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ARTICLE
Disease Ecology

Probability of parasite infection (Trombiculidae) across habitats and small mammal hosts

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Abstract

Parasite infection patterns within ecosystem networks are driven by habitat as well as host availability. However, the effect parasites have on host health is often unknown. Understanding host–parasite interactions across host species and habitat types can provide insights into complex host–parasite dynamics. To explore a poorly understood parasite–multi-host system, we investigated the probability of Trombiculid chigger infection depending on habitat, host species, and small mammal community structure. We also assessed relationships between infection and body mass. We live trapped small mammals in Algonquin Provincial Park, Ontario, Canada, across 4 years (2016, 2017, 2018, and 2020), within seven different habitat types. Results supported field observations that red-backed voles (*Clethrionomys gapperi*) are primary hosts for infection from Trombiculid chiggers, with deer mice (*Peromyscus maniculatus*) and woodland jumping mice (*Napaeozapus insignis*) being secondary hosts. Red-backed voles consistently showed higher probabilities of infection than deer mice and woodland jumping mice; additionally, infection rates were higher among secondary hosts in years when red-backed voles were more prevalent in small mammal communities. Differences in chigger infection across habitats were correlated with the abundance of red-backed voles, except for white pine/white spruce and white pine/red pine habitats. No relationship was identified between Trombiculid chiggers and body mass within either red-backed voles or deer mice. Overall, evidence suggests that red-backed voles are the primary hosts for Trombiculid chiggers, with some evidence that habitat type can further influence infection rates among host species.

KEYWORDS
Bayesian, body mass, chiggers, environment, infestation, parasites, prevalence, rodents, vegetation

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INTRODUCTION

Parasites have the potential to influence species interactions and community dynamics, particularly in multi-host systems. However, empirical evidence for these influences within networks of free-living species can often be scarce or absent (Stewart Merrill et al., 2022). Parasites often infect multiple host species within the same community, but the probability of these hosts becoming infected, supporting, or transmitting the parasite can greatly vary (Johnson et al., 2019). Parasites may encounter hosts of varying quality; some will be highly susceptible and act as competent hosts to facilitate parasite persistence and transmission, while others function as "dead-ends" and misdirect infectious stages (Dobson et al., 2006). Competent host density and overall host diversity can greatly influence parasite transmission and infection success (Johnson et al., 2012). Thus, quantifying the roles of different hosts within a multi-host parasite system is critical to advance our understanding of parasite and disease dynamics within changing communities (Stewart Merrill et al., 2022).

Beyond meeting the needs of the host, the external habitat can also be an important determinant for variation in parasite infection. In addition to occurring across multiple host species, many parasites are found within a wide variety of habitat types (Álvarez-Presas et al., 2018; Shao et al., 2023). Different habitat types can contain different environmental traits, such as soil and microclimate characteristics, that can influence parasite success (Bowman, 2000; Shao et al., 2023). For instance, habitat type can influence host-seeking behavior and parasite survival off-host (Richardson et al., 2022). Host habitat can also further contribute to parasite infection patterns by enhancing host density or diversity (Johnson & Haas, 2021). Ultimately, it is critical to consider both the host's habitat and the broader external environment in parasite infection patterns, as many parasites directly engage with both throughout their life cycle (Blache et al., 2025; Scott, 2023; Turner et al., 2021).

Trombiculid mite larvae, known as chiggers, are ectoparasites commonly found on vertebrate hosts (Chen et al., 2022; Stekolnikov et al., 2022; Traub & Wisseman, 1968). Once attached to hosts, chiggers feed exclusively on host bodily fluids (Kim et al., 2024), often only staying attached for 3–5 days (Morand et al., 2006; Stekolnikov et al., 2022), representing a distinct instar that is subsequently followed by active free-living life stages (i.e., nymph and adults; Matthee et al., 2020). The spatial and temporal emergence of chiggers can vary depending on environmental conditions and phenology (Blache et al., 2025; Chen et al., 2022; Jameson & Brennan, 1957). Warm and humid conditions, characterized by increased temperature and precipitation, are hypothesized to increase developmental rates and be favorable for chiggers (Maaz et al., 2018). Increased precipitation can also drive decomposition of leaf litter for more favorable habitat and promote the abundance of prey species for adult mites (Maaz et al., 2018; Wale et al., 2023). However, different species of chiggers can be adapted to different environmental conditions. Chigger species *Euschoengastia radfordi* and *Euschoengastia peromysci*, have both been found to parasitize deer mice (*Peromyscus maniculatus*); however, *E. radfordi* were found to prefer dry brush fields, whereas, *E. peromysci* showed preference towards the moist duff of forests (Jameson & Brennan, 1957). These differences in preferred habitat type between these chigger species are likely due to the environmental requirements of subsequent free-living adult life stages (Jameson & Brennan, 1957).

Parasites by definition impose costs on their hosts and can negatively affect host reproductive success (Gooderham & Schulte-Hostedde, 2011; Neuhaus, 2003) and survival (Lemaître et al., 2009). These costs can include reduced hemoglobin (Fellin & Schulte-Hostedde, 2022), elevated glucocorticoids (Veitch et al., 2021), and declines in body condition (Hakkarainen et al., 2007; i.e., an animal's body mass relative to structural size and can serve as an index for energy reserves [Schulte-Hostedde et al., 2001, 2005]). Furthermore, body condition can be influenced by sex and reproductive status, among other factors (Murray, 2002), including parasitism that forces energy to be allocated to the immune system (Sheldon & Verhulst, 1996). This leaves less energy for reproduction and growth (Sheldon & Verhulst, 1996). Nonetheless, the evidence for a direct impact of parasites on body condition in small mammal hosts remains mixed. Some studies have found a correlation between parasite infection and body condition (Mallinger et al., 2022), while others have not (Gorrell & Schulte-Hostedde, 2008; Perez-Orella & Schulte-Hostedde, 2005).

