.0000	0.0067	0.0024
August	0.0056	0.0022	0.0000	0.0000	0.0056	0.0022
September	0.0011	0.0027	0.0000	0.0000	0.0011	0.0027
October	0.0000	0.0000	0.0056	0.0012	0.0056	0.0012
November	0.0000	0.0000	0.0222	0.0038	0.0222	0.0038



**Appendix 4.** Summary statistics for ticks found in deciduous forests (per square meter) on Fort Drum Military Installation, New York, during April–November, 2015–2016.

Month	Larval		Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0067	0.0024	0.0067	0.0024
May	0.0000	0.0000	0.0052	0.0030	0.0089	0.0036	0.0141	0.0070
June	0.0133	0.0094	0.0356	0.0069	0.0022	0.0038	0.0511	0.0000
July	0.0000	0.0000	0.0078	0.0046	0.0000	0.0000	0.0078	0.0046
August	0.0144	0.0064	0.0044	0.0027	0.0000	0.0000	0.0189	0.0068
September	0.0222	0.0079	0.0011	0.0027	0.0000	0.0000	0.0233	0.0082
October	0.0089	0.0077	0.0022	0.0038	0.0011	0.0027	0.0122	0.0081
November	0.0000	0.0000	0.0000	0.0000	0.0156	0.0046	0.0156	0.0046
<b>2016</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0044	0.0054	0.0044	0.0054
May	0.0000	0.0000	0.0030	0.0034	0.0030	0.0034	0.0059	0.0030
June	0.0022	0.0038	0.0144	0.0027	0.0000	0.0000	0.0167	0.0036
July	0.0000	0.0000	0.0033	0.0032	0.0000	0.0000	0.0033	0.0032
August	0.0844	0.0230	0.0033	0.0032	0.0000	0.0000	0.0878	0.0231
September	0.0022	0.0038	0.0000	0.0000	0.0000	0.0000	0.0022	0.0038
October	0.0000	0.0000	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038
November	0.0000	0.0000	0.0000	0.0000	0.0122	0.0037	0.0122	0.0037

**Appendix 5.** Summary statistics for *B. burgdoreri*-positive ticks found in deciduous forests (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>						
April	0.0000	0.0000	0.0022	0.0024	0.0022	0.0024
May	0.0000	0.0000	0.0037	0.0030	0.0037	0.0030
June	0.0044	0.0054	0.0022	0.0038	0.0067	0.0067
July	0.0022	0.0024	0.0000	0.0000	0.0022	0.0024
August	0.0110	0.0027	0.0000	0.0000	0.0110	0.0027
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0011	0.0027	0.0011	0.0027	0.0022	0.0024
November	0.0000	0.0000	0.0067	0.0042	0.0067	0.0042
<b>2016</b>						
April	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038
May	0.0015	0.0031	0.0015	0.0031	0.0030	0.0029
June	0.0022	0.0024	0.0000	0.0000	0.0022	0.0024
July	0.0011	0.0027	0.0000	0.0000	0.0011	0.0027
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0011	0.0270	0.0011	0.0270
November	0.0000	0.0000	0.0044	0.0017	0.0044	0.0017

**Appendix 6.** Summary statistics for ticks found in Developed (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Larval		Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0100	0.0046	0.0100	0.0046
May	0.0267	0.0133	0.0122	0.0090	0.0119	0.0031	0.0567	0.0131
June	0.0000	0.0000	0.0067	0.0038	0.0000	0.0000	0.0067	0.0038
July	0.0000	0.0000	0.0078	0.0049	0.0000	0.0000	0.0078	0.0049
August	0.0000	0.0000	0.0100	0.0006	0.0000	0.0000	0.0100	0.0006
September	0.0167	0.0069	0.0011	0.0027	0.0000	0.0000	0.0178	0.0072
October	0.0000	0.0000	0.0011	0.0027	0.0233	0.0064	0.0244	0.0061
November	0.0000	0.0000	0.0000	0.0000	0.0367	0.0114	0.0367	0.0114
<b>2016</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0133	0.0072	0.0133	0.0072
May	0.0000	0.0000	0.0000	0.0000	0.0052	0.0039	0.0052	0.0039
June	0.0000	0.0000	0.0033	0.0032	0.0000	0.0000	0.0033	0.0032
July	0.0000	0.0000	0.0056	0.0040	0.0000	0.0000	0.0056	0.0040
August	0.0500	0.0094	0.0022	0.0038	0.0000	0.0000	0.0522	0.0095
September	0.0144	0.0074	0.0000	0.0000	0.0000	0.0000	0.0144	0.0074
October	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
November	0.0000	0.0000	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038

