The effect of stress level and parasite load on the movement pattern of the white-footed mouse within a fragmented landscape

Jorge Alejandro Gaitan Camacho

Department of Biology

McGill University, Montréal

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Abstract

Lyme disease is an infectious zoonotic disease caused by the spirochete bacterium *Borrelia burgdorferi* sensu lato. In North America, it has a number of vertebrate hosts including the white-footed mouse (*Peromyscus leucopus*). The disease is transmitted to other vertebrates, including humans, through the bite of an infected black–legged tick (*Ixodes scapularis*). In recent years there has been an increase in the incidence of *Borrelia burgdorferi* in southern Quebec, coinciding with the range expansion of the white-footed mouse and the black-legged tick in the region. This increasing distribution of reservoir and vector will undoubtedly favour the emergence and spread of Lyme disease in the parts of the province where they both become more abundant. As a generalist species, the white-footed mouse is favoured in fragmented landscapes like the Monteregie area, where it has been displacing the deer mouse (*Peromyscus maniculatus*), its local competitor. In this region we evaluated the effects of stress level, parasite load and some forest patch characteristics on white-footed mouse movement patterns. We found a negative effect of the adrenal gland size, a proxy for stress level, on the home range area and the movement rate of mouse individuals, suggesting that stressed mice cannot defend large home ranges. White-footed mouse population densities had a negative effect on the home range area and on the movement rate, consistent with higher competition rates and conflict avoidance behaviours in these sites. Population density also influenced the excursion (outside the forest patch) and exploration (outside the home range) rates, either directly or indirectly through its effect on home range area and movement rate. Finally, we found that the load of ticks had a negative effect on movement rate. *P. leucopus* densities and stress levels are good predictors of the movement patterns in this species and can be used to better understand its dispersal dynamics

at the front of its distribution range. This will contribute to better predict the rate and pattern of Lyme disease expansion and identify high-risk areas for the disease.

Résumé

La maladie de Lyme, une zoonose infectieuse causée par la bactérie spirochète *Borrelia burgdorferi* sensu lato. En Amerique du Nord, cette maladie implique plusieurs hôtes vertébrés, dont la souris à pattes blanches (*Peromyscus leucopus*). La maladie est transmise à d'autres vertébrés, dont l'humain, par la morsure d'une tique à pattes noires (*Ixodes scapularis*) infectée. Ces dernières années ont vu l'incidence de *Borrelia burgdorferi* augmenter dans le sud du Québec, coïncidant ainsi avec l'extension des aires de distributions de la tique et de la souris dans la région. L'augmentation de la distribution du réservoir ainsi que du vecteur va indubitablement favoriser l'émergence et la propagation de la maladie dans les zones de la province où ces deux acteurs deviennent plus abondants. En tant qu'espèce généraliste, la souris à pattes blanches est favorisée dans les paysages fragmentés comme en Montérégie, où elle a peu à peu remplacé la souris sylvestre (*Peromyscus maniculatus*), son compétiteur local. Dans cette région, nous avons évalué les effets du niveau de stress, de la charge parasitaire ainsi que de certaines caractéristiques environnementales propres aux différentes parcelles de forêt étudiées, sur le mouvement de la souris à pattes-blanches, et plus particulièrement sur sa dispersion à longue distance au sein de ce paysage. Nous avons trouvé un effet négatif de la taille des glandes surrénales, utilisée comme proxy pour le niveau de stress, sur la taille du territoire mais aussi sur le taux de mouvement des souris, suggérant ainsi que les souris stressées ne peuvent pas défendre un large territoire. Les densités de populations de souris à pattes blanches avaient elles aussi in effet négatif sur la taille du territoire et sur le taux de mouvement des individus, ce qui est consistant avec des taux de compétition plus élevés et des comportements d'évitement des conflits dans ces sites.

La densité de population influençait aussi les taux d'excursion (hors de la parcelle de forêt), et d'exploration (hors du territoire), que ce soit directement ou indirectement via son effet sur la taille du territoire et sur le taux de mouvement des individus. Enfin, nous avons trouvé que la charge de tiques avait un effet négatif sur le taux de mouvement des individus. La densité de *P. leucopus* ainsi que les niveaux de stress constituent ainsi de bons prédicteurs du mouvement pour cette espèce et peut donc être utilisé pour mieux comprendre les dynamiques de dispersion de l'espèce sur le front de colonisation de son aire de distribution. Cela contribuera à une meilleure prédiction du taux et des patrons d'expansion de la maladie de Lyme ainsi qu'à une meilleure identification des zones à haut risque pour cette maladie.

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Contribution of authors

This thesis consists of two chapters, including one manuscript to be submitted to a journal (Chapter 2). The candidate designed the study, collected and analyzed the data, and wrote the manuscript. Professor Virginie Millien supervised the project, collaborated actively in all the steps, and is co-author of the manuscript.

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INTRODUCTION

Animal dispersal is one of the main and most stressful events in the life of most animals (Lidicker & Stenseth 1992). It requires a considerable amount of energy and it poses many risks, including the abandonment of a familiar area in search for a new home, the risk of predation, the uncertainty when arriving to an unknown area, and the aggression of residents upon arrival (Ferriere *et al.* 2000). Because of these risks, the process is generally gradual for most species, but on some occasions, an individual can perform a rapid dispersion in a very short period of time (Hansson 1992). In recent years, molecular techniques have allowed to detect and trace dispersal patterns of different species that proved to be difficult to detect through more traditional direct methods because of their size or life habits (Rogic *et al.* 2013); small and nocturnal animals are more difficult to track for example (Harris *et al.* 1990). One weakness of these indirect techniques, however, is that they do not provide information on short-term movements, dispersal routes or on the traits of the individuals that are more prone to engage in a dispersal process (Soisalo & Cavalcanti 2006). This leaves a gap in knowledge if we are to understand the biology of a species, including space use in real time by individuals (Mcshea and Madison 1992), spatio-temporal segregation within and between species (Farías *et al.* 2012), and physiological and behavioural traits that are associated with movement (Creel *et al.* 2007).

The method of radio-tracking has been used to study animal movement for over 50 years to obtain this kind of information (Aebischer *et al.* 1993; Harris *et al.* 1990, Figure 1.1). With increasingly better technology that allows tracking further with lighter transmitters, the amount and quality of data has vastly improved for many species (Langrock *et al.* 2012). There has also been an increasing interest in the interaction of animal physiology with behaviours that have a larger impact on the structure of animal populations and of entire communities (Janin *et al.*2012).

This interest stems from growing evidence that individual and population stress can have marked effects on population dynamics, foraging patterns and species interactions, all of which in turn have an effect at community scale by changing the distribution, presence, ecological interactions, and population densities of plant and animal species (Creel *et al.* 2013).

By combining the radio tracking technology with the study of animal physiology, it is possible to identify the links between the physiological traits of an individual with its movement behaviour (Belthoff & Dufty 1998). Given that organisms with increased stress levels respond differently to a stimulus when compared to individuals under normal stress conditions (Sapolsky *et al.* 2000), including these measurements can provide a powerful additional tool for the understanding of animal behaviour and its consequences at many ecological levels, from individuals to communities (Creel *et al.* 2013).

There is increasing evidence that a number of species are shifting their distribution polewards in response to climate warming (e.g. Myers *et al.* 2009), which may have profound impacts on local communities that are colonised by southern species. One such example is the white-footed mouse (*Peromyscus leucopus*), a rodent species that has been expanding its northern range limit into the southern regions of Quebec, outcompeting the local deer mouse (Roy-Dufresne *et al.* 2013). The white-footed mouse is the main reservoir for the causal agent of Lyme disease (Ostfeld 2009), an emerging infectious disease in North America of growing concern (Center for Disease Control, 2012). The first reported human case of Lyme disease acquired in Quebec was in 2008, and the incidence of cases in the province has been steadily increasing since then (Simon *et al.* 2014). Milder climatic conditions over the last decade have been identified as the driver for the emergence and spread of Lyme disease in Southern Quebec, at the most northern limit of its occurrence in North America. Climate warming allows both the main host (the white-footed mouse *P. leucopus*) and vector (the black-legged tick *Ixodes scapularis*) of Lyme disease to establish populations in Quebec, thus providing a favourable setting for the establishment of the transmission cycle of the *Borrelia burgdorferi*, the causal agent of Lyme disease (Simon*et al.* 2014). The white-footed mouse is currently expanding its range poleward at a rate estimated at approximately10 km per year (Roy-Dufresene *et al*. 2013), and is colonizing a fragmented landscape, moving through forest patches within a mostly agricultural area in Southern Quebec. While the white-footed mouse is known to prefer forest habitat (Merriam & Lanoue 1990), it is also a relatively generalist species, able to disperse within agricultural fields or even urbanized areas (Marrotte *et. al*. 2014). Indirect molecular and modeling methods have proven useful at predicting the rate of dispersal of the white-footed mouse (Rogic *et al.* 2013, Marrotte *et al.* 2014) within such a fragmented landscape. However, little is known about the biological characteristics that are promoting dispersal among individuals of white-footed mouse.

The aim of my thesis is to explore this question, using direct tracking methods of individuals in the field to evaluate the effect of a number of stressors on the movement pattern of the white-footed mouse, and the consequences on the ongoing spread of Lyme disease in the region. More precisely my objectives are:

- To determine the effect of parasite load on mouse movement patterns,
- To evaluate the relationships between the stress levels of individual mice with their movement pattern,
- To identify the characteristics of forest patches that may favour or impede the dispersal of individuals onto other forests patches.

My thesis is divided in two chapters. In the first chapter, I review the literature on animal movement, including exploration, and the effect of parasites, habitat fragmentation or predators on movement stimulation or avoidance. I then review the literature on the mammalian response to stress, focusing on factors that can stimulate a stress response and its consequences for the survival of an organism. In the second chapter, I conducted an analysis of the relationship between movement patterns, stress level and parasite load in a number of white-footed mice, to identify factors that could explain the variation in their home range size, movement rate, exploratory behaviour, and excursions outside forest patches. I found that individuals carrying more ticks also had higher stress level and tended to move less and within a smaller area. These individuals were also more prone to disperse outside their home range. This result has implications for the prediction of the rate of spread of Lyme disease in a region where it is currently rapidly emerging. Without taking into account individual traits that are related to movement and dispersal of the white-footed mouse, we may underestimate its role in spreading the pathogen to communities of hosts found across forest patches in Southern Quebec. A better understanding of the dispersal behaviour of the white-footed mouse will thus be key for predicting future high-risk areas for Lyme disease.

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CHAPTER ONE: Literature review

Introduction

Movement and exploration in animals play important roles in the survival of individuals and their overall fitness by providing a means to find resources, new environments, mates, refuges and also the means to disperse (Archer & Birke 1983; McShea & Madison 1992). Additionally, they provide the necessary information and mechanisms to avoid predation (Whishaw *et al.* 2006) and familiarize the animals with their surroundings (Hughes 1968; Archer & Birke 1983), allowing the identification of important feeding grounds, escape routes and potential resources (McReynolds 1962). These potential locations can be used immediately after discovery or remembered for future trips (Mc Reynolds 1962; Krebs 1978), reducing both the energy and time spent searching for these locations and even increasing the survival chances against an attack by a predator (Metzgar 1967; Krebs 1978; Soisalo & Cavalcanti 2006).

