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Abstract

Lyme disease occurrence has increased rapidly in Canada in the past five years. The emergence of Lyme disease coincides with the range expansion of the primary host, the white-footed mouse (*Peromyscus leucopus* (Rafinesque, 1818)), in the region. We evaluated the effects of stress level, parasite load and forest patch characteristics on *P. leucopus* movement pattern. We found negative relations between on the one hand the adrenal gland size, a proxy for stress level, and population density, and on the other hand, home range area and movement rate of mouse individuals, suggesting that stressed mice cannot maintain a large home range. Population density was also related with excursion (outside the forest patch) and exploration (outside the home range) rates, either directly or through its effect on home range area and movement rate. Finally, movement rate and excursion rate were lower in individuals infested with more black-legged ticks. Our results have implication for the mechanism of Lyme disease emergence in the region: individual hosts that carry more ticks and are thus more likely to be spreading the bacterium responsible for Lyme disease are dispersing less than tick-free individuals. Lyme disease monitoring should thus consider how the characteristics of host communities modulate the spread of the disease across the landscape.

Key-words

Black-legged tick, dispersal, home range, *Ixodes scapularis*, *Peromyscus leucopus*, stress, white-footed mouse

Introduction

Lyme disease is an infectious zoonotic disease and is emerging in North America (Ostfeld (2011). In this region, the causing agent is the spirochete bacterium *Borrelia burgdorferi* (Johnson et al. 1984), which is transmitted to a number of vertebrate hosts through the bite of the black-legged tick (*Ixodes scapularis* Say 1821). The white-footed mouse (*Peromyscus leucopus*) is considered the main reservoir for the disease in Eastern North America, with a reservoir competence over 90% (Allan et al. 2003; Keesing et al. 2009; Ogden and Tsao 2009; Ostfeld 2009). Because tick vectors are very limited in their movement, they rely almost entirely on their hosts to disperse. The movement pattern of *P. leucopus* mice is thus expected to have a significant effect on the pattern of emergence and spread of Lyme disease in a region.

In recent years there has been a northward range shift and increase in abundance of the white-footed mouse in Québec (Roy-Dufresne et al. 2013). This expansion is expected to facilitate the emergence and spread of Lyme disease in areas where both the main reservoir and tick vector become more abundant (Ogden et al. 2009; Simon et al. 2014). Forest habitat is essential to the survival and reproduction of the white-footed mouse (Zollner and Lima 1999), and its movement across the landscape is constrained by geographical barriers such as large roads and rivers (Rogic et al. 2013; Marrotte et al. 2014). Habitat fragmentation has been linked to an increase in prevalence of Lyme disease (Keesing et al. 2009), as host species diversity is reduced but the

relative abundance of the white-footed mouse is larger in fragmented habitats (Van Buskirk and Ostfeld 1995; Ostfeld and Keesing 2000; Ostfeld 2009). As a result, the proportion of infected ticks feeding on *P. leucopus* increases, due to the lack or lower abundance of other small mammal hosts that are either less competent reservoirs for the disease, or better at removing ticks while grooming (Keesing et al. 2009). Smaller forest patches also favours the generalist mice over more specialist species, and many studies reported high densities of *P. leucopus* in small forest fragments (Nupp and Swihart 1996, 1998; Krohne and Hoch 1999; Wilder and Meikle 2005; Tanner et al. 2010). At a larger scale, movement pattern of a host species may vary across its distribution range, with individuals from populations at the leading edge of its distribution range having larger home range area and dispersal rate than in core populations (Lindstedt et al. 1986; Dytham 2009).

Beside habitat quality and landscape fragmentation, community-level interactions may alter the density and dispersal rate of *P. leucopus* populations. The white-footed mouse is a territorial species (Metzgar 1973; Lackey et al. 1985; Wolff and Lundy 1985; Xia and Millar 1989; Wolff 1992; Krohne and Hoch 1999; Barko et al. 2003), which defends its home range (Lackey et al. 1985; Nupp and Swihart 1996). Home range size tends to be smaller in areas with increased population density, due to increased intra-specific competition (Krohne and Hoch 1999; Wilder and Meikle 2005).