**Appendix 7.** Summary statistics for *B. burgdorferi*-positive ticks found in Developed (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>						
April	0.0000	0.0000	0.0056	0.0040	0.0056	0.0040
May	0.0000	0.0000	0.0044	0.0024	0.0044	0.0024
June	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
July	0.0022	0.0024	0.0000	0.0000	0.0022	0.0024
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0144	0.0055	0.0144	0.0055
November	0.0000	0.0000	0.0022	0.0094	0.0022	0.0094
<b>2016</b>						
April	0.0000	0.0000	0.0067	0.0067	0.0067	0.0067
May	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038
June	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
July	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
November	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

**Appendix 8.** Summary statistics for ticks found in mixed forest (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Larval		Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0256	0.0028	0.0256	0.0028
May	0.0000	0.0000	0.0150	0.0072	0.0126	0.0022	0.0292	0.0061
June	0.0156	0.0052	0.0556	0.0076	0.0089	0.0051	0.0800	0.0097
July	0.0000	0.0000	0.0244	0.0087	0.0000	0.0000	0.0244	0.0087
August	0.0211	0.0076	0.0078	0.0040	0.0000	0.0000	0.0289	0.0065
September	0.0467	0.0071	0.0033	0.0021	0.0022	0.0024	0.0522	0.0066
October	0.0000	0.0000	0.0011	0.0027	0.0411	0.0035	0.0422	0.0038
November	0.0000	0.0000	0.0000	0.0000	0.0611	0.0031	0.0611	0.0031
<b>2016</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0422	0.0064	0.0422	0.0064
May	0.0089	0.0077	0.0089	0.0052	0.0200	0.0030	0.0378	0.0044
June	0.0844	0.0090	0.0389	0.0051	0.0044	0.0027	0.1278	0.0085
July	0.0000	0.0000	0.0200	0.0026	0.0000	0.0000	0.0200	0.0026
August	0.1411	0.0107	0.0111	0.0058	0.0000	0.0000	0.1522	0.0115
September	0.0600	0.0011	0.0033	0.0021	0.0033	0.0047	0.0667	0.0009
October	0.0000	0.0000	0.0000	0.0000	0.0333	0.0052	0.0333	0.0052
November	0.0000	0.0000	0.0000	0.0000	0.0311	0.0048	0.0311	0.0048

**Appendix 9.** Summary statistics for *B. burgdoreri*-positive ticks found in mixed forest (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>						
April	0.0000	0.0000	0.0200	0.0024	0.0200	0.0024
May	0.0007	0.0022	0.0074	0.0022	0.0081	0.0022
June	0.0111	0.0034	0.0022	0.0038	0.0133	0.0047
July	0.0056	0.0035	0.0000	0.0000	0.0056	0.0035
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0022	0.0024	0.0000	0.0000	0.0022	0.0024
October	0.0000	0.0000	0.0167	0.0039	0.0167	0.0039
November	0.0000	0.0000	0.0311	0.0033	0.0311	0.0033
<b>2016</b>						
April	0.0000	0.0000	0.0356	0.0069	0.0356	0.0069
May	0.0037	0.0040	0.0096	0.0026	0.0133	0.0022
June	0.0056	0.0022	0.0000	0.0000	0.0056	0.0022
July	0.0067	0.0024	0.0000	0.0000	0.0067	0.0024
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0033	0.0021	0.0000	0.0000	0.0033	0.0021
October	0.0000	0.0000	0.0056	0.0035	0.0056	0.0035
November	0.0000	0.0000	0.0156	0.0046	0.0156	0.0046

**Appendix 10.** Summary statistics for ticks found in shrub forest (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Larval		Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0056	0.0040	0.0056	0.0040
May	0.0000	0.0000	0.0000	0.0000	0.0030	0.0044	0.0030	0.0044
June	0.0000	0.0000	0.0156	0.0052	0.0022	0.0038	0.0178	0.0054
July	0.0000	0.0000	0.0044	0.0027	0.0000	0.0000	0.0044	0.0027
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0111	0.0086	0.0011	0.0027	0.0000	0.0000	0.0122	0.0081
October	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
November	0.0000	0.0000	0.0000	0.0000	0.0078	0.0029	0.0078	0.0029
<b>2016</b>								
April	0.0000	0.0000	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038
May	0.0000	0.0000	0.0000	0.0000	0.0037	0.0026	0.0037	0.0026
June	0.0022	0.0038	0.0033	0.0032	0.0000	0.0000	0.0056	0.0048
July	0.0000	0.0000	0.0044	0.0040	0.0000	0.0000	0.0044	0.0040
August	0.0000	0.0000	0.0022	0.0038	0.0000	0.0000	0.0022	0.0038
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0000	0.0000	0.0044	0.0040	0.0044	0.0040
November	0.0000	0.0000	0.0000	0.0000	0.0078	0.0051	0.0078	0.0051