Movement is affected by a number of factors in wild animals. At the individual level these factors include behavioural constraints (Hansson 1992), parasite load (Burns *et al.* 2005), physiological constraints (Silverin 1997), and the overall health condition of an individual (Bowler & Benton 2005). Parasites for example can consume a considerable part of the energy budget of an organism (Khokhlova *et al.* 2002; St. Juliana*et al.* 2014), and this can be either translated into increased foraging to supply the increased metabolic demands (Munger & Karasov 1991), or into hindered movements on heavily parasitized organisms (Slansky 2007). In the same way, physiological requirements imposed on organisms can result in increased movements including sexual drive and hunger (Wood-Gush & Vestergaard 1989), while others may result on decreased activity, as it is the case of disease (Schwanz *et al.* 2011) or wounds (Sapolsky *et al.* 2000).

Parasitism, stress and an animal's health condition interact actively in a positive feedback (Charmandari*et al.* 2005). Stressed organisms for example are more prone to disease, which in turn deteriorates the animal's health (Sapolsky 2004). Sick animals can become stressed leaving them more vulnerable to parasites and disease, which further stress the organism (Romero 2004). Alternatively, non-stressed animals have stronger immune systems (Sapolsky*et al.* 2000), which make them better at defending themselves from disease and parasites, keeping their stress level low and their overall health in better shape (Romero*et al.* 2009). These feedbacks ultimately have consequences on the general fitness of the animal, which will results in a positive or negative effect on the animal movement (Belthoff & Dufty 1998).

Additional to internal factors that alter the movement patterns of animal, external factors can also alter an animal's behaviour (Barnum *et al.* 1992). In a fragmented habitat for example, animal movement is limited within the landscape by physical barriers to organisms of all sizes (Doak *et al.* 1992). Rural and urban habitats limit the movement of many animal species mainly because they are intolerant to the anthropogenic matrix (Barko *et al.* 2003; Marrotte *et al*. 2014; Rogic *et al.* 2013; Simon*et al.* 2014). In rural habitats, the fragmentation is generally limited to an agricultural matrix and forest patches crossed by roads and highways (Cummings & Vessey 1994), while the fragmentation by urban environments provide a significant barrier to most animal species (Barko *et al.* 2003; Marrotte *et al.* 2014), where only highly adaptable species can find refuge and cross them (Doak *et al.* 1992; Hansson 1992; Sinclair 1992).

At a wider geographical scale, as habitats are in constant change (Ronce 2007), dispersal has been in many cases an adaptation that has allowed some species to move from a worsening location to a more suitable one, and a key trait that allows species survival (Ferriere *et al.* 2000). Climate change is a major driver of species shift in distribution range (Walther *et al.* 2002), and with the increase in recent years of average global temperature, many species are currently shifting their range limits tracking their optimal climatic condition (Myers *et al.* 2009; Whitmee & Orme 2012; Roy-Dufresne *et al.* 2013). One example of such shift in the temperate northern hemisphere is the white-footed mouse (*Peromyscus leucopus*), a small mammal species known to rapidly expand its range into Southern Quebec, at a rate estimated at ~ 10 km per year (Simon *et al.* 2014).

The white-footed mouse

The white-footed mouse (*Peromyscus leucopus*) and the deer mouse (*Peromyscus maniculatus)* are the only *Peromyscus* species found in Quebec, and both share similar resources, including shelter, food, and nesting sites, but they are different in their response to the current changing environment. The white-footed mouse for example, is considered to be a generalist species (Lackey *et al.* 1985), very adaptable regarding its diet and habitat preferences (Metzgar 1973; Wolff 1985; Wolf & Batzli 2002), and better suited to warmer climates than the deer mouse (Myers *et al.* 2009; Roy-Dufresne *et al.* 2013). Due to the increasing temperature in the region, over the last 15 years *P. leucopus* has started to gain terrain over *P. maniculatus*, replacing it in most of the southern region (Roy-Dufresne *et al.* 2013), where past harsh winters and late springs used to favour the resident deer mouse. The expanding distribution of the white-footed mouse as well as the means by which it is achieving it, are of particular interest because of its role as a main reservoir host of the causal agent of Lyme disease.

Lyme disease in Quebec

Lyme disease, an infectious zoonotic disease caused by the spirochete bacterium *Borrelia burgdorferi* (Ostfeld 2009), involves a number of vertebrate hosts such as the eastern chipmunk (*Tamias striatus*), the short-tailed shrew (*Blarina brevicauda*), the masked shrews (*Sorex cinereus*), and the white-footed mouse (*Peromyscus leucopus*), considered to be the main reservoir for the disease in North America (Allan *et al.* 2003; Keesing *et al.* 2009; Ogden & Tsao 2009; Ostfeld 2009). The disease is transmitted to vertebrates, including humans, through the bite of the black–legged tick (*Ixodes scapularis*; Bouchard *et al.* 2011; Schwanz*et al.* 2011).

The first human case of Lyme disease acquired in Québec was reported in 2008 (Milord *et al*. 2013; INSPQ 2013), and the human disease incidence is increasing each year in the province, up to 148 cases in 2013 (INSPQ 2014). This increase in Lyme disease cases has been attributed to climate warming (Simon *et al*. 2014). With the recent northwards range shift and increase in abundance of the white-footed mouse in Quebec (Roy-Dufresne *et al.* 2013), we are witnessing the recent emergence and spread of Lyme disease in the parts of the province where both, reservoir and vector, have become more abundant (Simon*et al.* 2014).

Habitat fragmentation, white-footed mouse abundance and the prevalence of *Borrelia*

Although *P. leucopus* is a generalist species, it is considered that forest habitat is essential to its survival and reproduction (Zollner & Lima 1997). The presence of increasingly isolated forest patches with lower biodiversity in southern Quebec may increase the prevalence of Lyme disease (Keesing *et al.* 2009) in the region for two main reasons: (1) an increased abundance of infected white-footed mice relative to other small mammal hosts (Wilder & Meikle 2005; Wilder

& Meikle 2006) and (2) an increased movement of white-footed mice towards human populated areas (Hansson 1992). The Monteregie area south of Montreal is mainly agricultural with forest patches of different area that are isolated to different degrees and scattered throughout the landscape (Marrotte *et al*. 2014). Fragmentation of the habitat has been related to a loss of biodiversity (Ostfeld 2009), which may favor the white-footed mouse in small forest patches over other small mammal species (Bouchard *et al.* 2011; Simon *et al.* 2014). As a result, the proportion of *Borrelia spp*. infected ticks feeding on *P. leucopus* increases, due to the lack of other small mammal hosts that are either worse reservoirs for the disease or better at removing and killing ticks while grooming (Keesing*et al.* 2009). Smaller forest patches also favor the generalist species, and many studies reported higher densities of P. *leucopus* in small forest fragments when compared to larger patches (Nupp & Swihart 1996, 1998; Krohne & Hoch 1999; Nupp & Swihart 2000; Wilder & Meikle 2005; Wilder & Meikle 2006; Tanner *et al.* 2010). This increase in white-footed mouse density in small forest patches has been attributed to a decrease in interspecific competition (Wilder & Meikle 2005), increased reproduction rate in edge habitats and decreased predation pressure (Wolff 1985; Wolf & Batzli 2002; Wolf & Batzli 2004).

Habitat fragmentation and movement

Understanding how movement within the landscape of the white-footed mouse can modify the range dynamics at the most northern edge of its distribution is necessary to predict the future distribution of this species, and its role in the propagation of Lyme disease in the province. The dispersal matrix is of critical importance for an organism to engage into dispersal as it imposes different degrees of resistance to movement and limits the amount of dispersers between habitats. Animals are more likely to disperse into uniform habitats that provide the lowest level of resistance than in fragmented and less connected habitat (Marrotte *et al.* 2014).

Resistance, connectivity and habitat quality all vary across an heterogeneous landscape, which affects the pattern of dispersal across this landscape. Habitat fragmentation is the main limiting factor of dispersal of individuals in anthropogenic environments (Cummings & Vessey 1994; Barko *et al.* 2003; Ciuti *et al.* 2012). Small land animals such as the white-footed mouse face extra challenges when dispersing through a matrix composed of agricultural lands and urban areas (Barnum *et al.* 1992; Barko *et al.* 2003; Marrotte *et al.* 2014).

Urban areas pose the highest resistance to the mouse movement in a fragmented landscape (Marrotte *et al.* 2014) and gene flow through these barriers is very limited as they are generally hostile environments for this species (Marrotte *et al.* 2014; Rogic *et al.* 2014). Agricultural land on the other hand can either pose a resistance or facilitate the movement of the white-footed mouse (Wegner & Merriam 1990; Henein*et al.* 1998). This variation depends on the height of the crop, as mice will avoid traveling on open terrain, therefore limiting the movement of the species after harvest, during winter and early stages of growth. Once a crop provides a safe route unexposed to predators it becomes less of a barrier allowing mouse movement both through the crops and also through the hedgerows and ditches that by this time also have enough vegetation cover to work as paths for mouse dispersal (Cummings & Vessey 1994; Nupp & Swihart 1996; Zollner & Lima 1999).

Parasitism and its effect on *P. leucopus* movement

Parasitism plays an important role in regulating mouse population dynamics (Brown & Fuller 2006), influencing the behaviour and physiology of a host in different ways (Burns *et al.* 2005; Barnard & Behnke 2006; Cramer & Cameron 2007; Rejmanek *et al.* 2010). Parasites have been shown to affect the energy budget of the host (Brown & Fuller 2006; Careau *et al.* 2010), its immune system (Jaffe *et al.* 2005), and even direct changes in its behaviour that may favour different parasite species (Milinski & Heller 1978; Milinski 1985). Milinski and Heller (1978) found that stickleback fish changed their feeding strategy in the presence or absence of predators depending on their parasite load. When the fish were free of parasites, the presence of predators motivated them to focus their feeding activities in patches with lower concentrations of food (in this case *Daphnia sp*.) in order to allocate a large part of their perceptual input on their predators (Milinski & Heller 1978). In contrast, fish infested with the generalist parasite *Schistocephalus solidus* were fearless when compared with uninfected fish, a behaviour which will benefits the parasite. Fish infested by *Glugea anomala*, whose only host is the stickleback fish, exhibited more fear toward the predator and maintained themselves farther from it when compared with non-parasitized fish (Milinski 1985).

Parasites have also been observed to affect the behaviour of mammalian hosts (Rejmanek *et al.* 2010). One example comes from deer mice (*Peromyscus maniculatus*) infected with the nematode *Trichinella spiralis*. Mice lowered their activity at the onset of the infection but these effects changed when the adults were expected to release the larvae, leaving them more vulnerable to predators, which in turn benefit the parasite (Rau 1983). *Toxoplasma spp.* a known parasite of the white-footed mouse is another example of a behaviour-altering parasite and has been shown to alter the behaviour of their hosts to become fearless and to engage into a search for a predator (more commonly a cat) so that the parasite can enter the oocycst stage of its life cycle in the carnivore's digestive tract (Rejmanek *et al.* 2010).

