

UNTANGLING URBAN RAT-ASSOCIATED HEALTH RISKS IN  
DISADVANTAGED NEIGHBOURHOODS – FROM MOVEMENT TO  
MENTAL HEALTH

by

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Untangling urban rat-associated health risks in disadvantaged neighbourhoods – from movement to mental health

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## ABSTRACT

Urban Norway rats (*Rattus norvegicus*) carry a number of pathogens transmissible to people, and the prevalence of these pathogens can vary across fine spatial scales. While pathogen prevalence is an important determinant of human health risk, the transmission of these pathogens to people is closely linked to how rats and humans interact in cities.

In this thesis, I investigated how interactions between urban rats, their environment, and people could influence human health risks. To do this, I explored whether rat movement could explain heterogeneous patterns of pathogen prevalence. First, in **Chapter 2**, I synthesized the published literature and found that rat movement is largely restricted by resource availability and landscape barriers such as roadways. Then, in Chapters 3 – 5, I combined ecological and genomics-based approaches to describe rat movement in Vancouver’s Downtown Eastside, an area where pathogen clustering has been previously documented. In **Chapter 3**, I demonstrated that movement estimates derived from capture-mark-recapture methods are prone to bias due to smaller individuals more frequently re-entering traps than larger individuals. Given issues of unequal trappability, in **Chapter 4**, I evaluated the utility of using Global Positioning System tags to track urban rats and found that these tools are currently ineffective due to tag loss and signal obstruction. In **Chapter 5**, I used rat genetics to identify related individuals and the distances between them. I demonstrated that 99% of highly related rat pairs (i.e., parent-offspring and full-sibling pairs) were trapped in the same city block, revealing infrequent dispersal among blocks, which aligned with patterns of pathogen clustering in this population. Finally, in **Chapter 6**, I interviewed residents of this neighbourhood about their experiences living with rats and illustrated that frequent and close contact with rats negatively impacted the mental health of residents.

Overall, my research suggests that minimal movement of rats may lead to a clustering of rat-associated pathogens. Further, my work reveals that even in the absence of disease, interactions with rats may negatively impact the mental health of those living with them. Together, this information can be used to more effectively manage rat-associated health risks in cities.

## LAY SUMMARY

Urban rats transmit a number of disease-causing organisms, called pathogens, to people. Yet while rats are found throughout cities, the distribution of these pathogens can vary across neighbourhoods, with some city blocks having many affected rats and others having none. Understanding what drives these patterns is important because this information can inform rat management. In this thesis I combine ecological and genomics-based methods to study rat movement in Vancouver's Downtown Eastside. I demonstrate that rats rarely move among city blocks, suggesting that minimal movement may prevent pathogens from spreading to surrounding areas. Further, in interviews with residents of this neighbourhood, I document that rats can also negatively impact the mental health of those living with them. Together, my findings suggest that decisions to control rats should consider both their impacts on psychological and physical health, and that effective approaches should be scaled to encompass the extent of rat movement.

## PREFACE

**Ethics Approval:** Studies included as part of this thesis received approval from the UBC Research Ethics Board. Activities involving the trapping and handling of urban rats were approved by the University of British Columbia's Animal Care Committee (A11-0087 and A14-0265). Handling of rat tissues and hazardous materials were approved by the University of British Columbia's Biosafety Committee (B15-0097 and B15-0179). Research involving interviews with residents of Vancouver's Downtown Eastside was approved by the University of British Columbia's Providence Health Care Research Ethics Board (H16-02743).

**Published Chapters:** Most chapters in this thesis have been previously published in peer-reviewed academic journals. Below I have indicated my contributions to each manuscript.

A version of **Chapter 2** has been published as:

Byers KA, Lee MJ, Patrick DM, Himsforth CG (2019) Rats About Town: A systematic review of rat movement in urban ecosystems. *Frontiers in Ecology and Evolution*, 7,13.

I conceived of this literature review, and I identified the search criteria with MJL and CGH. Both MJL and I determined which literature to include and extracted the data from the relevant publications. I analyzed the resulting data and wrote the manuscript with assistance from MJL and comments from CGH. All co-authors contributed to revising the manuscript for publication.