**Appendix 11.** Summary statistics for *B. burgdorferi*-positive ticks found in shrub forest (per square meter) on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Nymph		Adult		Total	
	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>						
April	0.0000	0.0000	0.0044	0.0040	0.0044	0.0040
May	0.0000	0.0000	0.0015	0.0031	0.0015	0.0031
June	0.0067	0.0038	0.0022	0.0038	0.0089	0.0051
July	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
August	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
November	0.0000	0.0000	0.0022	0.0038	0.0022	0.0038
<b>2016</b>						
April	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May	0.0000	0.0000	0.0007	0.0022	0.0007	0.0022
June	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
July	0.0011	0.0027	0.0000	0.0000	0.0011	0.0027
August	0.0011	0.0027	0.0000	0.0000	0.0011	0.0027
September	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
October	0.0000	0.0000	0.0033	0.0032	0.0156	0.0038
November	0.0000	0.0000	0.0044	0.0054	0.0044	0.0054



**Appendix 12.** Summary statistics for environmental conditions in coniferous forest when ticks were obtained on Fort Drum Military Installation, New York, during April–November 2015–2016.

Month	Temperature (C)		Humidity		Wind speed (MPH)		Pressure (mmHg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	7.11	0.26	0.66	0.18	14.00	0.58	759.41	0.02
May	18.81	0.57	0.66	0.12	12.43	0.61	763.23	0.01
June	19.44	0.46	0.76	0.05	6.67	1.27	760.14	0.02
July	27.41	0.89	0.59	0.01	5.00	0.46	760.39	0.01
August	22.22	0.29	0.71	0.04	6.67	0.71	757.81	0.00
September	21.56	0.36	0.56	0.09	11.60	0.65	764.69	0.02
October	10.00	0.24	0.81	0.08	5.67	1.01	763.99	0.01
November	8.06	0.55	0.79	0.04	7.33	0.45	768.35	0.01
<b>2016</b>								
April	10.19	0.55	0.52	0.11	7.67	0.67	768.10	0.00
May	17.28	0.55	0.63	0.07	7.33	0.45	752.12	0.02
June	22.04	0.68	0.72	0.04	8.33	0.40	744.64	0.00
July	26.57	0.26	0.73	0.05	5.33	0.54	747.73	0.01
August	25.56	0.30	0.52	0.08	6.50	0.41	758.78	0.03
September	23.33	0.12	0.65	0.04	5.83	0.86	764.58	0.00
October	17.41	0.41	0.82	0.06	9.00	0.52	762.30	0.02
November	7.13	0.40	0.59	0.07	6.33	0.59	764.12	0.01

**Appendix 13.** Summary statistics for environmental conditions in deciduous forest when ticks

were obtained on Wheeler-Sack Army Airfield, New York, during April–November 2015–2016.

Month	Temperature (C)		Humidity		Wind speed (MPH)		Pressure (mmHg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	8.19	0.96	0.58	0.22	13.25	0.74	759.84	0.02
May	17.22	0.62	0.72	0.10	11.00	0.56	764.71	0.02
June	20.19	0.38	0.74	0.04	11.33	1.59	760.05	0.02
July	19.44	1.47	0.75	0.13	3.50	0.27	760.35	0.01
August	23.89	0.20	0.68	0.03	10.00	0.84	757.26	0.01
September	19.17	0.92	0.79	0.15	5.50	0.21	764.79	0.02
October	12.22	0.14	0.76	0.01	7.50	2.01	762.89	0.01
November	9.44	0.74	0.70	0.06	6.00	0.69	768.16	0.01
<b>2016</b>								
April	6.11	0.00	0.81	0.00	12.00	0.00	767.33	0.00
May	20.28	0.71	0.55	0.14	7.00	0.94	748.86	0.02
June	21.89	0.61	0.78	0.03	6.00	0.26	744.58	0.01
July	25.83	0.51	0.75	0.17	5.50	1.07	748.67	0.01
August	25.83	0.40	0.54	0.14	4.00	0.50	749.30	0.01
September	23.89	0.00	0.72	0.00	7.00	0.00	762.76	0.00
October	18.89	0.00	0.84	0.00	14.00	0.00	755.14	0.00
November	6.11	0.46	0.66	0.06	9.25	1.18	764.16	0.01

**Appendix 14.** Summary statistics for environmental conditions in Developed when ticks were obtained on Wheeler-Sack Army Airfield, New York, during April–November 2015–2016.