Algonquin Provincial Park possess a diverse small mammal community primarily composed of deer mice (*P. maniculatus*), southern red-backed voles (*Clethrionomys gapperi*; from hereon referred to as red-backed voles), woodland jumping mice (*Napaeozapus insignis*), eastern chipmunks (*Tamias striatus*), North American red squirrels (*Tamiasciurus hudsonicus*), meadow jumping mice (*Zapus hudsonius*), meadow voles (*Microtus pennsylvanicus*), northern flying squirrels (*Glaucomys sabrinus*), short-tailed shrews (*Blarina brevicauda*), and *Sorex* spp. shrews. Trombiculid chiggers have previously been identified as parasites on multiple small mammal hosts within Algonquin Provincial Park (Bobbie et al., 2017). Thus, host–parasite dynamics between Trombiculid and the small mammal community in Algonquin Provincial Park represents a multi-host system ideal for understanding relationships between primary and

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secondary hosts, as well as habitat type. Within this multi-host system, the primary host species remains unconfirmed. Nonetheless, field-based observations suggest that red-backed voles are the primary host for Trombiculid chiggers, because they typically have higher infection prevalence at greater intensities than other small mammal hosts (Elliott Schmidt, Jasmine Veitch, and Arianne Sawyer, personal observations). Additional information such as how habitat influences infection rates and what impact Trombiculid chiggers' infection has on host condition also remained unanswered. The objective of this study was to (1) identify the presence of Trombiculid chigger infection across host species, (2) identify the presence of Trombiculid chigger infection across habitats, and (3) determine the relationship between the presence of Trombiculid chigger infection and individual body condition among host species. To address these objectives, the presence of chigger infection was examined across three different host species (i.e., red-backed voles, deer mice, and woodland jumping mice) across seven different habitat types. As potential primary hosts, we further hypothesize that the abundance of red-backed voles (i.e., primary hosts) is positively associated with Trombiculid chigger infection prevalence among habitats. Lastly, we hypothesize that Trombiculid chiggers negatively impact host body condition.

METHODS

This study was conducted in Algonquin Provincial Park, Ontario, Canada (45°54′ N, 78°26′ W) over four field seasons (May–August 2016, 2017, 2018, and 2020). All protocols were approved by the Animal Care Committee (ACC) at Laurentian University, Sudbury, Ontario (Animal Use Protocol number 6011106).

Study sites

Algonquin Provincial Park is situated on a dome of Precambrian Canadian Shield bedrock (elevation 587 m) and contains a heterogenous mixture of habitat types created through diverse topography and geographic features; existing at the boundary of the northern boreal forest and southern deciduous hardwood forest (Ontario Ministry of Natural Resources, 2002). Field sites within this study consist of soils formed from glacial tills and mature forests dominated by hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), interspersed with softwood species such as hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*; Ontario Ministry of Natural Resources, 2002). Temperatures within Algonquin Provincial Park range from −35.9 to 32.34°C throughout the year. Over July–August, our study period, temperatures range from approximately 6 to 32°C, humidity from 30%–99%, and 14.5–15.2 h of daylight (Environment and Climate Change Canada, 2026). Seven traplines were sampled within this study: sugar maple hardwood, cut-over mixed wood, dense mixed wood, coniferous, white pine/white spruce, black spruce/aspen, and white pine/red pine. Trapline labels were designated based on defining species within each habitat when originally sampled in 1952; current vegetation communities are provided in Appendix S1: Table S1.

Host biology

The three small mammal species that serve as hosts for Trombiculid chiggers in Algonquin Provincial Park (deer mice [*P. maniculatus*], red-backed vole [*C. gapperi*], woodland jumping mice [*N. insignis*]) are all rodents (Rodentia), but from phylogenetically separate groups. Woodland jumping mice are in the family Zapodidae (Alhajeri, 2023), and while deer mice and red-backed voles are both in the family Cricetidae, they are in separate subfamilies: red-backed voles are in the subfamily Arvicolinae (Withnell & Scarpetta, 2024), whereas deer mice are in the subfamily Neotominae (Miller & Engstrom, 2008). The ecology and natural history of these syntropic species is described in Hughes et al. (2026) and Wilson et al. (2017). Deer mice are habitat generalists and are among the most widely distributed mammals in North America. Red-backed voles and woodland jumping mice tend to live in mixed deciduous and coniferous forest with complex habitat structure. Generally, all three species are polyandrous and produce multiple litters from May to August. Deer mice generally reproduce three to five times each breeding season, with each litter containing four to six pups. Deer mice have an average lifespan of 1–2 years and reach sexual maturity after 6–8 weeks. Their home range varies from 0.36 to 5.8 ha. Red-backed voles also live for 1–2 years and produce litter sizes that range from four to five pups, two to three times per reproductive season. Reported home ranges for red-backed voles are smallest among the three species, 0.01 to 0.5 ha. In contrast, woodland jumping mice live for 4–5 years and reproduce one or two times per season. They have home ranges of 0.4 to 3.6 ha. Woodland jumping mice also produce fewer offspring per reproductive event than deer mice and red-backed voles, producing two to four pups per litter. Woodland jumping mice are also unique because they hibernate, relying on fat stores during a winter hibernation period that can last over 6 months. In all three species, burrows are constructed under fallen logs and rocks, and nests

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are lined with grass, leaves, and sometimes moss or sphagnum.

Field methods

Small mammals were trapped as part of a long-term monitoring program using traplines that were established in the 1950s (Fryxell et al., 1998). Trapping occurred across seven habitat types: sugar maple hardwood, cut-over mixed wood, dense mixed wood, conifer, white pine/white spruce, black spruce/aspen, and white/red pine (Figure 1). The total study area (~8 × 2.5 km) was a continuously forested area that has not been logged or burned since the 1930s (Fryxell et al., 1998). Within each habitat type, traps were set over eight trapping sessions (three nights of consecutive trapping) between May and August. Each site was trapped every 2 weeks for a total of 16 weeks. Traplines were >0.3 km apart and rarely would an individual be caught on two different traplines. Each trapline contained transects that consisted of 10 trapping stations set at 10-m intervals (two traps per station). Small mammals were captured using Sherman traps (Rogers Manufacturing, Kelowna, BC, Canada) baited with water-soaked sunflower seeds. Polyester bedding was provided as nesting material. Traps were set 30–60 min prior to sunset and then checked in the morning starting just 30 min prior to sunrise. The designed trapping protocol targets species that are most active during corpuscular periods. Targeted species include deer mice, red-backed voles, and woodland jumping mice. Non-target species refers to species that are active outside of crepuscular time periods, rare or were unexpectedly captured and include eastern chipmunks, North American red squirrels, meadow jumping mice,