Reported ecto-parasites of the white-footed mouse include fleas (Siphonaptera), lice, soft ticks (Argasoidae), hard ticks (Ixodidae) and botfly larvae (Cuterebridae) (Figure 1.2). Even though they have a persistent presence on their hosts, there is little evidence of these parasites having an effect on the animal fitness (Hersh *et al.* 2013), even though many of these parasites are themselves vectors of other parasites and diseases (Keesing *et al.* 2009).

One exception for this neutral effect of the parasites on the movement of small mammal is botfly parasitism (Durden *et al.* 2004), a very common parasite in new world small mammals (Jaffe *et al.* 2005). These species starts their parasitic cycle as an endoparasite but ends as a subcutaneous larva. Owing it to its large size relative to the host, it had always been assumed that parasitism by these larvae should be very costly for the host (Lemaître *et al.* 2009), but empirical studies have produced mixed results on the impact of these parasites on small rodents (Brown & Fuller 2006). While some studies claim that botfly parasitism can have a positive impact on a species survival (Burns *et al.* 2005), others have found strong negative impacts (Brown & Fuller 2006; Lemaître *et al.* 2009), weak negative impacts (Careau *et al.* 2010) or neutral impacts (Brown & Fuller 2006; Slansky 2007). Overall, botfly parasitism seems to have a net negative impact on an individual's fitness (Burns *et al.* 2005, Slansky 2007).

The types and drivers of movement in animals

Movement in animals primarily aims at increasing fitness and providing an individual with immediate needs including food, shelter, mates and refuges, and non-immediate needs, including information gathering, identification of potential resources, tracking changes in the environment and chasing out invaders (Montgomery & Monkman 1955; Archer & Birke 1983). This is achieved in many species inside their home range, where an individual (or group of individuals) perform these daily activities (McNab 1963; Metzgar 1973; Bowman *et al.* 2002). The main advantage for having a home range, is the possibility of securing available resources for the owner of the area, and in territorial species, it is defended from competitors (McNab 1963; Wolff 1992).

Frequently in the wild, mice perform movements outside their home range (patrolling or excursions) into neighbouring territories (exploration) (Metzgar 1967; Archer & Birke 1983; Wood-Gush & Vestergaard 1989). These movements also provide a means to track changes outside their own home range, so that the behaviour can be modified to match the requirements of the animal, and in some cases it can mean the possibility to increase or change their own home range (disperse) into a vacant one (Krebs 1978; Krebs 1992; McComb *et al.* 2001; Scognamillo *et al.* 2003; Soisalo & Cavalcanti 2006); in some cases they can even displace less competitive individuals of the same or another species, as it is the case of the white-footed mouse in Quebec (Roy-Dufresne *et al.* 2013).

From exploration to dispersal

Dispersal is defined as a "migration beyond the pre-migration limits of a familiar area during which the ability to return to the familiar area is retained but not necessarily exploited" (Davies *et al.* 2012). It has been shown that for some species long range dispersal may result in a mortality of 50% and the costs include not only energy expenditure and predation risks, but also less favourable conditions experienced by resident individuals in the new environment (Goodenough *et al.* 2009). There are however a number of benefits of dispersal, including avoidance of kin competition, avoidance of inbreeding (Gadgil 1971; Greenwood 1980; Archer & Birke 1983; Bollinger *et al.* 1993; Mossman & Waser 1999), and an increased overall reproductive sucess of the dispersing individual (Van Vuren & Armitage 1994). It can also be a means for survival in rapidly changing environments where individuals of a given species may track optimal conditions and modify their distribution accordingly (Lidicker & Stenseth 1992).

Several factors have been found to influence both the migration pattern and habitat selection by an organism (Stenseth & Lidicker 1992), including sex and age of the individual

(Lidicker & Stenseth 1992; Wolff 1992; Nagy *et al.* 2007; Hanski & Selonen 2009), resources availability (Wolf & Batzli 2004), connectivity between departure site and the new settlement (Merriam & Lanoue 1990; Henein *et al.* 1998), weather variables during the dispersal (Rizkalla & Swihart 2007), personality (Dingemanse *et al.* 2003), competition (Mossman & Waser 1999), disease, natal experience (Stamps & Davis 2006), maternal nutrition (Massot & Clobert 1995) and the dispersal matrix (Barnum *et al.* 1992; Doak *et al.* 1992; Nupp & Swihart 1998, 2000). Additionally, natal experience has been reported to increase selectiveness by dispersers, since an organism will tend to establish itself in a place that is as good as, or better than the area where it was born (Stamps & Davis 2006; Mabry & Stamps 2008).

In species where dispersal is male biased such as *Peromyscus leucopus* (Wolff 1992), males tend to disperse more often because females tend to remain close to their breeding site, and males are forced to move further from it influenced by their mother (Wolff 1985; Wolff 1992; Massot & Clobert 1995) to avoid breeding among closely related individuals (Wolff 1992). Finally, individual differences have also been identified as determining factors of dispersal pattern, with individuals that tend to engage more in exploration being also more prone to disperse(Dingemanse *et al.* 2003; Réale *et al.* 2007).

Predator pressure and activity pattern

Underscoring the importance of predation risks and its effect on exploration, Whishaw *et al.* (2006) found that rats failed to explore from a secure starting position and were increasingly likely to escape as security decreased, not in order to perform a voluntary exploration but rather to find the much-appreciated security (Barnum *et al.* 1992). Their results suggest that a primary function of locomotor behaviour in a novel environment is to optimize security (Whishaw *et al.* 2006). In natural environments, such laboratory experimental conditions are expected to be fairly uncommon, but it sheds a light on the importance of perceived security to engage in foraging and activities (Willems & Hill 2009).

Van der Merwe and Brown (2009) designed an experiment to understand the effect of predators on the searching and foraging behaviours of ground squirrels (*Xerus inauris*), a small diurnal rodent foraging in open fields. They found that these animals did not tend to spend large amounts of time far from their burrows, suggesting that unless safety from predation was established, no exploratory movements were performed outside a set safe area, even in the presence of attractive food sources (Van der Merwe & Brown 2008). Similar results were found in fishes in coral reefs (Madin *et al.* 2011), arthropods in grasslands (Schmitz & Suttle 2001), mice in forest patches (Barnum *et al.* 1992; Willems & Hill 2009), or baboons in open savannas (Willems & Hill 2009). The results obtained in different taxonomic groups highlight the foraging limitations imposed by predation risk, shaping the actions of species and their distributions across communities.

The sense of security of an animal is related to its familiarity with its immediate environment. Metzgar (1967) found that white-footed mice (*Peromyscus leucopus*) that were allowed to become familiarized with the refuges and routes inside a small room had significantly higher chances of escaping a screech owl than mice that had not had the time to become familiarized with the space. These results show the other side of the coin in which exploration becomes a mechanism by which the animal can locate potential escape routes or shelters against predators, and in fact, overcome the costs of predation risk by providing the animal with a spatial map of its surroundings (Metzgar 1967).

Individual response to stress

Glucocorticoid hormones are in general regarded as "stress hormones" and the measurement of the changes in the concentration of these hormones is used as a proxy to determine how stressed an organism is (Romero 2004; Creel *et al.* 2013).

The glucocorticoid production however is not limited to stress-induced secretion. Glucocorticoid concentrations vary on a daily basis as a result of intrinsic factors like hunger or the urge to mate, and the release of glucocorticoids will prepare the required systems to perform the desired task (Romero *et al.* 2009). Some of these changes are regular cycles in the basal glucocorticoid level in the body, and studies have shown that these changes in basal level depended on the season and on the ontogenic stage of the individual (Boonstra *et al.* 2001). Under non-stress situations, the concentration of glucocorticoids increases after waking and prior to activities that increase the metabolic demand, such as foraging and mating, and decrease when these activities cease and other activities are engaged (Romero *et al*. 2009). Seasonal cycles in glucocorticoid level also modulate the type of behaviours that are adopted by the individual to match the changing requirement throughout the year, stimulating behaviours that include gathering and storing of food in a cache, seeking a mate in breeding season, competing for a mate, and preparing for torpor or hibernation (Romero 2004; Boonstra *et al.* 2001).

The stress response is an endocrine process, which ultimately has consequences at the physiological and behavioural levels of an individual (Sapolsky *et al.* 2000). It is a process widely spread throughout the vertebrates (Lafferty & Holt 2003; Careau *et al.* 2010; Creel *et al.* 2013) that starts with a perceived stressor (a wound, hunger, environmental pollutants, being chased by a predator, parasites, pathogens, habitat changes and aggression) (Christian 1956; Welch & Welch 1969; Avitsur *et al.* 2001; Brown & Fuller 2006; Ulrich-Lai *et al.* 2006; Barnard

& Behnke 2006; Gesquiere*et al.* 2008; Oitzl *et al.* 2010; Clinchy*et al.* 2011; Schwanz*et al.* 2011; Bauer*et al.* 2013) followed by the secretion of catecholamines and glucocorticoids (Charmandari*et al.* 2005; Lupien *et al.* 2009; Love *et al.* 2013) by the adrenal gland cortex (Romero *et al.* 2008, Sapolsky *et al.* 2000; Lafferty 1999).

The overall stress-response plays an important role at determining the fitness of an animal in a given environment (Oitzl *et al.* 2010; Creel *et al.* 2013), by altering the physiology of the animal as well as some of its behaviours (Charmandari*et al.* 2005; Romero *et al.* 2009; Crespi *et al.* 2013). In general this response provides an overall increase in the fitness of an individual (hence its widespread distribution among animals), but it can be deleterious in cases of prolonged exposure (Sapolsky 2004).

The phylogenetic background of the individual will also determine the consequences of the exposure to a given stressor (von Holst 1998). Animals in different taxa experience stressful events differently, and very stressful events to one species may not constitute a serious threat for individuals belonging to another species (Réale *et al.* 2007). Individuals of different ontogenetic stage, sex and reproductive status also react differently to a stressor, and the consequences of the response are also very different depending on the intrinsic characteristics of the organism. These consequences will be reflected at various levels of the organism, from its physiology to its behavioural patterns (Creel *et al.* 2007; Wada 2008).

The immediate stress response to the catecholamines boosts the immune activity, allowing for an increased inflammatory response and active leucocytes, macrophages and lymphocytes (Sapolsky *et al.* 2000). The advantage of this early response is to protect against pathogens that may enter the body through a wound (a common consequence of stressful encounters). But this reaction by the immune system can be so strong that it may result in the immune system overshoot, causing it to attack the body's tissues, and such an extreme inflammatory response may prove fatal for an individual (Sapolsky *et al.* 2000). If left unchecked, the strong immune response produced by the catecholamines can thus become deleterious for the organism (Sapolsky *et al.* 2000; Sapolsky 2004). A constant production of glucocorticoids regulates the response of the immune system, but at the same time leaves the organism vulnerable to diseases and parasites that may become opportunistic (Barnard *et al.* 1996). Disease and parasites are by themselves stressors, and in already stressed organisms, they induce a positive feedback between the glucocorticoids level and the immunity response, leading to a decreased fitness of the organism. There have been reports however that this feedback is hampered in animals with a fast pace of life syndrome such as mice, making them tolerant to more stressful situations (Réale *et al.* 2010), and that in fact they are resistant to the effects of the glucocorticoids on the immune system, while allowing the glucocorticoid production as a response to diseases and parasites.