Month	Temperature (C)		Humidity		Wind speed (MPH)		Pressure (mmHg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	8.33	1.06	0.65	0.24	7.67	0.52	756.41	0.03
May	17.59	0.83	0.65	0.09	9.67	0.40	764.29	0.00
June	20.28	0.54	0.88	0.03	14.50	2.49	758.32	0.03
July	20.93	0.86	0.76	0.10	5.00	0.26	759.80	0.01
August	19.44	0.24	0.79	0.02	13.00	0.28	757.81	0.00
September	19.72	1.16	0.63	0.09	7.50	0.91	762.89	0.04
October	10.00	0.35	0.75	0.09	7.25	1.53	764.67	0.01
November	9.44	0.00	0.67	0.08	8.00	0.41	767.59	0.03
<b>2016</b>								
April	13.89	0.79	0.45	0.10	2.50	0.32	768.99	0.00
May	20.28	0.79	0.72	0.01	9.50	0.16	747.14	0.00
June	20.00	1.33	0.87	0.02	5.50	0.21	745.11	0.01
July	30.56	0.21	0.61	0.36	6.50	1.37	750.06	0.00
August	22.59	0.16	0.71	0.06	5.00	0.45	755.99	0.05
September	18.33	0.12	0.79	0.05	6.00	1.22	765.81	0.01
October	17.31	0.22	0.86	0.03	7.77	0.48	760.73	0.01
November	8.89	0.00	0.55	0.00	5.00	0.00	760.98	0.00

**Appendix 15.** Summary statistics for environmental conditions in mixed forest when ticks were obtained on Wheeler-Sack Army Airfield, New York, during April–November 2015–2016.

Month	Temperature (C)		Humidity		Wind speed (MPH)		Pressure (mmHg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	8.98	0.49	0.50	0.17	15.33	0.71	759.04	0.02
May	17.50	0.49	0.63	0.10	11.63	0.78	762.89	0.01
June	20.56	0.54	0.70	0.05	9.33	1.15	743.20	0.14
July	22.50	0.67	0.76	0.07	8.00	0.29	760.03	0.01
August	16.39	0.15	0.93	0.05	7.25	0.85	758.57	0.01
September	19.33	0.52	0.68	0.13	7.60	0.58	765.35	0.02
October	10.46	0.18	0.82	0.07	7.33	1.44	764.71	0.01
November	8.43	0.64	0.79	0.05	8.17	0.40	767.93	0.01
<b>2016</b>								
April	12.22	0.28	0.46	0.11	5.33	2.10	768.52	0.01
May	17.90	0.71	0.62	0.10	8.33	0.45	750.63	0.02
June	20.37	0.55	0.77	0.01	6.83	0.42	743.50	0.00
July	24.22	0.52	0.74	0.09	5.20	0.49	745.79	0.01
August	25.09	0.31	0.56	0.06	8.00	0.52	758.11	0.03
September	20.65	0.35	0.70	0.07	5.67	0.68	766.36	0.01
October	9.67	1.00	0.93	0.05	3.80	0.55	761.90	0.02
November	8.47	0.24	0.60	0.09	6.75	0.55	762.00	0.01

**Appendix 16.** Summary statistics for environmental conditions in shrub forest when ticks were obtained on Wheeler-Sack Army Airfield, New York, during April–November 2015–2016.

Month	Temperature (C)		Humidity		Wind speed (MPH)		Pressure (mmHg)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>2015</b>								
April	11.11	2.77	0.51	0.48	16.50	2.09	757.17	0.04
May	23.89	0.00	0.70	0.00	9.00	0.00	764.54	0.00
June	22.22	0.24	0.77	0.02	14.00	2.67	758.19	0.02
July	21.85	0.65	0.69	0.07	4.33	0.89	760.22	0.01
August	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
September	19.17	1.04	0.81	0.15	6.00	0.00	764.67	0.02
October	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
November	10.69	0.85	0.75	0.02	12.00	0.79	764.41	0.00
<b>2016</b>								
April	6.67	0.00	0.90	0.00	8.00	0.00	767.08	0.00
May	14.63	0.57	0.73	0.12	5.00	0.26	754.63	0.01
June	25.83	0.17	0.77	0.01	9.00	0.33	744.35	0.00
July	23.06	0.52	0.77	0.09	3.50	0.27	747.14	0.02
August	27.22	0.00	0.65	0.00	4.00	0.00	749.81	0.00
September	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
October	18.89	0.00	0.94	0.00	15.00	0.00	754.63	0.00
November	4.72	0.24	0.69	0.03	9.50	0.16	760.86	0.00