A number of physiological characteristics and behaviours may also alter the movement pattern of mouse hosts individuals and ticks feeding on them, and studies have reported the stressful effect of high population density in mice (Christian 1956; Davis and Christian 1957; Wilder and Meikle 2005) and other mammals (e.g. Dettmer et al. 2014). Stressed individuals have been reported to either engage more actively in locomotion or to reduce it greatly (Barnum

et al. 1992; Belthoff and Dufty 1998; Oitzl et al. 2010; Nemati et al. 2013). Stress level in turn, may vary with parasite load (Brown and Fuller 2006; Schwanz 2006; Bauer et al. 2013, but see Crespi et al. 2013). The dispersal rate of an individual depends on several individual-level factors (Stenseth and Lidicker 1992), including age (Hansson 1992), sex (Wolff 1992), reproductive status (Gliwicz 1992), personality (Dingemanse et al. 2003), and external factors such as the weather (Rizkalla and Swihart 2007), or the type of matrix through which it would disperse (Mabry and Stamps 2008; Linzey et al. 2012; Marrotte et al. 2014). Juveniles are the individuals that most often leave their natal home range (Wolff 1992) and engage in dispersal movements (Hansson 1992; Sinclair 1992; Wolff 1992; Bollinger et al. 1993; Massot and Clobert 1995).

A series of factors operating from the continental scale down to the individual are thus determining the movement and dispersal behaviour of a species (Figure 1) and here, we apply this framework to the white-footed mouse and the role it plays in the emergence of Lyme disease in Southern Québec. The Montérégie area south of Montréal is mainly agricultural with forest patches of different area scattered throughout the landscape (Marrotte et al. 2014). The white-footed mouse is expanding north within this fragmented landscape (Ledevin and Millien 2013; Simon et al. 2014), and a better understanding of the movement and dispersal pattern of this species will help identify areas of higher risk for Lyme disease. We estimated stress level and parasite load in a number of white-footed mouse individuals to evaluate their relation with movement pattern within the fragmented landscape. We tested the hypothesis that a higher ectoparasite burden will impede the movement rate of their *P. leucopus* host. We also evaluated the relations between body condition and stress level on movement pattern in these mice. We tested the hypothesis that stress level is higher in individuals with reduced movement rate and home range area.

Materials and methods

Field methods and sampling

The study sites were located in forest fragments in the Montérégie region of Southern Québec, Canada, between 45°48' N and 45°56' N (Table S1), in an area covering approximately 0.29 km². We used the Système d'information écoforestière (MRNF 2004) database to extract patch area and edge proportion (ratio of the forest patch area to its perimeter) for each of these forest fragments (Table S1).

Small mammals were captured at six sites during the summers of 2012 and 2013. We used Sherman live traps baited with a mixture of peanut butter and oatmeal set in grids of 120 traps (24 x 5 traps placed 10 m apart) right before dusk and checked right after dawn the next morning. Trapping occurred at each site for three consecutive nights. Weight, external measurements and reproductive status were recorded on all captured individuals of *P. leucopus*, as well as the number of ectoparasites (ticks, fleas, lice and warble pores indicating the presence of *Cuterebra* sp. larvae). For each site, we estimated small mammal species diversity (Shannon index) and the abundance of *P. leucopus* (number of *P. leucopus* captured per 100 m²).

Upon capture, *P. leucopus* individuals were marked with an ear tag (The national Band and Tag company: model 1005s1), and fitted with a collar (BD-2C from Holohil systems Ltd). Only individuals of 15 grams or more were fitted with a collar and younger individuals were released immediately upon capture. The weight of the collar (1.1 g) thus represented a maximum of 7.3% of the body mass of the mouse individual. Once fitted with a collar, the individual was released after 40 minutes of observation to ensure that it did not show any sign of discomfort or distress.

Mice were tracked starting at dusk until 8 hours after sunset (Hicks et al. 1998), and bearings were taken every 4 or 5 minutes, depending on the number of individuals tracked simultaneously. We obtained the location of each animal every 20 minutes by immediate triangulation (Harris et al. 1990) using three 3-element Yagi antennas with an error of 1 meter. In 2012, mice were tracked at 6 sites during 4 non-consecutive nights for 2 weeks starting on July 23rd. In 2013 we reduced the number of sites to four, but increased the tracking period to four weeks, starting on July 15th.