A version of **Chapter 3** has been published as:

Byers KA, Lee MJ, Bidulka JJ, Patrick DM, Himsworth CG (2019) Rat in a cage: Trappability of urban Norway rats (*Rattus norvegicus*). *Frontiers in Ecology and Evolution*, **7**, 68.

This manuscript is co-first authored. The study was conceived of by myself, MJL and CGH, and I acquired the necessary funding to perform the fieldwork. Both MJL and I collected and analyzed the data for this paper. I wrote the majority of the manuscript with significant contributions from MJL. All co-authors contributed to revising the manuscript for publication.

A version of **Chapter 4** has been published as:

Byers KA, Lee MJ, Donovan CM, Patrick DM, Himsworth CG (2017) A novel method for affixing Global Positioning System (GPS) tags to urban Norway rats (*Rattus norvegicus*): Feasibility, health impacts and potential for tracking movement. *Journal of Urban Ecology*, **3**, 1-7.

I conceived of this study and acquired the necessary funding to perform the fieldwork. Data collection was performed by me, MJL and CMD. I analyzed the data and wrote the manuscript. All co-authors contributed to revising the manuscript for publication.

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I conceived of this study, which was designed in collaboration with TRB and MCW. Funding for this study was acquired by me, CGH, and JMS. Rat tissue samples were previously collected and tested for pathogens by CGH. To obtain genetic data from these samples, I performed the laboratory work, and the resulting genetic data was first filtered by MC. The data was analyzed by me, TRB, and MC with significant contributions from JMS and MCW. I wrote the majority of the manuscript with contributions from MC and significant edits from TRB. All co-authors contributed to revising the manuscript for submission.

A version of **Chapter 6** has been published as:

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I conceived of this study with CGH, and I designed the study with SMC and CGH. I acquired the necessary funding to perform this research. Both RL and I interviewed study participants, and I transcribed the interviews and analyzed the data with input from SMC. I wrote the manuscript with significant contributions from SMC. All co-authors contributed to revising the manuscript for publication.

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## LIST OF ABBREVIATIONS

AIC – Akaike Information Criterion

CMR – Capture-Mark-Recapture

ddRADseq – double digest Restriction Site Associated DNA sequencing

DTES – Downtown Eastside

GPS – Global Positioning System

MRSA – Methicillin-Resistant *Staphylococcus aureus*

OR – Odds Ratio

PCR – Polymerase Chain Reaction

PIT – Passive Integrated Transponder

RFID – Remote Frequency Identification

SNP – Single Nucleotide Polymorphism

SRO – Single Room Occupancy

VANDU – Vancouver Area Network of Drug Users

VHF – Very High Frequency

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*Dedicated to Lobester and Bertha,*