**Appendix 17.** Summary statistics of fall mast production on Fort Drum Military Installation, New York, 2015–2016.







**Appendix 18.** Summary statistics for stand variables on Fort Drum Military Installation, New York, during April–November 2015–2016.

Stand variable	Grassland		Coniferous		Mixed		Deciduous		Shrub		Developed landscape	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Tree density	0.000	0.000	24.313	2.004	19.750	2.005	19.875	1.819	21.688	2.672	9.750	1.822
Tree dbh (cm)	0.000	0.000	23.802	0.700	25.443	0.777	21.186	0.788	12.453	0.198	25.400	1.445
Basal area (square meters)	0.000	0.000	0.594	0.035	0.658	0.042	0.507	0.039	0.132	0.005	0.761	0.098
No. tree species	0.000	0.000	4.688	0.405	4.875	0.407	3.188	0.228	3.750	0.323	2.250	0.281
Canopy cover (%)	0.000	0.000	96.178	0.833	93.656	1.445	95.944	0.747	95.827	1.039	63.454	6.925
Snag density	0.000	0.000	6.000	0.742	6.813	0.993	3.125	0.455	4.938	0.777	1.125	0.272
Snag height (m)	0.000	0.000	3.814	0.325	4.868	0.344	4.977	0.419	4.047	0.339	4.478	0.797
Snag dbh (cm)	0.000	0.000	19.680	1.376	24.608	1.281	22.581	2.608	16.348	0.702	25.315	4.165
Decay stage of snags	0.000	0.000	6.177	0.225	5.541	0.213	5.360	0.271	5.506	0.195	6.222	0.495
Cover/vegetation density	1.500	0.129	2.406	0.228	2.422	0.201	2.188	0.196	3.547	0.327	1.875	0.294
CWD density	0.000	0.000	1.625	0.301	2.063	0.413	1.438	0.288	1.250	0.296	0.188	0.101
CWD length (m)	0.000	0.000	6.696	1.010	5.556	0.605	10.515	1.024	4.305	0.515	6.257	3.989
CWD dbh (cm)	0.000	0.000	20.857	1.961	19.065	0.961	28.669	4.041	15.761	1.673	29.464	12.293
Decay class of CWD	0.000	0.000	2.769	0.150	2.818	0.171	3.261	0.296	3.850	0.365	2.333	0.333
Leaf litter depth (cm)	0.000	0.000	3.306	0.328	2.345	0.335	3.781	0.445	0.356	0.108	1.681	0.639
Stem density	209.313	17.517	44.875	9.479	71.875	11.670	80.875	10.122	122.375	11.078	172.625	40.326
No. stem species	5.750	0.636	4.188	0.440	6.313	0.373	3.688	0.610	6.250	0.698	5.063	0.887

**Appendix 19.** Description of habitat variables to be measured nearby small mammal trapping grids for cover type characterization on Fort Drum Military Installation, New York, during April–November 2015–2016.

Spatial Level	Vegetative Parameter	Measurement Description
Stand	Species	Tree species; when determinable
	Dbh (cm)	Average dbh/0.04 ha plot; measured using calipers
	Crown class	When determinable (USDA Forest Service 2002)
	Canopy cover	Average % coverage, measurements at the center and 10-m in each cardinal direction from the center of each 0.04-ha plot; visually estimated using densiometer
	Snag density and volumes Decay stage of snags	# of snags/0.04 ha plot; measured using tape 1–9; see Maser et al. 1979, Thomas et al. 1979 for description
Midstory	Cover/vegetation density	% coverage/1-6; visually estimated using cover board
	Coarse woody debris (CWD)	Length and diameter; visually estimated using measuring tape and calipers at midpoint
	Decay class of CWD	1–5; see Maser et al. 1979, Thomas et al. 1979 for description
Understory	Leaf litter depth	When determinable, average of measurements from each corner of the 0.001-ha nested plot; visually estimated using ruler
	Ground cover composition	Relative abundance of stems; visually estimated

**Appendix 20.** Covariance of habitat variables on Fort Drum Military Installation, New York, during April–November 2015–2016. Colinearity of  $>0.70$  was considered high covariance.