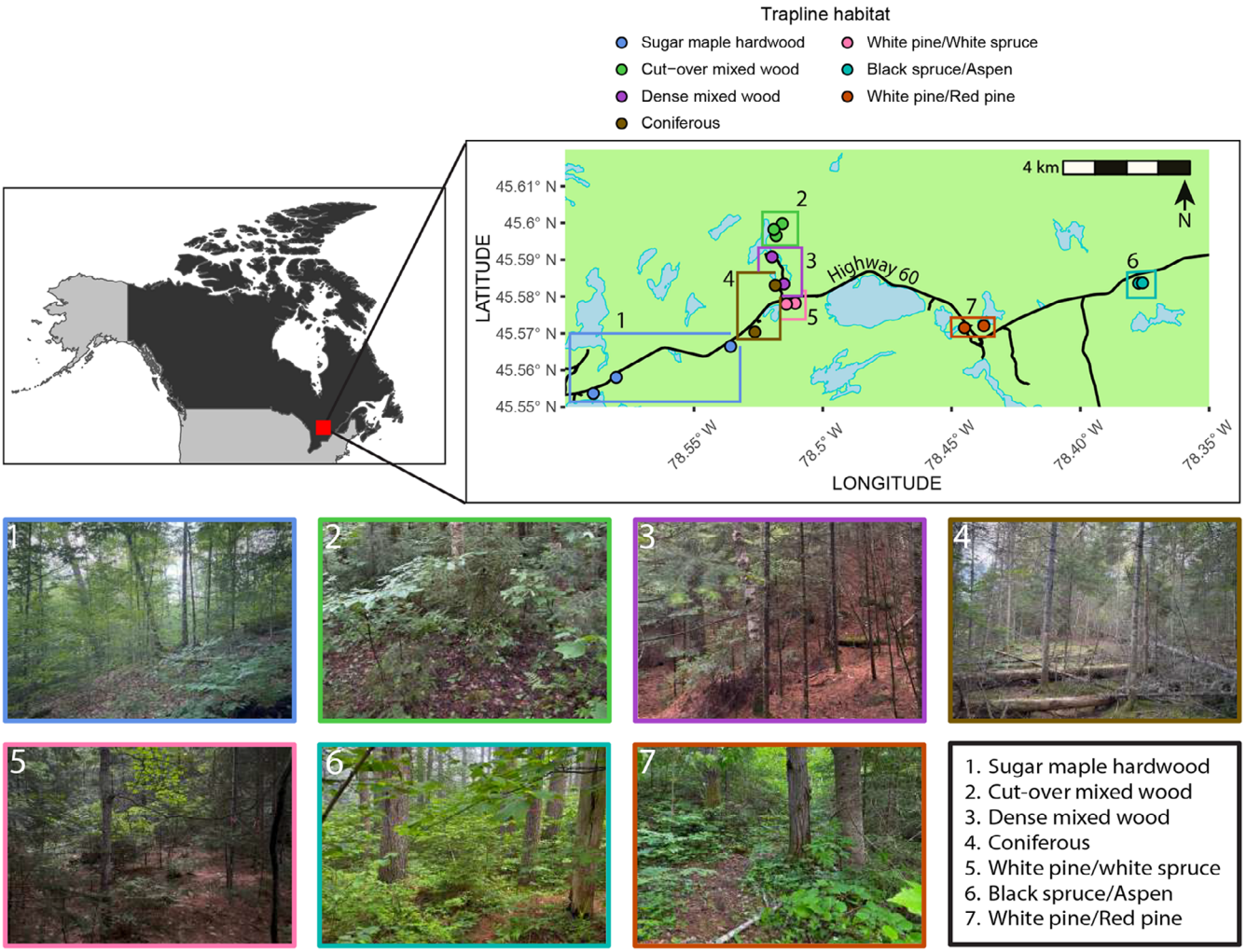

FIGURE 1 Map representing the location of different habitat types, as well as pictures associated with each habitat type. The red square represents location of Algonquin Provincial Park. The map was made in R using packages *sf* (Pebesma, 2018; Pebesma & Bivand 2023) and *rnaturalearth* (Massicotte & South, 2023), with additional road (Government of Ontario, 2025) and waterbody (Ontario Ministry of Natural Resources and Forestry (MNRF), 2025) datasets provided by open source datasets. Photo credit: Angela Bouranakos.

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meadow voles, northern flying squirrels, short-tailed shrews, and *Sorex* spp. of shrews.

Peromyscus mice have been sampled in Algonquin Park and genetically assessed for species identification (McKay, 2016). In areas that were sampled for this study, McKay (2016) reported only two of 149 (1.34%) *Peromyscus* mice that were identified as *P. leucopus*. The remainder were *P. maniculatus*. We therefore assume that all *Peromyscus* we sampled were *P. maniculatus*.

Upon first capture, individuals were tagged with unique alphanumeric ear tags (National Brand and Tag, Newport, Kentucky, USA) for future identification. Red-backed voles and woodland jumping mice received one ear tag. Deer mice were tagged on both ears, due to a greater tendency for tags to be ripped. Age (juvenile, sub-adult, and adult; determined by mass and/or pelage, depending on the species), mass (Pesola scale, to ±1 g), sex (determined by anogenital distance), and morphometric measurements including right hindfoot length (heel to tip of longest nail; ruler, to ±1 mm), skull length (distance from occipital crest to tip of nose; calipers, to ±0.1 mm), and skull width (distance from parietal bones; calipers, to ±0.1 mm) were collected for each individual. Captured individuals were visually examined for the presence of Trombiculid chiggers (typically located around the ear and/or genitals) during each capture event. Individuals were immediately released at their capture location once processing was completed.