The effect of stress on movement behaviour

In general, a stress response to an immediate threat will most likely result in some displacement of the individual away from the stressor (Whishaw *et al.* 2006). In most cases, these movements will rely on the spatial memory the animal has of its surroundings, and at this point, the hippocampus plays a central role (Moisan *et al.* 2013). This region of the brain is involved in spatial cognition and memory; therefore any process that affects the function of this region will have an indirect effect on movement-related behaviour (Champagne *et al.* 2008).

In mammals, the brain is a region of the body that is favoured by the increased blood flow as a consequence of the catecholamine release, which facilitates the oxygen and glucose delivery to all areas in this organ (reviewed in Sapolsky *et al.* 2000). The effect of glucocorticoids on the other hand is quite different as it causes a reduced glucose transport towards the brain. It is not clearly understood why this phenomenon occurs, but in this case, the glucocorticoids are suppressive when compared to the catecholamines (Oitzl *et al.* 2010). This effect seems to be related to memory formation by the hippocampus, where right after the onset of the stressor, memory is improved, but only for those memories that are relevant for the situation; everything else is ignored and does not remain a long-term memory as a consequence of the delayed action of the glucocorticoids (Oitzl *et al.* 2010; Champagne 2008; Moisan *et al.* 2013; Love *et al.* 2013).

Empirical and experimental studies, suggest that there is a lower degree of exploration in more stressed animals due to the decrease of hippocampal size in these individuals (Oitzl *et al.* 2001). Such chronic situations are rarely achieved in natural populations, and in fact, changes observed in exploratory behaviours by a naturally stressed animal could instead reflect stressor avoidance rather than a spatial memory and cognition related disorder from an atrophy of the hippocampus (Madin *et al.* 2011). Belthoff and Dufty (1998) found increased locomotor activity after exogenous glucocorticoids were administered to screech owls, and the effect of glucocorticoids on animal movement has to be interpreted for both short and long-term exposure to a stressor. The immediate effects of a glucocorticoid release (or administration) increase the energy available for the organism (Romero 2004), therefore allowing for an increase in locomotion. The presence of the stressor will generally cause an aversive reaction by the animal to avoid it, in cases resulting in locomotion (Creel *et al.* 2007), but prolonged exposure to a stressor (and to glucocorticoids) can in fact result in impeded locomotion due in part by the atrophy of the hippocampus (Oitzl *et al.* 2010).

The stress response therefore is a mechanism that allows organisms to respond to a changing environment in a way that they can adjust their physiologies and behaviours to this change. These responses have been maintained throughout evolution because overall they increase the survival chances and ultimately the overall fitness of an individual (Creel *et al.* 2013, Love *et al.* 2013; Guesquiere *et al.* 2008).

Conclusion

A number of factors have been identified as potential drivers of movement and dispersal in mammals. Stressors such as the competition for food resources or space may increase stress-level of an individual, which could lead to altering its movement behaviour, with exploration of territories outside its home range or even dispersal to a new breeding site. On the other hand, parasitism may impede movement rate, as well as the presence of inhospitable habitat around the foraging area. Clearly, the relationships between movement pattern, stress-level, parasitism, habitat characteristics and community assemblages are complex and context-dependant. A better understanding of these relationships will prove useful if we are to better characterize the pattern of dispersal of the white-footed mouse within the fragmented landscape of the Monteregie, at the most northern range edge of its distribution. This is especially critical within the current context of the rapidly expanding Lyme disease in the region, an expansion which is mostly attributed to the increase in abundance of the white-footed mouse (Simon *et al*. 2014).

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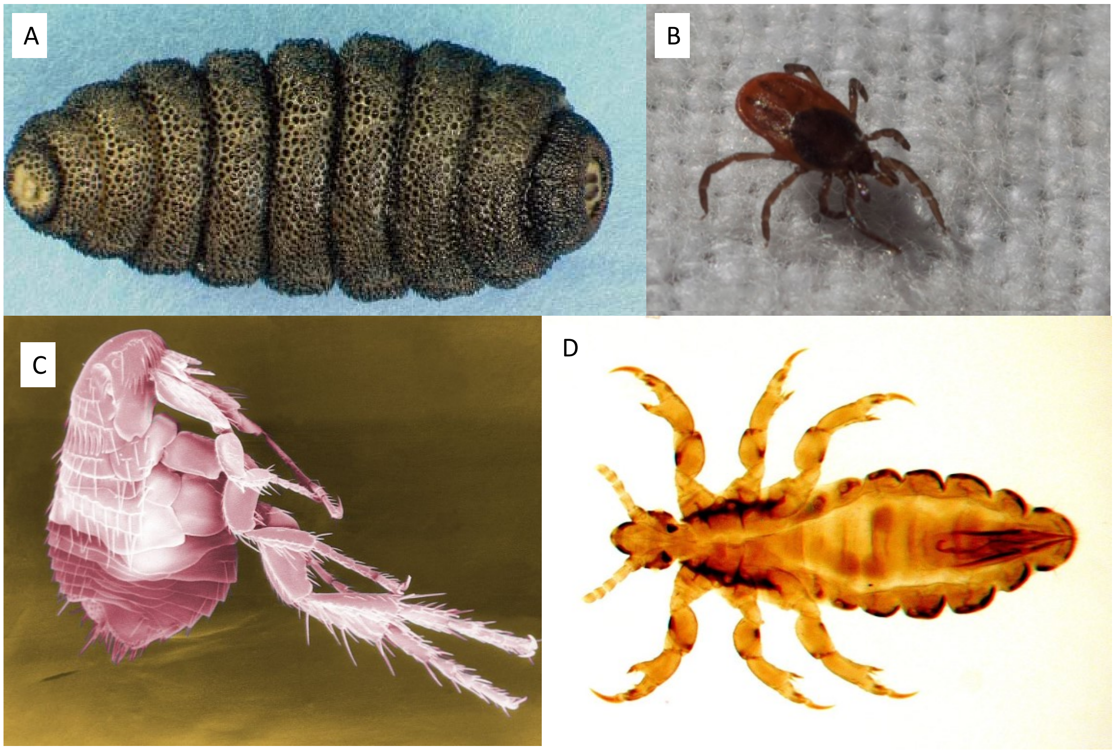
Figure Legends

Figure 1.1. A white-footed mouse fitted with a radio-transmitter (photo V. Millien, Mont Saint-Hilaire, Quebec, August 2012).

Figure 1.2. Common ecto-parasites of the white-footed mouse. 1: botfly larva (Slansky 2007); 2: black legged tick (photo V. Millien, Mont Saint Bruno, Quebec, September 2012); 3: flea (http://commons.wikimedia.org/wiki/File:Flea_Scanning_Electron_Micrograph_False_Color.jpg); 4: louse ("http://en.wikipedia.org/wiki/File:Fig._1._Male_of_head_louse.jpg#mediaviewer/File:Fig._1._Male_of_head_louse.jpg.)

Figure 1.1

Figure 1.2



Connective Statement

In the first chapter of this thesis, I reviewed the published evidence for drivers of movement in animals, focusing particularly on stressors that could modulate the type and rate of movement. Understanding the triggers that are leading to dispersal in animals is particularly relevant for species that are currently undergoing range shift in response to climate warming. There have been relatively few attempts to connect empirical data on movement behavior and the physiological condition of an individual, most likely because of the logistic cost of conducting such a study in wild animals.

In the next chapter, I present such data, using movement data obtained for 32 white-footed mice that were fitted with a radio-transmitter. I explored a number of hypotheses on how stress level and parasite-load may affect the movement pattern of these mouse individuals. I found that individuals carrying more parasites (in particular black-legged ticks) tended to move at a larger rate and were also more prone to explore territories outside their home range. Those individuals also had larger adrenal gland size, which was used as a proxy for stress-level. These results are of prime importance in the current context of Lyme disease emergence, as they suggest that individuals of white-footed mouse that are more prone to disperse are also the ones carrying more ticks; which in turn is likely to increase the rate of expansion of Lyme disease within the landscape.

CHAPTER 2: Stress level, parasite load and movement pattern in the white-footed mouse in forest fragments at its northern range limit

INTRODUCTION

Lyme disease, is an infectious zoonotic disease transmitted to vertebrates, including humans, through the bite of the black–legged tick (*Ixodes scapularis*; Bouchard *et al.* 2011; Schwanz *et al.* 2011). The causing agent is the spirochete bacterium *Borrelia burgdorferi* (Ostfeld 2009), which can be transmitted to a number of vertebrate hosts, including the eastern chipmunk (*Tamias striatus*), the short-tailed shrew (*Blarina brevicauda*), the masked shrews (*Sorex cinereus*), and the white-footed mouse (*Peromyscus leucopus*), the later being considered to be the main reservoir for the disease in the region (Allan *et al.* 2003; Keesing *et al.* 2009; Ogden & Tsao 2009; Ostfeld 2009).

In recent years there has been a northwards range shift and increase in abundance of the white-footed mouse in Quebec (Bouchard *et al*. 2011, Roy-Dufresne *et al.* 2013). This expansion is likely to favour the emergence and spread of Lyme disease in the parts of the province where both the main reservoir and vector become more abundant (Simon *et al*. 2014), thus increasing the probability of entering in contact with humans (Allan *et al.* 2003). Forest habitat is essential to the survival and reproduction of the white-footed mouse (Zollner & Lima 1997) and its movement across the landscape is constrained by geographical barriers such as large roads and rivers (Marrotte *et al*. 2014). It has been shown that habitat fragmentation is increasing the prevalence of Lyme disease (Keesing *et al.* 2009). First, fragmentation of the habitat has been related to a loss of biodiversity (Ostfeld 2009), which may favour the white-footed mouse in small forest patches over other small mammal species (Bouchard *et al*. 2011). As a result, the proportion of *Borrelia* infected ticks feeding on *P. leucopus* increases, due to the lack of other small mammal hosts that are either worse reservoirs for the disease or better at removing and killing ticks while grooming (Keesing *et al*. 2009). Smaller forest patches also seem to favour the generalist mice over more specialist species, and many studies reported higher densities of *P. leucopus* in small forest fragments when compared to larger patches (Nupp & Swihart 1996, 1998; Krohne & Hoch 1999; Wilder & Meikle 2005; Tanner *et al*. 2010). Several factors are known to increase the white-footed mouse density in smaller forest patches, including decreased interspecific competition (Wilder & Meikle 2005), increased reproduction, and decreased predation as a consequence of increased edge habitat (Wolf & Batzli 2002). Finally, habitat fragmentation has been related with increased movement of mice towards human populated areas (Bouchard *et al.* 2011), thereby increasing Lyme disease risk through larger contact rate between infected mice and humans.

The Monteregie area south of Montreal in Southern Quebec is mainly agricultural with forest patches of different area that are more or less isolated and scattered throughout the landscape. The white-footed mouse is expanding north within this fragmented landscape (Ledevin & Millien 2013; Simon *et al*. 2014), and a better understanding of the effect of habitat fragmentation on the pattern of expansion of this species will help identify areas of higher risk for Lyme disease where it is rapidly emerging. Here, we estimated stress level and parasite load in a number of white-footed mouse individuals sampled in forest patches, to evaluate their effect on movement pattern within the fragmented landscape of the Monteregie region. We tested the hypothesis that a higher ecto-parasite burden will impede the activity and movement of their *P.*

leucopus host. We also evaluated the effects of overall body condition and stress level on movement pattern in these mice. We then investigated the relations between individual stress level and parasite burden with a number of forest patch characteristics. We tested the hypothesis that overall stress level of an individual is positively related with higher densities of conspecific, while parasite load is affected by both habitat characteristics and the structure of the small mammal community.