	Temperature	Wind	Humidity	Pressure	Tree density	Tree species	Tree DBH	Canopy cover	Stem height	Stem dbh	Stem decay	Stem count	CWD length	CWD dbh	CWD decay	CWD count	Midstory	Leaf litter	Stem density	Ground species richness
Temperature	1.00	-0.04	-0.26	-0.46	0.04	0.01	-0.05	0.01	-0.07	-0.05	0.06	0.00	0.01	0.00	-0.01	-0.01	0.00	0.03	-0.03	-0.05
Wind	-0.04	1.00	-0.13	-0.07	0.02	-0.01	-0.02	0.03	0.01	-0.04	-0.06	0.00	0.00	-0.02	0.07	0.01	0.06	-0.03	0.01	0.02
Humidity	-0.26	-0.13	1.00	-0.05	-0.04	-0.04	-0.01	-0.02	0.03	-0.06	-0.03	-0.03	-0.03	0.07	-0.03	-0.03	0.06	-0.09	0.07	0.06
Pressure	-0.46	-0.07	-0.05	1.00	-0.02	-0.01	-0.01	-0.04	-0.04	0.07	-0.02	-0.02	0.00	0.03	-0.07	-0.03	-0.05	0.02	0.00	-0.03
Tree density	0.04	0.02	-0.04	-0.02	1.00	0.77	0.93	0.73	-0.46	-0.05	0.07	0.74	0.03	0.73	0.42	0.73	0.50	-0.90	0.00	-0.22
Tree species richness	0.01	-0.01	-0.04	-0.01	0.01	1.00	0.53	0.73	-0.20	-0.06	0.99	-0.37	-0.81	0.04	0.59	0.91	0.34	-0.84	0.07	0.00
Tree DBH	-0.05	-0.02	-0.01	-0.01	-0.09	0.53	1.00	0.08	0.57	-0.35	0.55	-0.35	-0.35	0.04	0.04	0.91	0.34	-0.84	0.00	0.28
Canopy cover	0.01	0.03	-0.02	-0.04	0.93	0.73	0.08	1.00	-0.11	-0.42	0.74	-0.15	0.13	-0.59	0.59	0.85	0.52	-0.86	-0.09	-0.09
Stem height	-0.07	0.01	0.03	-0.04	-0.46	-0.20	0.57	-0.11	1.00	-0.76	-0.17	-0.21	0.10	0.31	-0.61	0.15	-0.31	0.01	0.25	0.33
Stem dbh	-0.05	-0.04	-0.01	0.01	-0.68	0.21	0.67	-0.52	0.76	1.00	-0.17	-0.21	0.44	0.31	-0.61	-0.07	-0.72	0.06	0.32	0.28
Stem decay	0.06	-0.06	-0.06	0.07	-0.05	-0.06	-0.35	-0.42	-0.76	1.00	-0.15	-0.15	0.13	-0.66	-0.44	0.15	-0.32	0.09	0.25	0.38
Stem count	0.00	0.00	-0.03	-0.02	0.74	0.99	0.55	0.74	-0.15	1.00	1.00	1.00	-0.42	0.92	0.92	0.43	0.33	0.12	0.33	0.38
CWD length	0.01	0.00	-0.03	0.00	0.03	-0.37	0.13	0.30	0.10	-0.42	-0.42	1.00	0.72	0.10	-0.09	-0.49	0.76	-0.15	-0.79	-0.79
CWD dbh	0.00	-0.02	-0.02	0.03	-0.62	-0.81	-0.35	-0.59	0.31	0.44	0.13	0.13	1.00	-0.34	0.10	-0.67	0.35	-0.10	-0.59	0.08
CWD decay	-0.01	0.01	-0.03	-0.03	0.73	0.91	0.59	0.85	-0.07	0.24	0.24	1.00	0.80	0.30	1.00	0.30	0.33	-0.83	0.26	0.26
Midstory	0.00	0.06	0.06	-0.05	0.42	0.22	0.40	0.52	-0.31	-0.72	-0.32	0.43	-0.49	0.77	0.80	1.00	1.00	-0.53	0.41	-0.75
Leaf litter	0.03	-0.03	-0.09	0.02	0.50	0.34	0.15	0.40	0.01	0.06	0.09	0.12	0.76	0.35	-0.22	0.33	-0.53	1.00	-0.67	-0.75
Stem density	-0.03	0.01	0.07	0.00	-0.90	-0.84	-0.19	-0.86	0.25	0.32	0.03	-0.79	-0.15	0.46	-0.10	-0.83	-0.13	1.00	0.25	0.25
Ground species richness	-0.05	0.02	0.06	-0.03	-0.22	0.28	0.68	-0.09	0.33	0.28	-0.36	0.38	-0.79	-0.59	0.08	0.26	-0.41	-0.67	1.00	1.00