Trombiculid chiggers infecting small mammals were previously confirmed as the same species across multiple hosts by Bobbie et al. (2017) and morphologically to the family level Trombiculidae (Dr. Heather Proctor, personal communication). Across all sampling years, chiggers were initially observed at the beginning of July (July 11–13 depending on the year) and remained present on small mammal hosts for the remainder of the trapping season. Chiggers initially appeared on all focal species at the same time, suggesting the presence of an environmental cue triggering mite emergence. When assessing infection probability, only trapping data from the day chiggers were first observed and onwards was used to measure the probability of infection.

Prior to statistical analysis, data were subset between sample years to account for interannual variation in host abundances, using "minimum number known alive" as a proxy for abundance. Sample years 2016–2017 were designated as high red-backed vole years (referred to as high-RBV years), while sampling years 2018 and 2020 were designated as low red-backed vole years (referred to as low-RBV years). Subsetting the data into high- and low-RBV years was done to provide greater insight into how host–parasite dynamics in a multi-host system shift when the primary host possesses a high- or low-level abundance within the community. In high-RBV years, deer mice, red-backed voles, and woodland jumping mice comprised on average 49.5%, 24.6%, and 17.6% of the small mammal community, respectively (remaining 9.8% being composed of other rodent and shrew species). In low-RBV years, deer mice, red-backed voles, and woodland jumping mice comprised on average 69.6%, 5.9%, and 5.4% of the small mammal community, respectively.

Statistical analysis

All statistical analysis was completed using the statistical software R (v. 4.2.2; R Core Team, 2022). We ran Bayesian generalized linear mixed-effects models (GLMMs) using the package *brms* (Burkner, 2017). For each model, we selected distributions and link functions based on the response variable type (Appendix S1: Table S2), and used non-informative (i.e., centered on 0) weakly regularizing priors (Lemoine, 2019). Model convergence was assessed using visual inspection of Markov Chain Monte Carlo (MCMC) trace plots, autocorrelation plots, and Gelman-Rubin statistics (R-hat) with a threshold of 1.01, using the *rstan* package (Stan development Team, 2024). We assessed model fit via standardized residual checks from the DHARMa package (Hartig, 2022). Post hoc pairwise analysis was run using the *emmeans* package (Lenth, 2023).

Separate models were run to identify (1) infection probability across habitat types for high- and (2) low-RBV years, (3) how the percentage of red-backed voles within the small mammal communities influences infection probability, and (4) variation in mass among different parasitized groups.

Results from models are presented as mean effect sizes with 95% highest posterior densities [HPDs], to allow for intuitive comparisons with frequentist models. HPDs are analogous to 95% credible and CIs (in frequentist frameworks). However, instead of having equal-tailed intervals, HPDs contain the most probable 95% of values as defined by the narrowest interval in which included values have a higher posterior density than excluded values. HPDs are particularly useful when posterior distributions are skewed. We do not discuss results in terms of statistical "significance" but rather focus on the effect sizes as well as probability of direction (PD, i.e., the percentage of posterior distributions with the same sign as the estimated effect). Where PD results are presented, values greater than 90% are considered as strong evidence.

Analysis of body mass

Body mass was analyzed separately among deer mice and red-backed voles using data collected from the 2016

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trapping season. Woodland jumping mice were excluded as sample sizes were too small. Pregnant females as well as juveniles were excluded from the body condition analysis due to expected increased differences in mass and growth rates. As there were too few recaptures to examine individual changes in body mass before and after infection occurred, red-backed voles and deer mice were recorded as either "parasitized" or "not parasitized" based on initial capture events. We ran a principal components analysis (PCA) that included hindfoot length and skull length and width, and used the first component as a composite index of body size (Gorrell & Schulte-Hostedde, 2008). Body mass was then modeled (Gaussian distribution) using infection, body size, sex, and (Julian) date as fixed effects, including an interaction between sex and date, with 2500 warmup samples, 5000 iterations, and four chains to determine how mite infections influenced body mass.

RESULTS

Over July–August (time period that chiggers can be observed) within the 4 sampling years, a total of 1210 small mammals were captured (excluding shrews) across 9494 trap nights. In total, 698 deer mice, 202 red-backed voles, 152 woodland jumping mice, 121 eastern chipmunks, 32 American red squirrels, 2 northern flying squirrels, 2 meadow jumping mice, and 1 meadow vole were captured. Across all sample years, deer mice comprised the majority of the small mammal community ($n_{2016/2017}$: 332; $n_{2018/2020}$: 366) in most habitats. Red-backed voles ($n_{2016/2017}$: 170; $n_{2018/2020}$: 32) and woodland jumping mice ($n_{2016/2017}$: 123; $n_{2018/2020}$: 29) were subsequently the next largest contributors to the small mammal community in 2016/2017; however, they were less abundant in 2018/2020 trapping seasons (Table 1). Deer mice showed a stronger affinity to sugar maple hardwood habitats compared to other species, while red-backed voles preferred more coniferous-based habitats.

Infection probability during high-RBV years

During trapping seasons where red-backed voles represented a greater proportion of the small mammal community (high-RBV years), red-backed voles had higher infection probabilities than deer mice and woodland jumping mice (PD >99%), within all habitats except sugar maple hardwood and white pine/red pine (Appendix S2: Table S1). Infection presence was overall lower within the sugar maple hardwood habitat (Appendix S2: Table S2). There was strong evidence that red-backed voles were more likely to be infected than deer mice (0.51 [HPD: −0.028, 0.90]; PD = 93%), but limited evidence suggesting red-backed voles were more likely to be infected than woodland jumping mice (0.20 [HPD: −0.43, 0.72]; PD = 68%; Appendix S2: Table S3). All host species had the highest probabilities of infection in conifer habitats (RBV: 99%; DM: 90%; WJM: 94%), followed by dense mixed wood (RBV: 99%; DM: 66%; WJM: 84%), black spruce/aspen (RBV: 99%; DM: 47%; WJM: 48%), and cut-over mixed wood (RBV: 99%; DM: 32%; WJM: 59%; Figure 2, Table 2). The lowest probabilities of infection occurred within white pine/white spruce (RBV: 97%; DM: 12%; WJM: 12%), white/red pine (RBV: 81%; DM: 12%; WJM: 66%), and sugar maple hardwood (RBV: 65%; DM: 12%; WJM: 44%). Within sugar maple hardwood habitats, despite

TABLE 1 The proportion of species within the small mammal community during high red-backed vole years (2016/2017) and low red-backed vole years (2018/2020).