MATERIALS AND METHODS

Sampling and field procedures

The study site were all located in forest fragments in Southern Quebec, Canada, between 45.035° N and 46.298°N in latitude (Figure 2.1), in an area covering approximately 24000 sq km. We used the Système d'information écoforestière (SIEF) geospatial database to extract the forest patch area and the edge proportion (the ratio of the forest patch area to its perimeter) for each of these forest fragments.

Small mammals were captured at 17 different sites during the summer of 2012 (Figure 2.1).

At each site, we used Sherman live traps baited with a mixture of peanut butter and oatmeal. Traps were 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* that were later brought back to the laboratory for sampling of ectoparasites. We recorded the number of ticks, fleas, lice and warble pores (indicating the presence of *Cuterebra sp*. larvae) on each individual. Adrenal gland hyperplasia provides an indirect estimate of glucocorticoids levels in an individual (Christian 1956; Davis & Christian 1957; Sapolsky *et al.* 2000; Ulrich-Lai *et al* 2006), and is an estimate on how often and for how long 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 & Christian 1957; Sapolsky *et al*. 2000). The use of fecal glucocorticoid metabolites (FCM) was not deemed appropriate because it is a measure of short-term stress and would have required constant monitoring of the cages to make sure that the obtained FCM was due to former exposure to stressors and not a consequence of the trapping itself. Adrenal glands were sampled on each captured individual of *P. leucopus* 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 used the average weight of both glands (AG) for each individual. The body condition index (the residuals of the linear relation between of body mass and head and body length) was used as a proxy for the general health status of each individual (Jakob *et al.* 1996). For each site, we also obtained small mammal species diversity (estimated with the Shannon index) and the abundance of *P. leucopus* estimated as the number of *P. leucopus* captured per 100 sq. meters.

Radio tracking was performed in the summers of 2012 and 2013 at six of our sites in the Monteregie region (Figure 2.1). Mice were sampled near the edges or close to clearings of the forests to detect excursions, and were recaptured in the surroundings of their diurnal refuges. These refuges always compromised one of three options: rocks and crevices, in burrows under the roots of trees, or inside dead trees (standing or tree stumps). Upon capture, individuals were checked for the presence of external parasites, individually marked with an ear tag (The national

Band & 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 all released immediately upon capture. 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 approximately 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 at each site. We obtained the location of each animal every 20 minutes by immediate triangulation using three 3-element Yagi antennas with an error of 1 meter. This method insured the independence of each bearing recorded in the field (Harris *et al.* 1990). In 2012, mice were tracked in 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 re-captured after the third or fourth night of tracking (two weeks after the first tracking night in 2012 and 4 weeks after the first tracking night in 2013). The recapture was achieved by searching for the diurnal refuge during the afternoon and placing Sherman traps surrounding the refuge overnight. Recaptured individuals were euthanized and brought back to the laboratory for further study.

All procedures performed were approved by the McGill center for animal research ethics (McGill AUP#5420) and the government of Quebec (SEG permits2012-07-16-1417-16-17-SF and 2013-07-04-1530-04-14-16-17-SF).

Movement data

We estimated the geographic coordinates of each location of the mice using the location of the antennas and each of the simultaneous bearings in the LOAS 4.0 software (Ecological

Software Solutions LLC). We then used BIOTAS 2.0 (Ecological Software Solutions LLC) to obtain the home range of each individual we tracked in the field. Given its importance in dispersal prediction (Bowman *et al.* 2002) and following Millspaugh and Marzluff (2001), we used a 80% fixed kernel to define the home range area of a mouse (HR), which is the area where the probability of finding a given individual is a 80%. The fixed kernel method therefore, focuses on areas where the mouse concentrates its activity rather than the outermost location points as in other methods (Worton 1989). We analysed the nightly activity of each individual using movement rate (MR), or the average distance moved between bearings in a night divided by the time interval between those bearings (4 or 5 minutes depending on the site). We also estimated the exploratory movements of each individual (EXP), as the proportions of locations that fell outside the home range. Excursions (EXC) were defined by the proportion of the locations that fell outside the forest patch into other habitats. By definition, some of the excursion locations may also be exploration outside the home range, or fall within the home range.

Statistical analyses

We used linear mixed effects models (LME) to estimate the effect of parasite load, body condition and stress level on the movement pattern in *P. leucopus*, using the package *nlme* (Pinheiro *et al.* 2013) in R statistical software version 3.0.3 (R Core Team 2014).We first tested for the presence of sexual dimorphism in all our first response variables (home range, movement rate, proportion of exploration and excursion). We then included stress and parasite variables as fixed factors, as well as site and year as random factors in our models. We ran distinct models for each of our four different movement variables (home range, movement rate, exploration and excursions) and first checked for the independence of all continuous fixed factors using the *vif* function in the *HH* package in R (Heiberger & Holland 2014). We simplified the models by backwards selection using the function *drop1* from the *stats* package in R version 3.0.3 (R Core Team 2014). For each set of models (HR, MR, EXP and EXC as response variables), we retained the model with the lowest Akaike Information Criterion (AIC) as the final model.

We then investigated the effect of patch level characteristics on stress variables that were found to be significantly driving movement pattern. Larger forest patches with more edge habitat have been found to favour the white-footed mouse (Krohne & Hoch 1999; Wilder & Meikle 2005; Wolf & Batzli 2002). We used the forest patch area and the proportion of edge (the ratio of the area to the perimeter of the patch) to describe the physical characteristics of the patch and as a proxy for habitat quality for the mouse. Inter- and intra-specific competition pressure can increase stress level (Creel *et al.* 2013), and we thus used the diversity of small mammals (estimated by the Shannon diversity index) in a patch and the abundance of *P. leucopus* (estimated by the number of *P. leucopus* captured by 100 sq. meter) to estimate competition pressure. Breeding status (breeding versus non-breeding) and parasite load were also included as explanatory factors, as both can influence the stress level of an individual (Romero *et al.* 2008).

Because our system involves multiple pathways between factors, we then used structural equation modeling (SEM) using all our measured variables (stress, parasites and patch characteristics) to further explore these causal pathways simultaneously. For physiological variables, we considered the size of the adrenal gland and body condition. Parasite counts of fleas, lice, ticks and botfly larvae were included to evaluate the effect of parasite load. Small mammal species richness, white-footed mouse density and forest patch area were used to describe the patch characteristics. All four movement variables were considered in this exploratory model. We evaluated the model significance using the package *lavaan* (Rosseel 2012) in R. A Chi-Square with a significance value larger than 0.05 indicated that our model could not be rejected (Shipley 2000). We then estimated all the path coefficients and associated significance level in our model, as well as the variance contribution of each of these paths.

RESULTS

We captured five different species of small mammals (*Peromyscus leucopus, Blarina brevicauda, Sorex sp., Tamias striatus, Tamiasciurus hudsonicus*) and the species richness at a given site ranged from 1 to 4. In total, we captured 193 individuals (128 males and 65 females) of white-footed mouse and this species was found at all our 17 sites (Table 1).

Thirty-two white-footed mouse individuals (15 males and 17 females) were radio tracked, half of them in 2012 and the other half in 2013 (Table 2). We were not able to recapture all individuals that had been fitted with a collar (17 mice were recaptured), however all collars were located and recovered with the exception of 5 that were either inaccessible (2 deep under boulders, 1 inside a tree), or which signals disappeared (2 collars). 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 carcase of the mouse and two other collars exhibited strong predation signs (broken and perforated). It has recently been reported that the mortality for white-footed mice is generally 50% after a period of one month in the wild (Collins & Kays 2014), which fits the mortality rate in our study, since we were able to recover about 50% of the animals.

Stress level and parasite load

Overall, the adrenal gland size ranged from 0.00025 to 0.0027g, and males had significantly larger adrenal glands than females (mean ratio F = 0.0011, mean ratio M = 0.0013;

t=-3.48; p<0.0001; n=193). However we found that the mass of the adrenal gland was not different between sexes when we considered only the tracked mice (t=-0.61; p=0.55; n=17). We further explored the relation between stress level and a number of patch-level characteristics: the small mammal diversity, the abundance of *P. leucopus*, the forest patch area and proportion of edge habitat. There was no significant effect of any of these patch–level variables on the adrenal gland size (Table 3).

The adrenal gland size was not correlated with body condition (p=0.2). Body condition ranged from 0 to 0.76 and averaged 0.34. There was a difference in this index between sexes where females have a higher body condition index (t=3.230; p<0.01; n=193). We also found that the sex difference could not be observed in the tracked mice (t=-0.012; p=0.99; n=32), for which the body condition index ranged from 0 to 0.6. As for the adrenal gland size, there was no effect of patch-level factors on body condition.

Most of our sampled individuals of white-footed mouse were free of ecto-parasites. Over a third (37%) of the trapped mice were infested with black-legged ticks, with a tick burden ranging from 0 to 30 (average tick burden per individual of 2.5). Twenty percent of the mice carried botfly larvae, some of them being infested with multiple larvae (up to four). Fleas were detected in 13% of the mice, while lice were less frequent, and detected only on 7% of the individuals.

Movement pattern

The variance inflation factor of all independent variables used the models were all lower than 5, and so were all included in the initial full models, for each of the four movement variables we used (Table 3).

Home Range. The average home range area (measured as the 80% fixed kernel) was 7605 sq. m, from 792 to 20730 sq. m (Table 2), and it did not significantly differ between males and females in our sample (*p* = 0.89). The fixed factors kept in our model after simplification were the size of the adrenal gland, the body condition index, the breeding status as well as the flea, tick and lice burdens (Table 3). The adrenal gland size had a negative effect on home range area, and no other factor was significant in our model.

Movement rate. The maximum distance moved per night by an individual varied greatly within and between individuals. This distance was as low as 48 meters and up to 1.9 km in a single night by a one mouse (Table 2). The average movement rate per mouse ranged from 1.8 to 7.3, and was on average 3.6 meters per minute. There was no significant difference in the movement rate between males and females (*p*=0.36). The final model with movement rate as a response variable included the size of the adrenal gland, the body condition, the breeding status as well as the number of fleas and botfly larvae (Table 3). Mice with larger adrenal glands and that carried more fleas tended to move less. Mice that had botfly larvae had significantly larger movement rate (Table 3).

Exploration. Exploratory movements, the proportion of locations spent outside the home range, varied between 1% and 50% with an average of 22.2% (Table 2). There was no difference in the exploratory behaviour between the tracked males and females (*p*=0.37). None of the factors included in our model (stress and parasite variables) had a significant effect on the proportion of exploration (Table 3).