Mice were then re-captured by searching for diurnal refugees during the afternoon and placing Sherman traps surrounding the refuge overnight. Upon recapture, individuals were euthanized and brought back to the laboratory. Both adrenal glands were sampled on each individual and kept in 95% ethanol for four weeks before being dried at 90°C for 24h. The mass of each adrenal gland was then measured with a precision scale (0.0001g precision), and we calculated the average mass of both glands for each individual. Adrenal gland hyperplasia and hypertrophy provide an indirect estimate of glucocorticoids levels in an individual (Christian 1956; Davis and Christian 1957; Sapolsky et al. 2000; Ulrich-Lai et al. 2006), and of the frequency and duration during which an organism has been exposed to stressors in its environment. We used the adrenal gland size as a proxy for stress level because it provides a measurement of prolonged production of glucocorticoids (Davis and Christian 1957; Sapolsky et al. 2000). The body condition index (residual of the linear regression between log-transformed body mass and head-and-body length) was used as a proxy for the general health status of each individual (Jakob et al. 1996). All external measurements were taken using the same protocol in the field. Body length was measured using a ruler, while body mass was measured with a Pesola scale to the nearest 0.5 g.

All procedures were approved by the McGill University Animal Care Committee (McGill AUP#5420) and the government of Québec (SEG permits 2012-07-16-1417-16-17-SF and 2013-07-04-1530-04-14-16-17-SF).

Movement data

We estimated the geographic coordinates of each location of individual mouse using the location of the antennas and each of the simultaneous bearings using the LOAS 4.0 software (Ecological Software Solutions LLC). We then used BIOTAS 2.0 (Ecological Software Solutions LLC) to estimate the home range area of each individual. Following Millspaugh and Marzluff (2001), we used an 80% fixed kernel, the area where the probability of finding a given individual is 80%, to estimate home range area. We estimated the nightly activity of each individual with movement rate (the average distance moved between bearings in a night divided by the time interval between those bearings), the exploratory movements of each individual (the proportion of bearings that fell outside the home range) and excursions (the proportion of bearings that fell outside the forest patch into other habitats).

Statistical analyses

We used linear mixed effects models to estimate the effect of forest patch characteristics, parasite load, body condition and stress level on the movement pattern of *P. leucopus* using the package *nlme* (Pinheiro et al. 2013) in R version 3.0.3 (R Core Team 2014). We first tested for the presence of sexual dimorphism in all response variables (home range area, movement rate, proportions of exploration and excursion). We included explanatory variables as fixed factors,

and site and year as random factors in our models. We ran distinct models for each movement variable and first checked for the independence of all fixed factors using the *vif* function in the *HH* package (Heiberger 2015) in R. We simplified the models by backwards selection using the function *drop1* from the *stats* package (R Core Team 2014). For each model, we retained the model with the lowest Akaike Information Criterion (AIC) as the final model.

We used forest patch area and the proportion of edge to describe the physical characteristics of the patch and as a proxy for habitat quality for the mouse (Simon et al. 2014). We used the diversity of small mammals in a patch and the abundance of *P. leucopus* to estimate competition pressure. We determined breeding status as breeding (pregnant or perforated vagina in females or dropped testes in males) versus non-breeding for all mouse individuals. Breeding status and parasite load (number of ticks, bot-fly larvae, fleas and lice) were also included as explanatory factors, as well as the adrenal gland mass and body condition index.

We then used structural equation modeling using all four movement variables and explanatory variables (stress, parasites and patch characteristics) to further explore the pathways in our system simultaneously. We included explanatory variables that were found to be significant in previous analyses. Specifically, we included the mass of the adrenal gland and body condition as physiological variables, the count of ticks to evaluate the effect of parasite load, and small mammal species richness and white-footed mouse density as patch-level characteristics. We evaluated the model significance and calculated path coefficients and their significance level using the package *lavaan* (Rosseel 2012) in R.

Results

We captured six species of small mammals (*Peromyscus leucopus*, *Peromyscus maniculatus* (Wagner 1845), *Blarina brevicauda* (Say 1823), *Myodes gapperi* (Vigors 1830), *Sorex cinereus* (Kerr 1792) and *Napaeozaous insignis* (Miller 1891)) and species richness at a given site ranged from 2 to 5.