		Proportion of small mammal community	
Species	**Latin name**	**2016/2017**	**2018/2020**
Deer mouse	*Peromyscus maniculatus*	0.495	0.696
Red-backed vole	*Clethrionomys gapperi*	0.246	0.059
Woodland jumping mouse	*Napaeozapus insignis*	0.176	0.054
Eastern chipmunk	*Tamias striatus*	0.060	0.145
American red squirrel	*Tamiasciurus hudsonicus*	0.017	0.037
Meadow jumping mouse	*Zapus hudsonius*	<0.01	0
Meadow vole	*Microtus pennsylvanicus*	<0.01	<0.01
Northern flying squirrel	*Glaucomys sabrinus*	0	<0.01

Note: Shrew species were not tagged for individual identification and therefore were not included within the small mammal community proportion calculations.

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being much less abundant, red-backed voles and woodland jumping mice were 4.20 and 2.54 times more likely to be parasitized compared to deer mice (Appendix S2: Table S4). Notably, within sugar maple hardwood habitats, red-backed voles only had a sample size of four individuals. However, in white pine/red pine habitat where abundances were more balanced, similar results were observed, with red-backed voles and woodland jumping mice being 5.43 and 4.22 times more likely to be parasitized than deer mice. Alternatively, in white

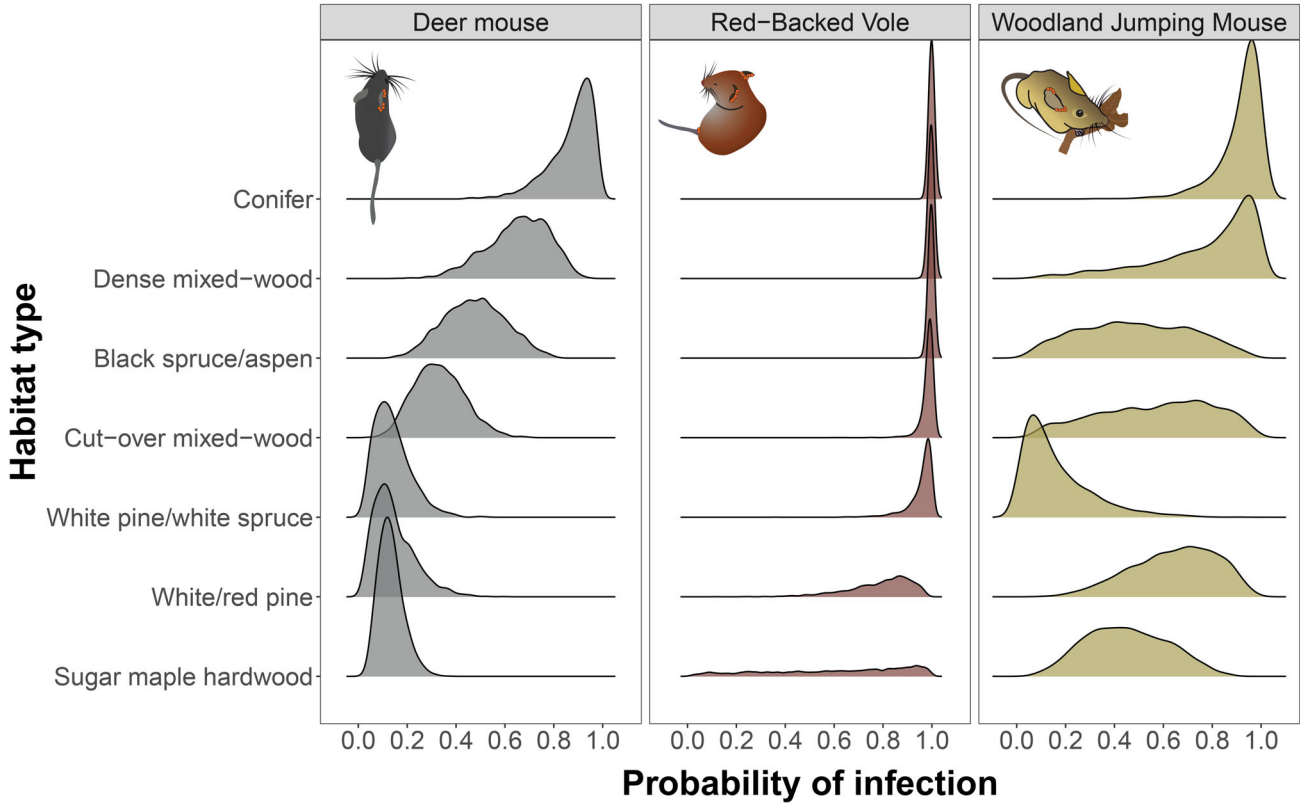

FIGURE 2 Probability of infection within deer mice, red-backed voles, woodland jumping mice, across seven different habitat types during high red-backed vole (high-RBV) years. Posterior distribution curves identify the range (width) and frequencies (height) of modeled infection probabilities within Bayesian model simulations. Within high-RBV years, red-backed voles composed approximately 25% of the total small mammal community across all habitats. Abundance and probabilities of infection across species and habitat can be seen in Table 2.

TABLE 2 Abundance (minimum number known alive) of deer mice, red-backed voles, and woodland jumping mice during high red-backed vole years (2016/2017) across seven different habitat types.