**Appendix 21.** Coniferous forest cover type.



**Appendix 22.** Deciduous forest cover type.



**Appendix 23.** Developed cover type.



**Appendix 24.** Grassland cover type.





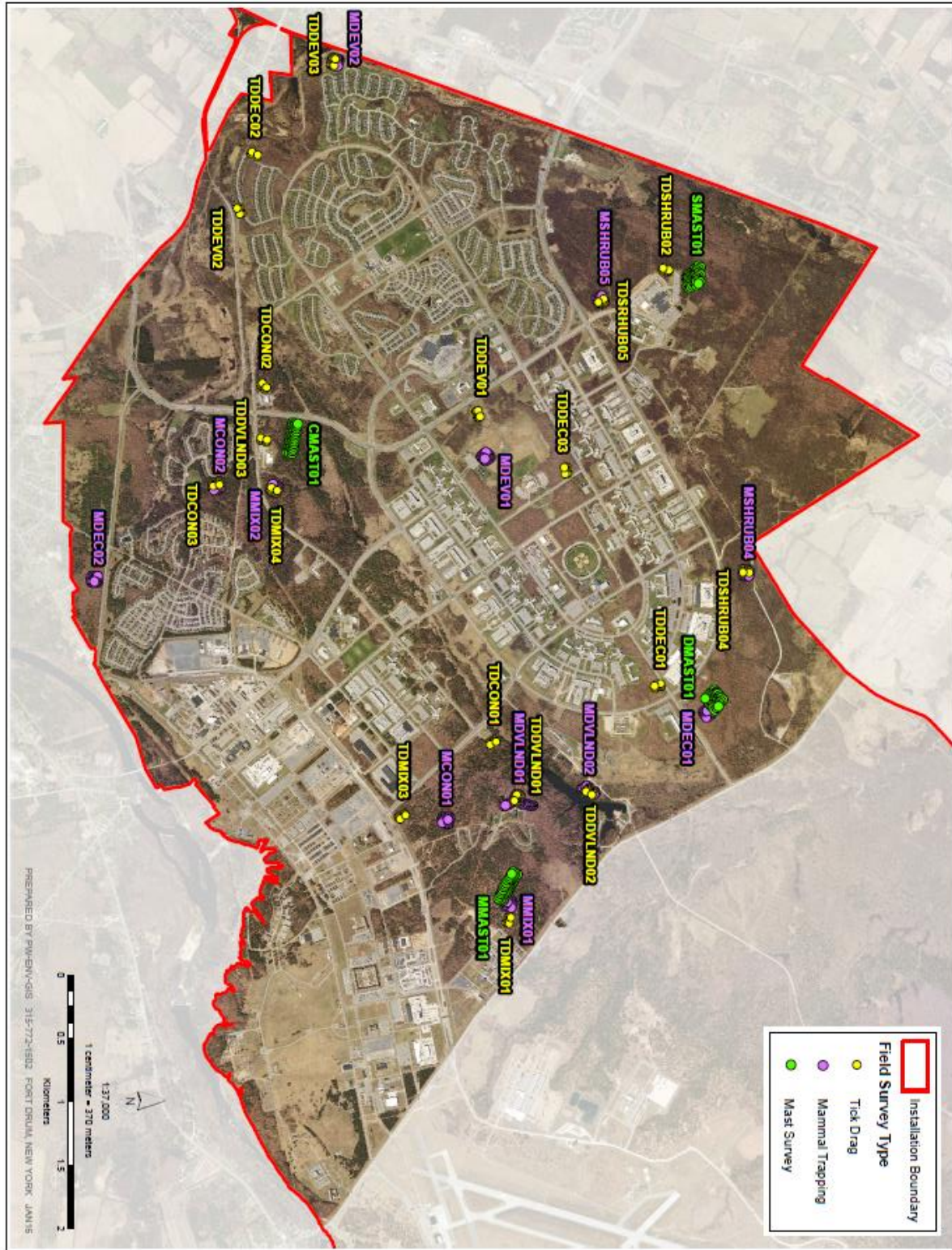
**Appendix 25.** Mixed forest cover type.