Species diversity increased with forest patch area (Pearson $r = 0.62$, $p < 0.0001$, $n = 32$) and perimeter (Pearson $r = 0.61$, $p < 0.0002$, $n = 32$), and decreased with proportion of edge habitat (Pearson $r = -0.60$, $p < 0.0002$, $n = 32$). We thus kept species diversity as an explanatory variable, but excluded patch area, perimeter and proportion of edge habitat in further analyses.

Thirty-two white-footed mouse individuals (15 males and 17 females) were radio-tracked (Table 1). We were able to recapture 17 mouse individuals and to recover an additional 8 collars. Five other collars were located but inaccessible, and the signal of the last two collars had disappeared. The recovered collars showed high degree of wearing (to a similar degree than in the recaptured mice), suggesting that the collars had been on the mouse for a long time. One of the collars was found with the carcass of the mouse and two other collars exhibited predation signs. Mortality rate in the white-footed mouse is generally 50% after one month in the wild (Collins and Kays 2014), which fits the mortality rate in our study.

Stress level and parasite load

The adrenal gland mass ranged from 0.0008 to 0.0019g (mean = 0.00125g, $sd = 0.00034$) and did not differ with breeding status ($t = -0.69$, $p = 0.51$, $n = 17$) or sex ($t = -0.62$, $p = 0.56$, $n = 17$). Body condition ranged from 0 to 0.60 and averaged 0.28 ($sd = 0.14$) and did not differ between

sex ($t = -0.012$, $p = 0.99$, $n = 32$). Breeding mice tended to have a larger body condition index than non-breeding mice ($t = -2.89$, $p < 0.01$, $n = 32$). The adrenal gland size was not correlated with body condition (Pearson $r = 0.23$, $p = 0.37$, $n = 17$) and there was no effect of patch-level characteristics (small mammal diversity, abundance of *P. leucopus*, forest patch area and proportion of edge habitat) on the adrenal gland size or on body condition (Table S3).

Fourteen out of our 32 individuals of white-footed mouse were free of ectoparasite upon capture. A small proportion of mice (5 out of 32) were infested with black-legged ticks, with a tick burden ranging from 0 to 11 (average tick burden per individual of 4.8). All the ticks collected on mice were larvae, except for one nymph. Forty percent of the mice carried botfly larvae, some of them being infested with multiple larvae (up to four). Fleas (1 to 3 fleas per individual) and lice (1 to 11 per individual) were detected in 15% of the mice.

Movement pattern

Home range area was on average 7605 m², ranging from 792 to 20730 m² (Table 1), and it did not significantly differ between males and females ($t = 0.14$, $p = 0.89$, $n = 32$). The maximum distance moved per night by an individual varied greatly, from as low as 48 meters up to 1.9 km in a single night (Table 1). The average movement rate per mouse ranged from 1.8 to 7.3, and was on average 3.6 m.min⁻¹. There was no significant difference in movement rate between males and females ($t = -0.93$, $p = 0.36$, $n = 32$). The proportion of exploratory movements outside the home range varied between 1% and 50% with an average of 22.2% (Table 1) and did not differ between sexes ($t = -0.79$, $p = 0.43$, $n = 32$). The proportion of excursions outside the

forest patch ranged from 0 to 55% and was on average 11% (Table 1). No difference was detected between sexes ($t = 0.33$, $p = 0.74$, $n = 32$).

Individual models of movement pattern

We first run a series of linear models on the four movement variables (home range area, movement rate, exploration and excursion rates) separately. The fixed factors included in our models were species richness, small mammal diversity, the abundance of *P. leucopus*, body condition, adrenal gland mass, breeding status, and parasite counts (number of ticks, fleas, lice and botfly larvae). The variance inflation factors of these variables were all lower than 5, which justify keeping these variables in further models (Miles 2005). We were able to measure the mass of the adrenal gland only for the 17 mice we recovered, so sample size was 17 in all these models. We first included all the factors in our models (Table S4) and present below the four final models, after simplification by backward selection.

After simplification of the model for home range area, the factors kept in the final model were *P. leucopus* density, adrenal gland mass, body condition, breeding status, flea, tick and lice burdens (Table 2). The adrenal gland mass had a negative effect on home range area, and no other factor was significant. The final model for movement rate included the mass of the adrenal gland, body condition, breeding status as well as the number of fleas and botfly larvae (Table 2). Mice with larger adrenal glands and a lower body condition index tended to move less. Mice infested with botfly larvae had significantly larger movement rate, but individuals moved less when carrying a large number of fleas (Table 2). None of the factors included in our final model had a significant effect on exploration rate. The final model for excursion rate included the mass

of the adrenal gland, *P. leucopus* density and tick burden. Of these variables, only ticks had a significant negative effect on excursion rate (Table 2).