	Abundance		
Habitat type	**Deer mice**	**Red-backed voles**	**Woodland jumping mice**
Sugar maple hardwood	99 [0.12|0.038, 0.22]	4 [0.65|0.10, 0.99]	35 [0.44|0.13, 0.76]
Cut-over mixed wood	56 [0.32|0.13, 0.52]	22 [0.99|0.94, 1.00]	11 [0.59|0.13, 0.94]
Dense mixed wood	40 [0.66|0.41, 0.88]	38 [0.99|0.99, 1.00]	9 [0.84|0.31, 1.00]
Coniferous	15 [0.90|0.68, 0.99]	40 [0.99|0.99, 1.00]	17 [0.94|0.73, 1.00]
White pine/white spruce	40 [0.12|0.025, 0.29]	18 [0.97|0.84, 0.99]	13 [0.12|0.0040, 0.43]
Black spruce/aspen	45 [0.47|0.25, 0.72]	24 [0.99|0.99, 1.00]	17 [0.48|0.091, 0.88]
White pine/red pine	35 [0.12|0.019, 0.31]	26 [0.81|0.55, 0.98]	21 [0.66|0.32, 0.94]

Note: Values in brackets are the model-estimated mean probability of infection followed by lower and upper highest posterior densities (HPDs) for each species in respective habitats.

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pine/white spruce, red-backed voles were approximately seven times more likely to be parasitized compared to both deer mice and woodland jumping mice.

Infection probability during low-RBV years

In 2018 and 2020, red-backed vole abundances were low and small mammal communities were heavily dominated by deer mice. Woodland jumping mouse abundances were often too low to make meaningful comparisons in these trapping seasons. Similarly, red-backed voles were completely absent from sugar maple hardwood habitats, and only one individual was captured within white pine/red pine habitats, making comparisons within these habitats unreliable. Red-backed voles retained high levels of infection probability across habitats where present: conifer (97%), black spruce/aspen (97%), cut-over mixed wood (96%), dense mixed wood (90%), and white pine/white spruce (92%). Conversely, the probability of infection among deer mice across habitats was below 1% (Table 3; Appendix S1: Figure S1). Pairwise contrasts across these habitats between red-backed voles and deer mice identified a greater probability (0.90–0.96) of red-backed voles being infected compared to deer mice across all habitats except sugar maple hardwood and white pine/red pine; however, deer mice and woodland jumping mice showed little difference (Appendix S2: Table S5).

Association between red-backed vole abundance and infection probability

Red-backed voles (trend: 8.25, [HPD: 4.87, 11.52]), deer mice (trend: 5.44, [HPD: 3.49, 7.25]), and woodland jumping mice (trend: 9.54, [HPD: 6.28, 13.32]) all showed an increase in the probability of infection as the proportion of red-backed voles within the small mammal community increased (Figure 3). Comparatively, deer mice showed a shallower slope than woodland jumping mice (−4.08, [HPD: −8.23, −0.13]) as the proportion of red-backed voles increased within the small mammal community.

Body condition

For red-backed voles, the first component (eigenvalue 1.71) of the PCA explained 57.0% of the variance in the data, and loaded positively with hindfoot length (0.56), skull length (0.60), and skull width (0.57); it was therefore used as a proxy for the body size of red-backed voles. For deer mice, the first component (eigenvalue 1.36) of the PCA explained 45.2% of the variance in the data, loaded positively with hindfoot length (0.66), skull length (0.58), and skull width (0.48), and was used as a proxy for deer mouse body size.

No relationship was found when comparing the body mass of red-backed voles that were infected ($n = 65$) and uninfected ($n = 21$; −0.13, [HPD: −2.72, 2.65]; Figure 4). Female red-backed vole body mass was shown to be generally greater than that of males (2.44, [HPD: 0.76, 4.01]). No relationship was found between the body mass of deer mice and Trombiculid chigger infection when comparing infected ($n = 9$) and non-infected deer mice ($n = 79$; −0.19, [HPD: −1.71, 1.04]). No difference was identified in body mass between the sexes of deer mice (0.14, [HPD: −0.67, 0.99]). Similarly, no relationship was identified between body mass and Julian date within red-backed voles (trend: 0.049, [HPD: −0.038, 0.12]) and deer mice (trend: −0.0075, [HPD: −0.034, 0.20]).

TABLE 3 Abundance (minimum number known alive) of deer mice, red-backed voles, and woodland jumping mice during low red-backed vole years (2018/2020) across seven different habitat types.

	Abundance		
Habitat type	**Deer mice**	**Red-backed voles**	**Woodland jumping mice**
Sugar maple hardwood	74 [0.00|0, 0.000021]	0 [0.53|0.0015, 1.00]	0 [0.00|0.00, 0.66]
Cut-over mixed wood	67 [0.01|0.000024, 0.024]	4 [0.96|0.41, 1.00]	0 [0.00|0.00, 0.92]
Dense mixed wood	46 [0.00|0.00000040, 0.0048]	3 [0.90|0.11, 1.00]	0 [0.00|0.00, 0.86]
Coniferous	31 [0.01|0.000017, 0.056]	5 [0.97|0.70, 1.00]	4 [0.00|0.00, 0.10]
White pine/white spruce	49 [0.00|0.00000030, 0.0074]	8 [0.92|0.40, 1.00]	3 [0.00|0.00, 0.031]
Black spruce/aspen	56 [0.00|0.0000020, 0.0071]	11 [0.97|0.70, 1.00]	13 [0.00|0.00, 0.0018]
White pine/red pine	40 [0.00|0.00, 0.0053]	1 [0.42|0.0000047, 0.99]	9 [0.00|0.00, 0.0016]

Note: Values in brackets are the model-estimated mean probability of infection followed by the lower and upper highest posterior densities (HPDs) for each species in respective habitats.