Excursions. The proportion of excursions outside the forest patches ranged from 0 to 55% and was on average of 11% (Table 2). No difference was detected between sexes for this variable (*p*=0.86). Excursions did not depend on the type of habitat around the forest patch and occurred in mowed lawn, orchards, tall grasses, crop field or clearings. The final model included the size of the adrenal gland, population density and tick burden. Of these variables, only ticks had a significant negative effect on excursion rate (Table 3).

Exploratory model

We used a Structural Equation modeling approach to further explore the effect of individual-level and patch-level characteristics on movement pattern, while taking into account simultaneously the four types of movement variables (Figure 2.2).

Our model was not rejected (*p*=0.47, Table 4). The variation in home range size depended on individual level factors, such as the adrenal gland size (*p*<0.004) and the body condition (*p*<0.026). Individuals with larger home ranges tended to have smaller adrenal gland size and larger body condition index. The home range size and movement rate were both negatively related with the white-footed mouse density (*p*<0.014 and *p*<0.044, respectively). Individuals with larger movement rate tended to have smaller adrenal gland size (*p*<0.047). Finally, movement rate decreased with increased tick load (*p*<0.027). The proportion of exploration was related with higher movement rate (*p*<0.003) and smaller home range size (*p*<0.014). The proportion of excursions increased with the density of white-footed mouse (*p*<0.001), and home range size (*p*<0.02).

DISCUSSION

Stress level and parasite loads

The study of parasites and their effect on biotic communities has gained special attention in recent years (Morand *et al*. 2006; Pedersen & Fenton 2007), especially for their role as modifiers of ecological interactions (Hatcher *et al*. 2006; Munger & Karasov 1991) as well as the effect on individuals. Several studies for example have reported variations in the stress level of animals with differing loads of parasites (Bauer *et al*. 2013; Brown & Fuller 2006; Schwanz 2006), further adding to the growing evidence of the important role of the parasites in the ecosystems. Others, on the other hand, have found no significant effect of the parasite load on the stress level (Crespi *et al*. 2013) especially in small fast-paced species like the white-footed mouse (Hersh *et al.* 2013; Réale *et al*. 2010). Here, we also found no significant relationship between the adrenal gland size and parasite burden in our sample, confirming these later results on *P. leucopus.*

Reported evidence shows that both a significant and non-significant effects of the parasite load on stress can be observed in different populations, as both can occur depending on the intensity, frequency and type of parasite load, as well as their combination with other non-parasite related stressors (Clinchy *et al*. 2011; Sapolsky 2004; Tanner et al. 2010). In absence of other stressors, parasites may be identified as powerful stressor even in small fast-paced animals (St. Juliana *et al*. 2014), but in natural environment, parasites may not have such a strong effect (Burns *et al*. 2005; Réale *et al*. 2010), when compared with other factors such as competition, predation pressure, habitat quality or weather variables (Addis *et al.* 2011; Ben-Nathan & Feuerstein 1990; Brown 2012; Christian 1956; Laundré *et al*. 2001; Monclús *et al*. 2009; Réale *et al*. 2010; Romero *et al*. 2009). Furthermore, the change in the production of glucocorticoid level is known to occur due to the interactions of several ecological, physiological and behavioural factors that we did not measured directly here (Charmandari *et al*. 2005; Lupien *et al.* 2009; von Holst 1998), including food and shelter availability (Love *et al*. 2013; Metzgar

1967), internal parasite loads (Brown & Fuller 2006) and genetic differences (Creel *et al*. 2013) as well as abiotic variables (Ben-Nathan & Feuerstein 1990).

Home range and movement rate

Our estimates of home range area are larger than most values previously reported for *P. leucopus* (from 590 sq. m to 12600 sq. m; Madison 1977; Mineau & Madison 1977; Stickel 1962; Wolff 1985). Several factors can influence home range estimates in tracked animals, such as the weight of the collar, the type of transmitter used, the frequency of tracking and the method used to estimate home range area. The collars we used were lighter than the collars used by Mineau and Madison (1977), they did not require surgery and were also lighter than those used by Wolff (1985), and the frequency of our sampling allowed to detect locations that may be missed when tracking an animal only once per night such as in Madison (1977). Compared to home range estimation methods that rely on capture techniques, radio telemetry provides a real time picture of the activity (Harris *et al.* 1990), therefore, our telemetry results were expected to differ from other methods that rely on capture-marking-recapture (Stickel 1962). The method we used provided real time and accurate measurements on the locations of the animals at least three times each hour for at least 6 hours per night, with light-weight collars (about 5% of the mouse weight), therefore providing a more accurate estimate of the home range of the animals.

The adrenal gland size was negatively correlated with home range area and movement rate. Stressed individuals have been reported to either engage more actively in locomotion or to reduce it greatly (Barnum *et al*. 1992; Belthoff & Dufty 1998; Nemati *et al*. 2013; Oitzl *et al.* 2010). Our data are in accordance with these last results, with individuals with larger adrenal glands concentrating their activity in smaller areas and tending to move at a smaller rate. Along this line of results, we found that body condition was positively related with home range area.

The body condition is correlated to the energetic state of an organism (Schulte-Hostedde *et al*. 2005), therefore, organisms with a better body condition have better endurance and can forage more efficiently than their congeners (McNab 1963).

We also detected a negative relation between the white-footed mouse density in a forest patch and home range area. This finding suggests that density of *P. leucopus* limit the home range area each individual of this species may maintain in a given site, a result in line with the fact that the white-footed mouse is a territorial species (Barko *et al*. 2003; Krohne & Hoch 1999; Lackey *et al*. 1985; Metzgar 1973; Wolff 1992; Wolff & Lundy 1985; Xia & Millar 1989). The white-footed mouse has been reported to defend its home range (Lackey *et al.* 1985; Nupp & Swihart 1996), and in areas with increased population densities it is likely that the size of the home range will be reduced due to increased intra-specific competition (Krohne & Hoch 1999; Wilder & Meikle 2005). The white-footed mouse density also had a negative effect on movement rate in our sample, suggesting a negative effect of the increased intra-specific competition in the forest patch on this behaviour.

Although a relationship between mouse density and adrenal gland size was not apparent in our data, the negative relationship between the adrenal gland size and home range area and the negative relationship between the adrenal gland size and movement rate we observed may also be related with increased population densities. Several studies have reported the stressful effect of high population densities in mice (Christian 1956. Davis & Christian 1957; Wilder & Meikle 2005) and other species such as macaques (Dettmer *et al*. 2014). Even though we did not find a direct link between the 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 neighbours (Wolf & Batzli 2004; Wolff 1985).

It has been shown that increased movement could lead to more exposure to parasites in the Siberian chipmunk *(Tamias sibiricus)* (Boyer *et al*. 2010) Interestingly, the movement rate in our study individuals was negatively related with parasite load, where increased loads of ticks decreased the movement rates of the individual as well as their excursion rates. Animals with higher tick loads have not been reported before to have an increased metabolic demand or to be significantly stressed (Barnard & 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

For a mouse or any animal to disperse from a forest patch to another, it is first necessary that it leaves the familiar area for a new one (Cockburn 1992; Ferriere *et al*. 2000; Gadgil 1971; Dytham 2009; Stickel 1968). The probability of an individual to leave a forest patch depends on several internal factors (Stenseth & Lidicker 1992b), including age (Hansson 1992), sex (Wolff 1992), reproductive status (Gliwicz 1992), personality (Dingemanse *et al.* 2003), and some external factors like weather (Rizkalla & Swihart 2007), and type of matrix through which it would disperse (Linzey *et al*. 2012; Mabry & Stamps 2008; Marrotte *et al*. 2014).

Juveniles are often the individuals that engage in dispersal movements (Bollinger *et al.* 1993; Hansson 1992; Massot & Clobert 1995; Sinclair 1992; Wolff 1992) and that are forced to leave their natal home range to search for their own (Wolff 1992). The increased proportion of excursions expected by younger individuals in our study would have reflected either their search of a new home range, or the exploratory excursive movements that can allow them to perform a dispersal movement outside the forest patch. Here, we found that breeding status or sex did not have any effect on the propensity to forage outside the home range in our sample.

We observed that population density was positively related with excursive behaviours in *P. leucopus*. Higher mouse densities in a forest mean that any given area inside the forest will have to be shared by more individuals, which in turns reduces the home range area that an individual can defend (Krohne & Hoch 1999; Lackey *et al*. 1985), and may stimulate excursions outside of the forest in order to get access to resources which are highly contested (Henein *et al*. 1998; Stenseth & Lidicker 1992a). Accordingly, we found that animals with a larger excursion rate also had a larger home range. Home range size has been positively correlated with dispersal (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 and tall grasses. Neither crop fields, nor small clearings were observed to limit the mouse movement, suggesting that these kinds of habitat are not strong barriers against mouse movement between forest patches. Several authors have observed *P. leucopus* individuals moving outside the forest patches through edge rows (Merriam & Lanoue 1990; Wilder & Meikle 2006) and tall crop fields (Cummings & Vessey 1994; Wolf & Batzli 2002, 2004; Marrotte *et al*. 2004), 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 (Dingemanse *et al*. 2002; Jedrzejewski *et al.* 2001; McReynolds 1962). These kinds of movements allow for information gathering that can be used to track changes in the environment that eventually will have consequences on the modification of the behaviour of an animal, one of such behaviours being shift or change of the home range (Archer & Birke 1983). The exploration rate in our model was positively related with the movement rate and negatively related with the home range. The later suggests that organisms with larger home range areas 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 ranges will need to engage more often in exploration movements to look for resources that may not be available in their own home range (Archer & Birke 1983; Stickel 1968; Wolf 1985), or to look for new areas on which they can expand their small home range (Doak *et al*. 1992; Ferriere *et al.* 2000; Gliwicz 1992; Nathan 2001).

Our model also indicated that animals that move more and faster are more likely to perform exploratory movements than those who have lower movement rates, a required feature for an animal that is exploring for resources or dispersing (Maier 2000; McShea & Madison 1992).The opposite effects of the home range area and the movement rate on the exploratory movement 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 very adaptable species that is currently increasing its range and most likely will continue to do so in the current context of changing environment and 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 previous studies, including larger home ranges, real time tracking outside forest patches and evidence of the effect of the stress levels on movement patterns. We found that this species is capable of very long movements in a single night, and that there are very few habitats it will avoid for foraging or even crossing. We could not find any effect of most parasites on the variation in the adrenal gland size of the individuals we tracked in the field, nor on their movement patterns with the exception of the negative effect of tick load on movement rate and excursion rate. This result suggests a decrease in mobility that may decrease the chances of a mouse to expand or change its home range. We found evidence that environmental factors affecting the population density of this species play a major role in regulating their home range size, movement rate and excursion rate. The excursive movements and the population density together with the type of habitat surrounding a forest patch may be the best predictors of sites with individuals that have a higher chance of entering in contact with people and of engaging into a dispersal movement. Given the central role of the white-footed mouse in the transmission cycle of Lyme disease in North-America, our results provide a set of data and useful information of how this species move within the fragmented forested landscape found in southern Quebec. Our findings have implications for the prediction of the rate of spread of Lyme disease in a region where it is currently rapidly emerging. Without taking into account individual traits that are related to movement and dispersal of the white-footed mouse, we may underestimate its role in spreading the pathogen to communities of hosts found across forest patches in Southern Quebec. A better understanding of the dispersal behaviour of the white-footed mouse will thus be key for predicting future high-risk areas for Lyme disease, and help to develop management plans and mitigate its impact on the public health in the region.