In sum, the adrenal gland size had a negative effect on home range area and movement rate, while body condition had a positive effect on movement rate. Mice infested with more ticks tended to move less outside the forest patch (excursion rate).

Exploratory model

We then used a structural equation modeling (SEM) approach to explore the effect of individual- and patch-level characteristics on movement pattern, while taking into account simultaneously the four types of movement variables and all pathways between them (Fig. 2). We used the results of previous individual analyses to build this more comprehensive model. While the strength of the coefficients (i.e. their value) or their significance level may differ between these two approaches, there was no major difference in the nature of the relations (i.e. the sign of the coefficients) we obtained using either individual linear models, or the SEM.

While we did not detect any factor that had a significant effect on exploration rate (outside the home range area) taken alone (individual model above), exploration rate was positively correlated with movement rate ($\rho = 0.39$, $p < 0.026$) and negatively correlated with home range area ($\rho = -0.65$, $p < 0.0001$), so exploration rate was kept in the SEM model (Fig. 2). Our model was not rejected ($p = 0.47$, Table 3). The variation in home range area depended on individual level factors, such as the adrenal gland mass and body condition. Individuals with a larger home range tended to have smaller adrenal glands and larger body condition index. Home range area and movement rate were both negatively related with white-footed mouse density. Individuals with smaller adrenal gland mass and lower tick load tended to have larger movement

rate. The proportion of exploration was positively related with movement rate and smaller home range area. The proportion of excursions increased with *P. leucopus* density, and home range area.

Discussion

Stress level and parasite load

Parasite load may have a significant or no effect on stress, depending on the intensity, frequency and type of parasite burden, as well as their combination with other stressors (Sapolsky 2004; Tanner et al. 2010; Clinchy et al. 2011). In natural environments, parasites may not have a strong effect (Burns et al. 2005; Réale et al. 2010), especially in small fast-paced animals (St. Juliana et al. 2014), relative to other factors such as competition, predation pressure, habitat quality or weather variables (Christian 1956; Ben-Nathan and Feuerstein 1990; Laundré et al. 2001; Monclús et al. 2009; Romero et al. 2009; Réale et al. 2010; Addis et al. 2011; Brown 2013). Here, we also found no significant relation between the adrenal gland mass and parasite burden, confirming these later results for *P. leucopus*. Furthermore, changes in glucocorticoid level are driven by the interaction of several ecological, physiological and behavioural factors that we did not measure directly here (von Holst 1998; Charmandari et al. 2005; Lupien et al. 2009), including food and shelter availability (Metzgar 1967; Love et al. 2013), internal parasite load (Brown and Fuller 2006), genetic differentiation (Creel et al. 2013), as well as abiotic variables (Ben-Nathan and Feuerstein 1990).

Home range and movement rate

Our estimates of home range area are larger than most values reported for *P. leucopus* (2780 m² on average, ranging from 590 to 18210 m²; Table S2). The type of data (trapping data versus radio-telemetry), or the protocol used to track animals (the weight of the collar, the type of transmitter used or the frequency of tracking) can influence home range area estimates (Madison 1977; Ribble et al. 2002), and home ranges estimated from radio-telemetry have been reported to be larger than home ranges estimated from trapping data (Ribble et al. 2002). The method we used provided real time and accurate measurements on the locations of each animal at least three times each hour for at least 6 hours per night, with light-weight collars (about 5% of the mouse weight). Interestingly, our results are in line with previous work on range estimates for *P. leucopus* in Southern Québec (12600 m², Mineau and Madison 1977) and confirm the hypothesis that individuals from populations at the leading edge of the northern limit of a species range may have increased dispersal rate, and therefore larger home range areas.

We found that individuals with larger adrenal glands concentrated their activity in smaller areas and tended to move at a smaller rate, supporting the hypothesis that stressed individuals engage less actively in locomotion (Barnum et al. 1992; Belthoff and Dufty 1998; Oitzl et al. 2010; Nemati et al. 2013). We also found that body condition was positively related with home range area. Body condition is correlated with the energetic state of an organism (Schulte-Hostedde et al. 2005), therefore, individuals with a better body condition have better endurance and can forage more efficiently than their congeners (McNab 1963).