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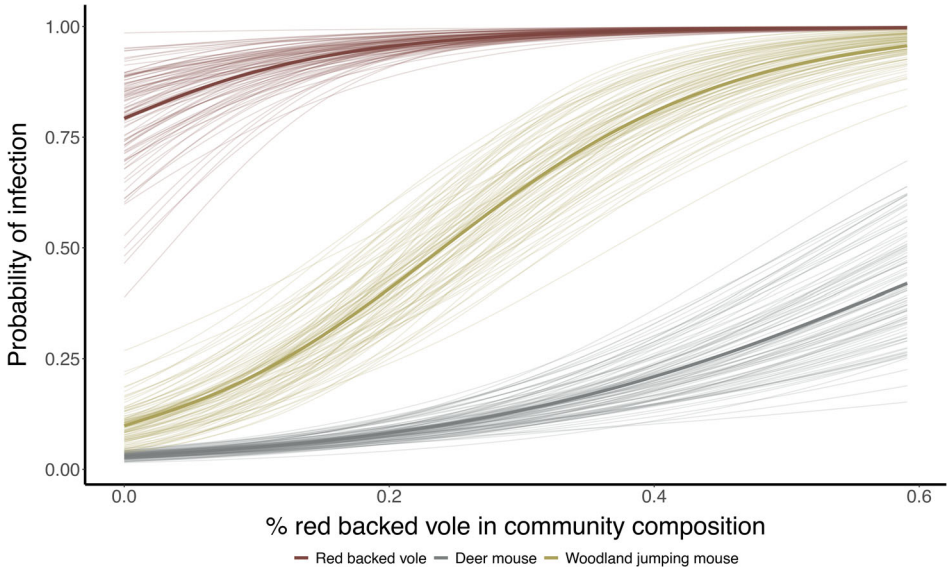

FIGURE 3 Probability of infection within deer mice, red-backed voles, and woodland jumping mice as the percentage of red-backed voles within the small mammal community changes.

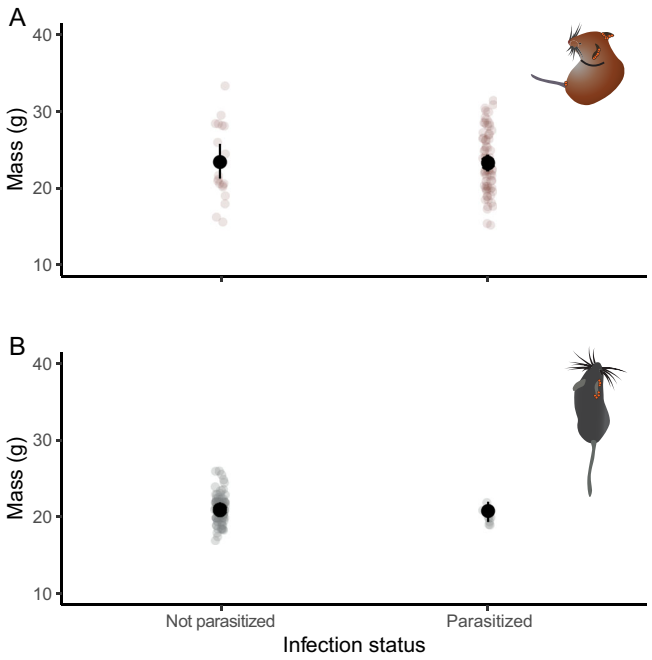

FIGURE 4 Body mass of (A) red-backed voles and (B) deer mice measured over infection stage. Measurements included the body condition of individuals in parasitized and not parasitized groups. Both red-backed voles (95% highest posterior density regions [HPD: −2.65, 2.72]; probability of direction = 46%), and deer mice ([HPD: −1.04, 1.71]; probability of direction = 40%), showed no differences in body condition across different infection status groups. Bars represent HPDs. The mean mass of red-backed voles that were never infected and infected was 23.35 ($n = 21$, [HPD: 21.20, 25.71]) and 23.25 ($n = 65$, [HPD: 22.18, 24.27]), respectively. The mean mass of deer mice that were never infected and infected was 21.05 ($n = 79$, [HPD: 20.65, 21.50]) and 20.87 ($n = 9$, [HPD: 19.44, 22.07]), respectively.

DISCUSSION

Host–parasite dynamics within multi-host systems are often complex yet poorly understood, particularly when examining interactions across multiple environments. Our study compared the infection probability of known Trombiculid chiggers among three different small mammal species including deer mice, red-backed voles, and woodland jumping mice across seven different habitat types. Red-backed voles were identified as candidates for primary hosts, showing consistently high infection rates across habitats and years. Additionally, chiggers were more prevalent among all species when red-backed voles comprised a larger proportion of the small mammal community. Chigger prevalence also seemed to be influenced by habitat type; however, this pattern may have been driven by red-backed vole abundances within respective habitats. Additionally, no correlation was found between infection and body mass.

Red-backed voles had consistently higher infection probabilities across habitats and years compared to woodland jumping mice and deer mice. When red-backed voles were abundant within small mammal communities, the probability of infection was >97% within most habitats. Comparatively, the probability of infection among deer mice (12%–90%) and woodland jumping mice (12%–94%) in the same habitats were much more variable, with higher probability associated with habitats with higher red-backed vole abundances. Field observations also describe red-backed voles typically having higher infection intensities (density of chiggers; Elliott Schmidt, Jasmine Veitch, Arianne Sawyer, personal

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observations); however, the density was not scored or quantitatively examined within this study. The role of red-backed voles as primary hosts to Trombiculid chiggers may be partly due to shared habitat among parasites and hosts. Active deutonymphs and free-living adult Trombiculid mites reside in soil and leaf litter (Alkathiry et al., 2022; Morand et al., 2006) where red-backed voles frequently create nesting sites. The need to forage within the leaf litter, interspecific interactions, and potential use of shared trails and habitats could serve as contact points for infection among secondary host species (Adrus et al., 2021; Jameson & Brennan, 1957). Host species have previously been shown to possess different relationships with mites in terms of infection intensity and prevalence (Antonovskaia et al., 2024). Within a similar host–parasite system in southwest China, Yunnan red-backed voles (*Eothenomys miletus*) were also found to have greater probabilities of infection from chiggers compared to local field mouse (*Apodemus chevrieri*) populations (Chen et al., 2022). Concurrently, greater infection prevalence of *Neotrombicula autumnalis* chiggers was recorded among bank voles (*Clethrionomys glareolus*) compared to wood mice (*Apodemus sylvaticus*) in the Netherlands (van Bronswijk, 1977). Despite vole species often showing greater infection prevalence over cohabitating small mammal host species, a detailed understanding of the mechanisms driving disparity between host species, such as host behavior and habitat, remains to be thoroughly investigated.