**Appendix 26.** Shrub forest cover type.



**Appendix 27.** Locations of small mammal, tick drag and mast trap grids within the Cantonment Area of Fort Drum Military Installation, NY.



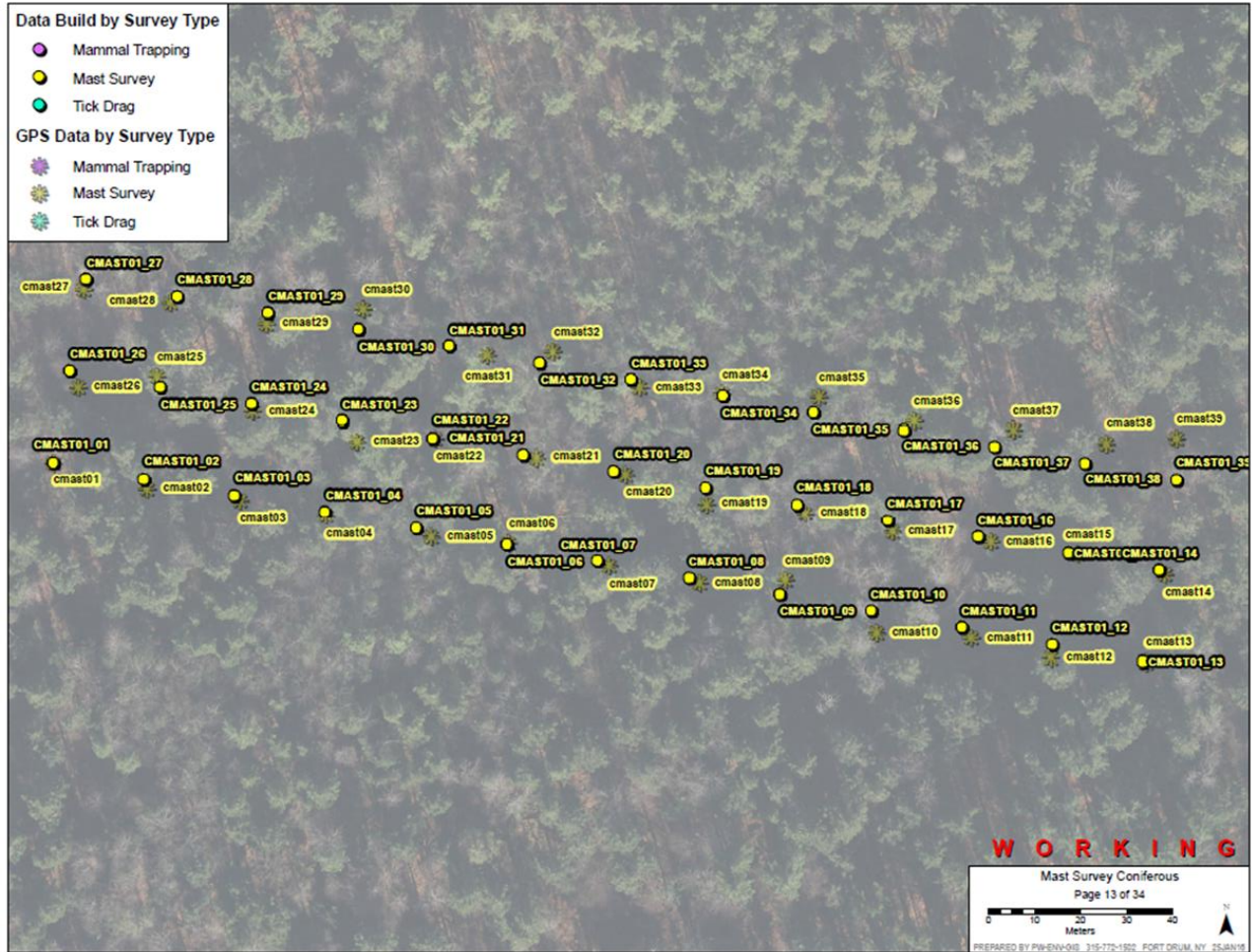
**Appendix 28.** An example of a tick drag grid within the Cantonment Area of Fort Drum Military Installation, NY.



**Appendix 29.** An example of a small mammal trapping grid within the Cantonment Area of Fort Drum Military Installation, NY.



**Appendix 30.** An example of a mast collection grid within the Cantonment Area of Fort Drum Military Installation, NY.



**Appendix 31.** An example of a mast trap within the Cantonment Area of Fort Drum Military Installation, NY.