Home range area decreased in forest patches with higher density of white-footed mice at our study sites. Studies have reported the stressful effect of high population density in mice (Christian 1956; Davis and Christian 1957; Wilder and Meikle 2005) and other mammals (e.g. Dettmer et al. 2014). Even though we did not find a direct link between mouse density and the adrenal gland size, the adrenal gland size and mouse density negative relationships with both home range area and movement rate support this hypothesis. Altogether, our findings indicate that stressed individuals in heavily populated areas tend to engage less into locomotion, most likely to avoid aggression by conspecifics (Wolff 1985; Wolf and Batzli 2004).

Increased movement led to more exposure to parasites in the Siberian chipmunk (*Tamias sibiricus*) (Boyer et al. 2010). Interestingly, movement pattern in our study individuals was related with parasite load, where increased loads of ticks decreased the movement rate of the individual, as well as their excursion rate. Animals with higher tick loads have not been reported before to have an increased metabolic demand or to be significantly stressed (Barnard and Behnke 2006; Hersh et al. 2013). Accordingly, our results indicate that larger tick-load does not lead to an increased movement rate, as it would be expected if foraging needs of these individuals were increased.

Dispersal

We found that breeding status or sex did not have any effect on the propensity to forage outside the home range in the white-footed mouse. However, we did not fit any juvenile individual (below 15g) with a collar, and may have thus missed those individuals that are the most prone to dispersal.

We observed that population density was positively related with excursive behaviours in *P. leucopus*, while animals with a larger excursion rate also had a larger home range. Home range area has been positively correlated with dispersal (Trehella et al. 1988; Bowman et al. 2002), and our results are in line with these studies, as an excursive movement is necessary for dispersal beyond the limits of the forest.

At our study sites, excursions did not depend on the type of habitat and occurred in mowed lawn, orchards, tall grasses, crop field or clearings. Several authors have also observed *P. leucopus* individuals moving outside the forest patches through edge rows (Merriam and Lanoue 1990; Wilder and Meikle 2006) and tall crop fields (Cummings and Vessey 1994; Wolf and Batzli 2002, 2004; Marrotte et al. 2014), observations that were confirmed in our study. Individuals performing excursions towards crop fields were very common, and wherever available, they would be used to forage at night.

Movement outside the home range of an animal is often referred as an exploratory movement or commuting movement (McReynolds 1962; Jedrzejewski et al. 2001; Dingemanse et al. 2002). This type of movements allows for information gathering that can be used to track changes in the environment that eventually will have consequences on the behaviour of an individual, such as a shift or change in home range (Archer and Birke 1983). Exploration rate in our model was positively related with movement rate and negatively related with home range area. The later suggests that organisms with larger home range have more resources available in their own home range, therefore have a lower need for leaving it to engage in commuting trips (Stickel 1968), whereas those with smaller home range need to engage more often in exploration movements to look for resources that may not be available in their own home range (Stickel 1968; Archer and

Birke 1983; Wolf 1985), or to look for new areas on which they can expand their small home range (Doak et al. 1992; Gliwicz 1992; Ferriere et al. 2000; Nathan 2001).

Our study also indicated that animals that move more and faster are more likely to perform exploratory movements than those who have lower movement rate, a required feature for an animal exploring for resources or dispersing (McShea and Madison 1992; Maier 2002;). The opposite effects of home range area and movement rate on exploratory rate indicate that exploration will be engaged through increased locomotion in situations where the home range area is not sufficient to supply the requirements of an individual.