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Tables

Table 1. Study sites characteristics (area, perimeter and edge proportion (perimeter/area)) as well as small mammal diversity (estimated by the Shannon diversity index), the number of captured white-footed mouse and tracked white-footed mouse at each site.

Site	Area (km2)	Perimeter (m)	Edge proportion	Small mammal diversity	*P. leucopus*	
					Number captured	Number tracked
Boat	0.02	660	33000	0.47	14	8
DV	0.46	3708	8060.86	1.33	11	
FH	11.08	108180	9763.53	1.19	8	
HR	5.09	41820	9589.47	0.0002	6	
HV	0.9072	9540	10515.87	1.37	18	
JA	0.37	3840	10457.52	1.23	23	
JP	2.47	27060	10942.18	1.18	12	5
KD	0.48	6480	13584.91	0.27	14	3
MSH	16.12	74280	4606.94	0.68	12	6
NO	0.68	4363	6397.361	0.97	25	
OR	0.31	3780	12103.75	0.38	8	
PdC	0.56	4105	7278.369	0.67	20	
RM	21.56	48480	2248.848	1.04	15	7
SB	14.40	97920	6799.15	0.73	26	3
SE	0.86	7398	8642.523	0.82	16	
SFR	0.86	7398	8642.523	0.87	4	
VA	3.62	31560	8729.566	1.46	6	

Table 2. Individual characteristics of the 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 (m2)	% EXP	% EXC	EXC to	MR	Maximum distance in a night (m)
B59	F	Boat	2013	22	18885.83	1	48	Farmland (corn)	1.99	384.62
B423	F	Boat	2013	18	3386.73	27	27	Farmland (corn)	3.92	621.89
B429	F	Boat	2013	32	6848.24	5	20	Farmland (corn)	1.94	265.81
B61	M	Boat	2013	19.5	792.69	35.4	22.6	Farmland (corn)	3.27	1385.91
B422	M	Boat	2013	20	6964.69	50	20	Farmland (corn)	1.81	465.29
B2	M	Boat	2012	24	20733.01	21.8	50	Farmland (corn)	4.65	1201.77
B1	F	Boat	2012	20.5	13278.53	12.12	33.3	Farmland (corn)	3.41	729.3
B4	F	Boat	2012	15	10077.25	6.45	54.8	Farmland (corn)	3.16	648.56
A1	F	SB	2012	17.5	12035.01	25	2.7	Tall grasses	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	Tall grasses	2.16	751.2
C1	M	JP	2012	23.5	5888.1	16.43	1.3	Mowed lawn	4.39	895.08
C2	F	JP	2012	24	2421.95	50	6.4	Mowed lawn/ Backyards	6.69	1274.61

J118	M	JP	2013	21	7984.71	13.55	8	Mowed lawn	2.17	670.07
J64	F	JP	2013	18	4875.88	13.79	8.62	Mowed lawn	2.51	715.41
J65	M	JP	2013	17	16802.98	17.85	14.28	Mowed lawn/ Backyards	5.92	1231.09
R427	M	RM	2013	15.5	2379.74	25	11.11	Farmland (corn)	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	Farmland (corn)	7.26	1361.96
E1	F	RM	2012	26.5	12021.68	9.43	1.88	Orchard	2.49	689.6
E3	F	RM	2012	19.5	1687.48	40	3.63	Orchard	2.76	1134
E4	M	RM	2012	15.7	5940.14	15.78	1.75	Orchard	2.54	848.48
D1	M	MSH	2012	17.2	8265.43	20	0		4.45	890.89
D3	F	MSH	2012	21.5	14544.72	19.56	0		4.55	1252.1
M428	M	MSH	2013	21.5	3243.68	28.57	0		2.93	584.5
M62	F	MSH	2013	18.5	8138.06	12.9	0		3.27	557.36
M66	M	MSH	2013	19	5622.75	18.51	0		3	48.37
M70	F	MSH	2013	15	12348.15	28	0		4.51	1635.65
F1	M	KD	2012	22	11686.24	12.5	0		3.07	970.33
F2	F	KD	2012	18	1960.66	32.83	0		2.95	1467.93
F3	F	KD	2012	25	2393.99	36.76	0		2.53	955.66

Table 3. Summary results of the linear mixed models; AG: adrenal gland size; BC: body condition; BRD: breeding condition; PLD: density of *P. leucopus*; HR: Home range area, EXP: proportion of exploration outside the home range, EXC: proportion of excursions outside the forest patch, MR: movement rate; BF: number of botfly larvae; SH: small mammal diversity; EG: edge proportion. P values in bold are significant.

Home Range			
Full model			
AG +BC + Fleas + Ticks + Lice + BF + SH + PLD + Area + EG + BRD	AIC = 173.18		
	slope	t	p
AG	-1085.76	-4.38	0.1424
BC	-130.99	2.81	0.2170
Fleas	-25.24	-2.05	0.2878
Ticks	-3.93	-2.508	0.2415
Lice	6.35	2.94	0.2084
BF	12.83	0.983	0.5051
SH	-90.06	-0.77	0.581
PLD	91.35	0.06	0.957
Area	36.4	0.576	0.667
EG	93.06	0.571	0.669
BRD	-50.51	-1.83	0.3176
Final model			
AG + BC + Fleas + Ticks + Lice + BRD	AIC = 170.80		
	slope	t	p
AG	-848.73	-6.78	**0.0211**
BC	88.73	3.26	0.0826
Fleas	-13.4	-2.62	0.12
Ticks	-3.58	-2.46	0.1332
Lice	4.64	3.38	0.0777
BRD	-22.57	-2.04	0.1776
Movement Rate			
Full model			
AG + BC + Fleas + Ticks + Lice + BF + SH+ PLD +	AIC = 36.5782		

Area + EG + BRD

	slope	t	p
AG	-12.673	-5.19	0.1210
BC	1.875	3.223	0.1915
Fleas	-0.481	-3.368	0.1837
Ticks	-0.005	-0.176	0.8889
Lice	0.069	3.486	0.1778
BF	0.550	3.9860	0.1565
SH	-0.672	-3.3416	0.1851
PLD	8.896	1.3453	0.4069
Area	0.520	1.6746	0.3427
EG	0.798	1.0578	0.4821
BRD	-1.155	-4.282	0.1461

Final model

AG + BC + Fleas + BF + BRD AIC = 3.468

	slope	t	p
AG	-4.12	-5.26	**0.0134**
BC	0.59	3.14	0.0515
Fleas	-0.15	-3.55	**0.0381**
BF	0.22	4.7	**0.0182**
BRD	-0.27	-3.01	0.0572

Exploration

Full model

AG + BC + Fleas + Ticks+ Lice + BF + SH + PLD + Area + EG + BRD AIC = 31.047

	slope	t	p
AG	-3.4715	-2.4203	0.2494
BC	0.3956	1.1781	0.4480
Fleas	-0.1474	-1.7877	0.3247
Ticks	-0.0033	-0.2010	0.8737
Lice	0.0078	0.6689	0.6247
BF	0.2771	3.5814	0.1733
SH	-1.4835	-3.3687	0.1837
PLD	7.6340	2.1614	0.2759
Area	0.3061	1.8336	0.3179
EG	0.4882	1.2082	0.4401
BRD	-0.2851	-1.8171	0.3203

Final model

BF	AIC = -7.427		
	slope	t	p
BF	0.0246	0.8132	0.4429

Excursions

Full model

AG + BC + Fleas + Ticks + Lice + BF + SH + PLD + Area + EG + BRD	AIC = 32.3811		
	slope	t	P
AG	-3.2614	-2.4421	0.2474
BC	0.1756	0.5422	0.6837
Fleas	-0.1138	-1.3773	0.3998
Ticks	-0.0260	-0.1623	0.3515
Lice	0.0126	1.1660	0.4513
BF	0.1200	1.4079	0.3932
SH	-0.3349	-0.4652	0.7228
PLD	6.3935	0.8336	0.5576
Area	0.1966	0.5584	0.6758
EG	0.5967	0.6631	0.6272
BRD	-0.2609	-1.7064	0.3375

Final model

AG + Ticks + PLD	AIC = -1.8151		
	slope	t	p
AG	-1.0585	-1.4282	0.2032
Ticks	-0.0263	-2.5456	**0.0437**
PLD	2.9805	1.3948	0.2355

Adrenal glands

Full model

BC + Fleas + Ticks + Lice + BF + SH + PLD + Area + EG + BRD	AIC= -58.5152		
	slope	t	p
BC	0.1352	1.7326	0.2253
Fleas	-0.0249	-1.1786	0.3598
Ticks	-0.0021	-0.4696	0.6848
Lice	0.0030	-0.9780	0.4312
BF	0.0324	1.8429	0.2067
SH	-0.1690	-1.6150	0.3529
PLD	1.1486	1.2918	0.4194
Area	0.0618	1.5368	0.3672

EG	0.1312	1.2902	0.4197
BRD	-0.0550	-1.4277	0.2895

Final model
BC + Fleas + Lice + BF + SH + PLD + Area + EG + BRD AIC= -59.9014

	slope	t	p
Area	0.0523	1.5962	0.3563
BC	0.1372	1.8680	0.1586
BRD	-0.0580	-1.6183	0.2040
EG	0.1056	1.3052	0.4162
SH	-0.1691	-1.7145	0.3361
PLD	0.9882	1.2770	0.4229
Fleas	-0.0281	-1.4861	0.2339
Lice	0.00316	1.0949	0.3536
BF	0.0345	2.1484	0.1209

Table 4. Summary results of the structural equation model (SEM); AG: adrenal gland size; BC: body condition; BRD: breeding condition; PLD: density of *P. leucopus*; HR: Home range area, EXP: proportion of exploration outside the home range, EXC: proportion of excursions outside the forest patch, MR: movement rate; BF: number of botfly larvae; SH: small mammal diversity; EG: edge proportion. P values in bold are significant. AIC = 456.77

Home range **HR ~ AG + PLD + Ticks + BC**	**Estimate**	**Std. Err**	**Z-value**	**P(>|Z|)**
AG	-0.592	0.208	-2.849	**0.004**
PLD	-0.372	0.151	-2.464	**0.014**
Ticks	0.094	0.158	0.596	0.551
BC	0.334	0.15	2.225	**0.026**
Exploration **EXP ~ HR + MR + BC + PLD + SH + Ticks**				
HR	-0.478	0.193	-2.469	**0.014**
MR	0.536	0.178	3.005	**0.003**
BC	-0.143	0.16	-0.895	0.371
PLD	0.026	0.124	0.212	0.832

SH	-0.024	0.129	-0.185	0.854
Ticks	0.008	0.08	0.097	0.923
Movement rate **MR ~ AG + PLD + SH + Ticks + BC**				
AG	-0.551	0.278	-1.983	**0.047**
PLD	-0.354	0.176	-2.01	**0.044**
SH	0.379	0.279	1.359	0.174
Ticks	-0.257	0.116	-2.211	**0.027**
BC	0.052	0.204	0.253	0.8
Excursions **EXC ~ HR + MR + BC + PLD + SH + Ticks**				
HR	0.426	0.183	2.326	**0.02**
MR	0.21	0.175	1.194	0.232
BC	-0.195	0.174	-1.117	0.264
PLD	0.61	0.178	3.424	**0.001**
SH	-0.26	0.212	-1.225	0.221
Ticks	-0.164	0.11	-1.49	0.136
Ticks **Ticks ~ PLD + SH**				
PLD	-0.274	0.232	-1.18	0.238
SH	-0.063	0.139	-0.453	0.651

Figure legends

Figure 2.1. A: Map of Southern Quebec with the location of the study sites; B: section of the Monteregie delimited in A. The red dots indicate sites where mice were captured and tracked. The white dots indicate sites where mice were captured.