Increased relative abundance of red-backed voles within the small mammal community was correlated with increased probabilities of infection for all species. The probability of infection was higher in high-RBV years compared to low-RBV years, despite both high- and low-RBV possessing comparable overall small mammal abundances. This trend in the data presents further evidence that red-backed voles are primary hosts for Trombiculid chiggers that may spread via secondary contact or shared resources among hosts (e.g., tunnels, burrows; Jameson & Brennan, 1957). Furthermore, within the low-RBV years, red-backed voles' infection probability remained high. In contrast, deer mice, which composed the majority (69%) of the small mammal community in low-RBV years, had low probabilities of infection across habitats. The fluctuating patterns of red-backed vole abundances within the examined small mammal community is not well understood. When attempting to link red-backed vole populations with masting year of trees, previous studies have shown mixed results (Boonstra & Krebs, 2011). A positive link was identified between red-backed vole abundance and white pine seed (22 years of data; Elias et al., 2006), as well as red maple seed crops (3 years of data; Schnurr et al., 2014). However, other studies failed to identify any relationship between red-backed vole abundance and red oak, red maples, or white pine crops (10 years of data; McCracken et al., 1999).

The probability of infection was highest across coniferous, dense mixed wood, cut-over mixed wood, and black spruce/aspen. However, these trends may have been driven by the abundance of red-backed voles within small mammal communities. In contrast, only sugar maple hardwood, white pine/white spruce, and white pine/red pine habitats displayed low probabilities of Trombiculid mite infection, particularly among secondary hosts. While red-backed vole abundance can explain the low probability of infection within sugar maple hardwood, it does not explain the lower probabilities of infection within white pine/white spruce and white pine/red pine habitats, suggesting soil characteristics may play a role in chigger abundance. The properties of soil habitats and leaf litter are reflective of the requirements for the active, free-living adult life stage of mites (Alkathiry et al., 2022; Jameson & Brennan, 1957; Morand et al., 2006) within the soil or leaf litter that predate soft-bodied arthropods or eggs of small arthropods (Shatrov & Kudryashova, 2006). Without further analysis of soil properties and associated leaf litter biodiversity, it remains challenging to provide a mechanism driving the scarcity of Trombiculid chiggers within sugar maple hardwood and white/red pine habitats. A further understanding of soil properties including soil moisture, temperature, and microinvertebrate biodiversity, could provide further insight into environmental properties that are potentially favorable to Trombiculid chiggers. Additionally, little is known about adult mite life stages as adults are rarely found in natural habitats (Morand et al., 2006). Habitat preference among chiggers has previously been identified among mite species parasitizing rats in Papua New Guinea and the Philippines (Luzon; Mohr, 1947), however, the difference in habitat types between the studies makes it difficult to draw parallels.

Environmental variables play an important role within the life cycle of chiggers. Despite data being collected over four different field seasons, the date Trombiculid chiggers were first observed varied by just 3 days, suggesting that environmental conditions that occur over June and July (highest temperatures and levels of precipitation; Environment and Climate Change Canada, 2026) may be responsible for triggering chigger emergence. Previous evidence suggests that environmental conditions, particularly warmer temperatures and increased humidity, represent favorable environmental conditions for development as well as host abundance (Maaz et al., 2018; Wale et al., 2023). Results from this study support this hypothesis, as within temperate regions of the northern hemisphere, July represents the warmest time of the year and coincides with elevated levels of rainfall and humidity.

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However, without sampling in similar habitats across larger geographical distances and different environmental conditions, it is difficult to determine which environmental conditions act as cues for Trombiculid chigger emergence.

Body mass of deer mice and red-backed voles showed no correlation with infection. Previous studies within a similar system found little or weak evidence of macroparasites influencing body mass (Gorrell & Schulte-Hostedde, 2008; Perez-Orella & Schulte-Hostedde, 2005); however, previous parasite removal studies have found reproductive benefits when parasite loads are reduced (Neuhaus, 2003; Patterson et al., 2013). A previous study examining Trombiculid infection on red-backed voles with the Apostle Island archipelago (Wisconsin, USA) determined infection prevalence to be best predicted by host density and body condition, suggesting that individuals with poor body condition displayed greater probability of Trombiculid infection (Mallinger et al., 2022). Trombiculid chiggers parasitize hosts for a short period of time (estimated to be 1–2 weeks), which could explain the lack of a relationship between presence of infection and body mass in this study. Additionally, within this study, infection intensity was not examined, which may provide further insight into the relationship between Trombiculid chigger infection and host body mass.

Infection from Trombiculid chigger parasites is influenced by a combination of factors including host species, and environmental and climate factors. Within this study, the proximity of sites removed the influence of climatic factors, allowing greater focus on host species and environmental variables. Evidence suggests that red-backed voles are the primary host of Trombiculid chiggers, as they retained high probabilities of infection across habitats and years. Additionally, red-backed vole abundance within the small mammal community was correlated with increased infection within all host species. White pine/white spruce and white pine/red pine habitats had lower probabilities of infection among hosts, despite possessing similar abundances of red-backed voles as other habitats. This suggests that soil or leaf litter characteristics may further influence the presence of Trombiculid chiggers. This pattern may be an indication of different microhabitat use among hosts within these habitat types, or potentially lower Trombiculid densities due to unfavorable soil conditions.

AUTHOR CONTRIBUTIONS

Elliott Schmidt: Conceptualization; methodology; validation; formal analysis; investigation; data curation; writing—original draft; writing—review and editing; visualization; project administration. **Jasmine S. M. Veitch:** Formal analysis; investigation; writing—original draft; writing—review and editing; project administration. **Hannah V. Watkins:** Methodology; validation; formal analysis; writing—review and editing; visualization. **Arianne Sawyer:** Conceptualization; methodology; investigation; writing—original draft. **Jeff Bowman:** Resources; writing—review and editing; supervision; project administration; funding acquisition. **Albrecht I. Schulte-Hostedde:** Conceptualization; methodology; writing—review and editing; supervision; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Schmidt et al., 2026) are available from Dryad: https://doi.org/10.5061/dryad.v6wwpzhc4.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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