Conclusion

The white-footed mouse is a generalist species currently increasing its range and most likely to continue to do so in the current context of changing climate (Roy-Dufresne et al. 2013). The constant tracking for extended periods of time we conducted here revealed activity patterns that had not been often seen in the wild, including larger home range, real time tracking outside forest patches and empirical evidence for the relation between stress level and movement pattern. White-footed mouse individuals were capable of very long movements in a single night, and there were very few habitats it avoided. We did not detect any effect of most parasites on the size of the adrenal gland in the individuals we tracked in the field, nor on their movement pattern with the exception of a negative relation between tick load and movement rate and excursion rate. While stemming from relatively limited data, our result suggests a decrease in mobility that may decrease the chance of a mouse with large tick-burden to expand or change its home range and a decreased chance for a mouse to be parasitized by ticks when foraging only within its

home range. We also found that the population density of the white-footed mouse played a major role in regulating individual home range area, movement, and excursion rates. Population density, which is modulated by habitat quality within the patch and the type of habitat surrounding a forest patch (Simon et al. 2014), may thus be a good predictor of sites where individuals have a higher chance of engaging into a dispersal movement and entering in contact with people (Fig. 1).

Given the central role of the white-footed mouse in the transmission cycle of Lyme disease in eastern North-America, our findings have implications for the prediction of the rate of spread of Lyme disease in a region where it is currently rapidly emerging. We conclude that in addition to landscape and habitat variables, individual traits affecting the movement and dispersal of the white-footed mouse, should be taken into account to better estimate the role of this species in spreading the pathogen to tick vectors and communities of hosts found across the landscape. This is an important outcome of our work, since a better understanding of the dispersal behaviour of the white-footed mouse is key for predicting future high-risk areas for Lyme disease, and helping to develop management plans and mitigate its impact on the public health in the region.

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Tables

Table 1. Individual characteristics of tracked mice; HR: Home range area, %EXP: proportion of exploration outside the home range, %EXC: proportion of excursions outside the forest patch, MR: movement rate.

Mouse ID	Sex	Site	Year	Weight (g)	HR (m ²)	%EXP	%EXC	MR (m.min ⁻¹)	Maximum distance in a night (m)
B59	F	Boat	2013	22	18885.83	1	48	1.99	384.62
B423	F	Boat	2013	18	3386.73	27	27	3.92	621.89
B429	F	Boat	2013	32	6848.24	5	20	1.94	265.81
B61	M	Boat	2013	19.5	792.69	35.4	22.6	3.27	1385.91
B422	M	Boat	2013	20	6964.69	50	20	1.81	465.29
B2	M	Boat	2012	24	20733.01	21.8	50	4.65	1201.77
B1	F	Boat	2012	20.5	13278.53	12.12	33.3	3.41	729.3
B4	F	Boat	2012	15	10077.25	6.45	54.8	3.16	648.56
A1	F	SB	2012	17.5	12035.01	25	2.7	2.97	1019.9
A3	F	SB	2012	18.7	8553.59	12.9	0	2.88	626
A4	M	SB	2012	19	10996.56	2.5	2.5	2.16	751.2
C1	M	JP	2012	23.5	5888.1	16.43	1.3	4.39	895.08
C2	F	JP	2012	24	2421.95	50	6.4	6.69	1274.61
J118	M	JP	2013	21	7984.71	13.55	8	2.17	670.07
J64	F	JP	2013	18	4875.88	13.79	8.62	2.51	715.41
J65	M	JP	2013	17	16802.98	17.85	14.28	5.92	1231.09
R427	M	RM	2013	15.5	2379.74	25	11.11	4.39	1116.75
R432	M	RM	2013	20	3868.14	41.5	0	5.93	1896.85
R67	F	RM	2013	24.5	5063.43	14.9	0	5.11	1479.02
R57	M	RM	2013	18	811	43.75	28.12	7.26	1361.96
E1	F	RM	2012	26.5	12021.68	9.43	1.88	2.49	689.6
E3	F	RM	2012	19.5	1687.48	40	3.63	2.76	1134

<i>E4</i>	M	RM	2012	15.7	5940.14	15.78	1.75	2.54	848.48
<i>D1</i>	M	MSH	2012	17.2	8265.43	20	0	4.45	890.89
<i>D3</i>	F	MSH	2012	21.5	14544.72	19.56	0	4.55	1252.1
<i>M428</i>	M	MSH	2013	21.5	3243.68	28.57	0	2.93	584.5
<i>M62</i>	F	MSH	2013	18.5	8138.06	12.9	0	3.27	557.36
<i>M66</i>	M	MSH	2013	19	5622.75	18.51	0	3	48.37
<i>M70</i>	F	MSH	2013	15	12348.15	28	0	4.51	1635.65
<i>F1</i>	M	KD	2012	22	11686.24	12.5	0	3.07	970.33
<i>F2</i>	F	KD	2012	18	1960.66	32.83	0	2.95	1467.93
<i>F3</i>	F	KD	2012	25	2393.99	36.76	0	2.53	955.66