Figure 2.2. Structural equation model of the individual-level variables (stress, body condition, tick load; blue and black boxes) and forest patch-level characteristics (white-footed mouse density, small mammal species diversity; green box) on four movement variables (home range, movement rate, excursion rate and exploration rate; red and grey boxes). Variance explained by the model for: home range=0.3774; exploration=0.5961; movement rate=0.2954; excursions=0.6341; ticks=0.0812. Coefficients are indicated on the figure by the paths. The paths leading to dispersal and Lyme disease risk (white and yellow boxes) were not included in the model and are depicted with dashed arrows.

Figure 2.1

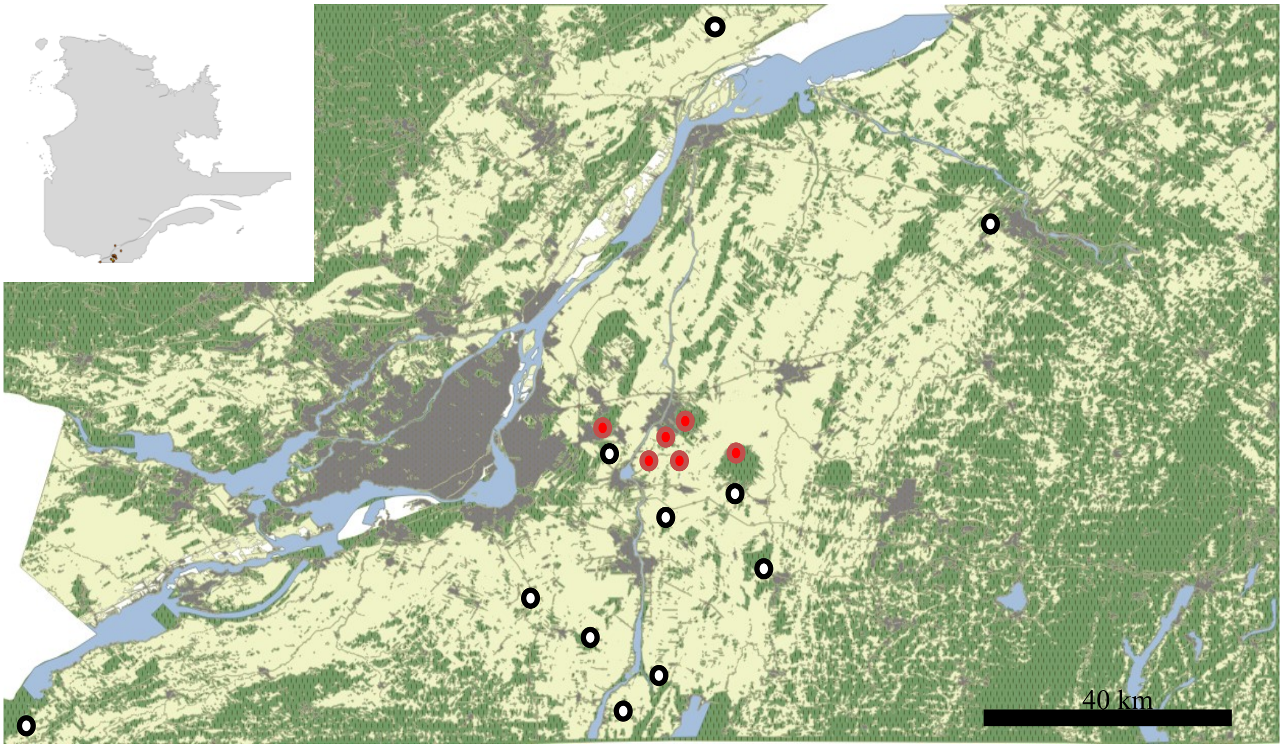
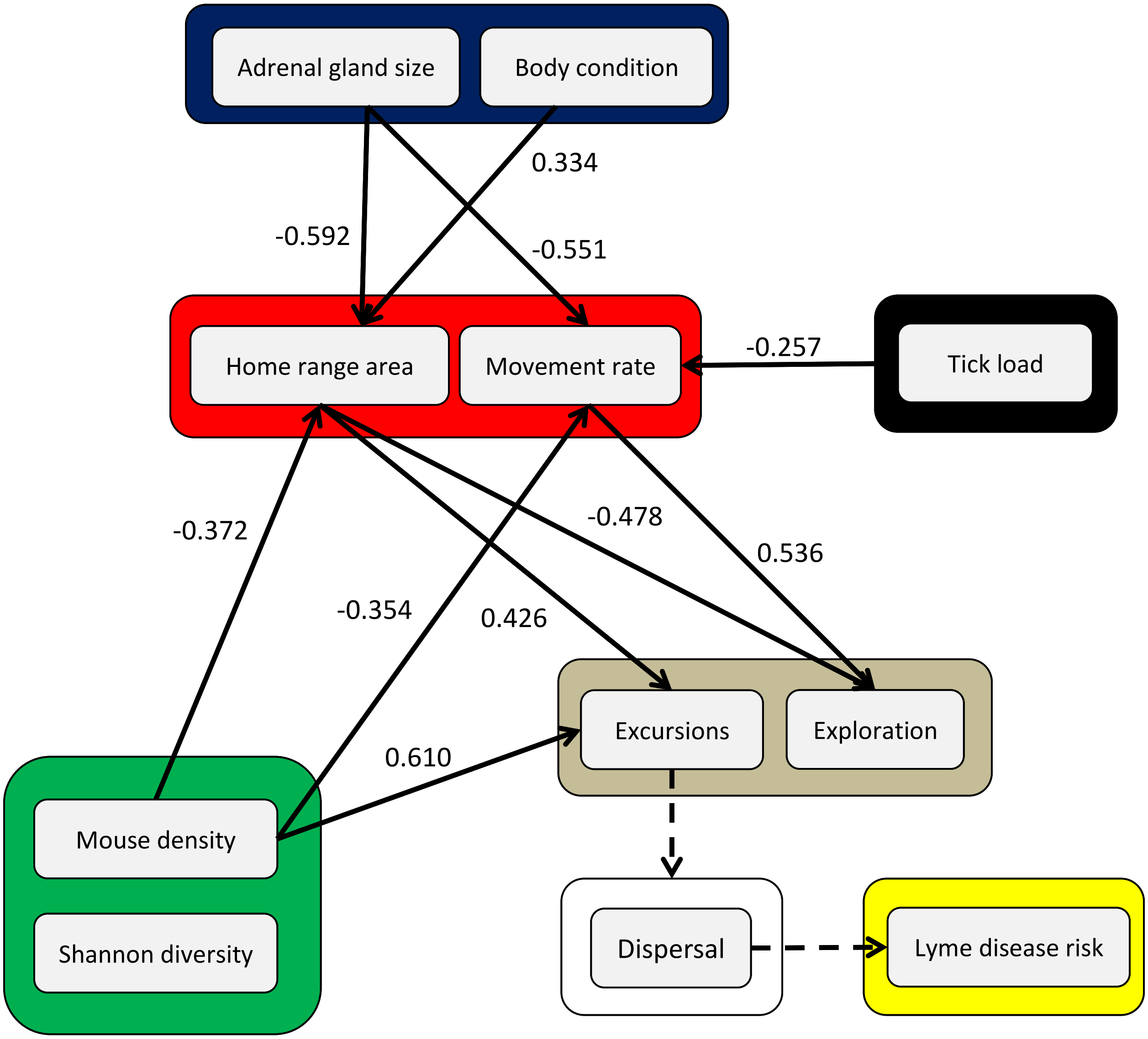


Figure 2.2


Adrenal gland size
Body condition
0.334
-0.592
-0.551
Home range area
Movement rate
-0.257
Tick load
-0.372
-0.478
0.536
-0.354
0.426
Excursions
Exploration
0.610
Mouse density
Shannon diversity
Dispersal
Lyme disease risk

GENERAL CONCLUSION

In this thesis I investigated the movement patterns of the white-footed mouse at the northernmost limit of its current distribution, as a part of a series of projects on the biology of this species as a main reservoir for the emerging Lyme disease in southern Quebec. I used direct tracking method in the field, to evaluate the effect of a number of factors on the movement pattern of the white-footed mouse. I considered individual level-factors such as the adrenal grand size as a proxy of the glucocorticoid production of the animal; the body condition as an indicator of the energetic capabilities of the organism. I also included in the analyses community-level factors such as the population densities of white-footed mice in the sampling areas as an indirect measurement of intra-specific competition; the micro-mammal species richness as an indicator of inter-specific competition; the parasite load of four ecto-parasites; and some forest patch characteristics including forest patch area and edge proportion (Romero *et al.* 2008).

Radio-telemetry tracking proved to be a powerful tool to document real-time movements inside and beyond forest patches. The advantage of this technique overcomes the problems of constantly capturing-recapturing procedures where a captured individual is immediately stopped from proceeding with its activities (Hicks *et al*. 1998). This technique also avoids constant manipulation by the researcher, which add to the biological accuracy of the observations (Harris et al. 1990).

Even though we did not find the combination of stressors that the cause the change on the adrenal gland sizes, my results suggest that factors affecting this aspect of their physiology have marked consequences on locomotor behaviours. These results add to the line of evidence of Belthoff and Dufty (1998) who found the cortisol levels and body condition of screech-owls to influence their locomotor activity. The measurement of stress hormones in small mammal can be informative even when other aspects of the stress physiology for fast-paced animals seem to make them impervious to the negative effects of stress (Réale *et al*. 2010). Further work on the physiology of the white-footed mouse may provide us with the information we need to explain the variation in stress level, including measuring directly factors like intra and inter-specific competition, resources availability and predator pressure.

The effect of the population density on the movement pattern was also an interesting finding. Although we did not detect a significant relation between mouse density and stress level estimated from the adrenal gland size, the mouse density in a forest patch appears to be a good predictor on the locomotor behaviour of the white-footed mouse. Patches with higher densities had mice that moved less and had smaller home ranges, but also mice that left the forest patches more often. Considering the importance of this reservoir in the Lyme disease dynamics (Ostfeld 2009), these findings can be used to plan and prepare for this emerging disease, considering that areas with higher white-footed mouse densities will also have mice more prone to leave them. Incidentally, those mouse individuals that tended to disperse more also carried more black-legged ticks, the vector for Lyme disease. These excursions of the white-footed mouse outside the forest patch will have two important consequences on the spread of the disease: first, mice will have more chance to enter in contact with human populations; and second, these individuals will be colonizing new habitats, further accelerating the rate of spread of Lyme disease in its area of emergence (Simon *et al.* 2014).

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