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Table 2. Final linear mixed models with Home range area, Movement rate and Excursion rate outside the forest patch as response variables. The fixed factors included in the initial full models were the adrenal gland mass, body condition, breeding status, density of *P. leucopus* (PLD), small mammal diversity, and counts of ticks, fleas, lice and botfly larvae. In all models, site and year were included as random effects. The model with Exploration rate as a response variable is not presented here since none of the factors was significant and included in the final model after model simplification. Sample size was $n = 17$ in all models. p-values in bold are significant.

Coefficient	Estimate	Standard Error	<i>t</i>	<i>p</i>
Home range model (AIC = 168.42)				
Intercept	-310465.23	48868.68	-6.353	0.0031
Adrenal gland mass	-856.99	134.83	-6.356	0.0239
Body condition	89.42	29.24	3.058	0.0923
Fleas	-13.94	5.55	-2.514	0.1284
Ticks	-3.45	1.55	-2.223	0.1563
Lice	4.62	1.46	3.153	0.0876
PLD	-644.18	358.69	-1.796	0.1469
Breeding status	-23.60	12.01	-1.964	0.1884
Movement rate model (AIC = 2.95)				
Intercept	-1513.23	275.85	-5.486	0.0027
Adrenal gland	-4.18	0.76	-5.492	0.0119
Body condition	0.61	0.18	3.321	0.0450
Fleas	-0.15	0.04	-3.728	0.0336
Botfly larvae	0.22	0.05	4.917	0.0161
Breeding status	-0.28	0.09	-3.183	0.0500
Excursion rate model (AIC = -8.35)				
Intercept	-361.96	270.20	-1.34	0.2289
Adrenal gland mass	-0.99	0.75	-1.34	0.2298
Ticks	-0.03	0.01	-2.53	0.0445
PLD	3.01	1.97	1.53	0.2017

Table 3. Summary regression statistics of the structural equations model; PLD: density of *P. leucopus*; p-values in bold are significant; Variance explained by the model: home range=0.380; exploration=0.596; movement rate=0.295; excursions=0.633; ticks=0.0812; Model AIC = 457.006.

	Estimate	Standard error	Z	p
Home range				
Adrenal gland	-0.591	0.207	-2.858	0.004
PLD	-0.373	0.151	-2.476	0.013
Ticks	0.094	0.157	0.602	0.547
Body condition	0.338	0.152	2.222	0.026
Exploration rate				
Home range	-0.477	0.194	-2.464	0.014
Movement rate	0.535	0.178	3.009	0.003
Body condition	-0.140	0.161	-0.874	0.382
PLD	0.027	0.124	0.220	0.826
Mammal diversity	-0.024	0.129	-0.185	0.853
Ticks	0.008	0.081	0.104	0.918
Movement rate				
Adrenal gland	-0.548	0.277	-1.978	0.048
PLD	-0.354	0.177	-1.996	0.046
Mammal diversity	0.377	0.279	1.355	0.176
Ticks	-0.258	0.117	-2.202	0.028
Body condition	0.044	0.202	0.216	0.829
Excursion rate				
Home range	0.427	0.184	2.325	0.020
Movement rate	0.209	0.176	1.188	0.235
Body condition	-0.192	0.176	-1.091	0.275
PLD	0.611	0.179	3.419	0.001
Mammal diversity	-0.260	0.213	-1.221	0.222
Ticks	-0.164	0.111	-1.480	0.139
Ticks				
PLD	-0.274	0.232	-1.180	0.238
Mammal diversity	-0.063	0.139	-0.453	0.651

Figure captions

Fig. 1. The factors driving individual movement and distribution are operating at different spatial scales, from continental and landscape scales, down to community and individual levels.

Fig. 2. Structural equation model of the individual-level variables (stress, body condition, tick load) and forest patch-level characteristics (white-footed mouse density) on four movement variables (home range area, movement rate, excursion rate and exploration rate). Only the paths with a significant p-value for the regression coefficient are depicted on the figure. Regression statistics for the model are provided in Table 3. Dotted lines on the two paths at the bottom were not tested in the model.