*For filling my life with love, opportunity, and endless Brule shore sunsets;*

*and to Sheila,*

*For handing me a microscope and encouraging me to look through it*

*“Rats!*

*They fought the dogs, and killed the cats,*

*And bit the babies in the cradles,*

*And ate the cheeses out of the vats,*

*And licked the soup from the cooks’ own ladles,*

*Split open the kegs of salted sprats,*

*Made nests inside men’s Sunday hats,*

*And even spoiled the women’s chats*

*By drowning their speaking*

*With shrieking and squeaking*

*In fifty different sharps and flats.”*

*Robert Browning, 1842, The Pied Piper of Hamelin*

# CHAPTER 1: INTRODUCTION

## 1.1 EMERGING INFECTIOUS DISEASES AND ‘ONE HEALTH’

In late 2019, a novel coronavirus (SARS-CoV-2) emerged in people in the city of Wuhan, China (Centres for Disease Control and Prevention 2020). In just a few months, this virus rapidly spread to 212 countries and territories, infecting over three and a half million people (Worldometer, 2020). Although human-to-human transmission is driving the current public health crisis, genetic evidence suggests that SARS-CoV-2 is zoonotic (transmitted from animals to people) (Andersen *et al.* 2020), with the virus originating in bats (Zhou *et al.* 2020). Coronavirus Disease 2019 (COVID-19) is just the most recent in a string of infectious diseases that first arose in animals (e.g., Ebola, MERS, SARS, Zika) (Jones *et al.* 2008b). Indeed, there have been over 87 new zoonotic agents discovered since 1980 (Gebreyes *et al.* 2014), with over 75% of emerging infectious diseases in people originating in animals (Taylor *et al.* 2001). The current global health emergency, as well as trends indicating an increased frequency in pandemics in recent years (Jones *et al.* 2008b) underscore that zoonoses, particularly those associated with wildlife, pose a significant and growing threat to human health (Daszak *et al.* 2000).

To tackle the complexity of emerging zoonoses, an interdisciplinary ‘One Health’ approach has widely been recognized as a valuable framework for assessing and mitigating zoonotic risks. Although lacking a formal definition, One Health considers the health of humans, animals, and ecosystems to be interdependent (Daszak *et al.* 2000; Gibbs 2014; Cunningham *et al.* 2017). Within this framework, urban environments are increasingly studied as hotspots for emerging zoonoses, as they serve as hubs for pathogen introductions (Rachowicz *et al.* 2005), and they provide optimal habitat for certain wild species, bringing wildlife into close contact with people

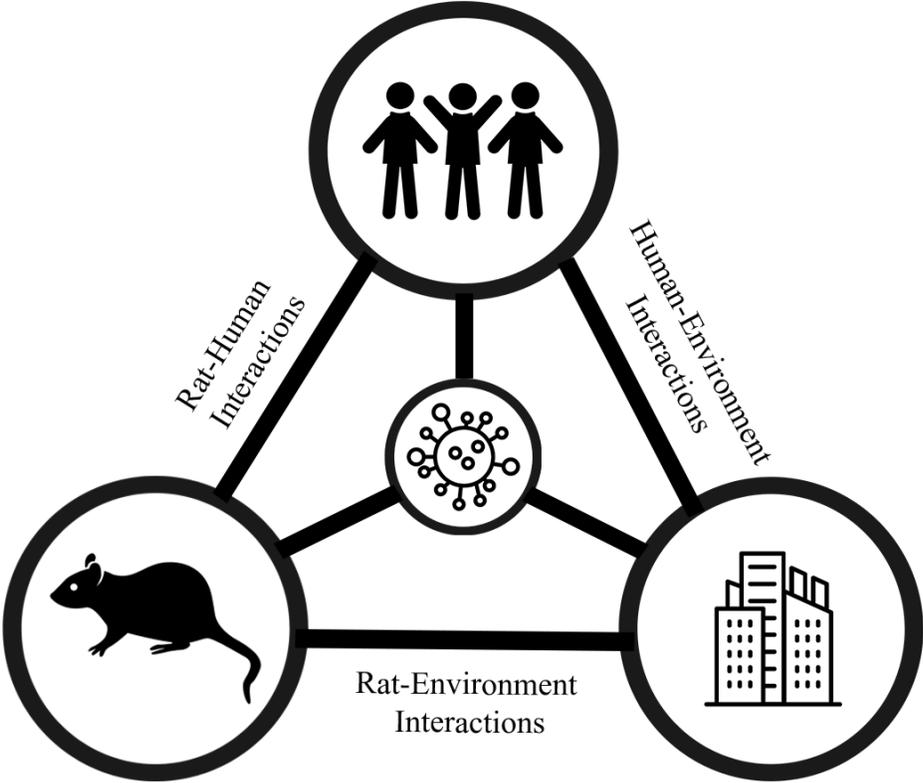
(Luniak 2004). Given the unprecedented rate of global urbanization (United Nations 2018) an understanding of urban zoonotic disease risks is essential for early outbreak detection and control.

## 1.2 THE CASE FOR STUDYING URBAN RATS

Of the wild animals that live in cities, rats (*Rattus* spp.) are perhaps the most notorious because of the frequency and severity with which they infest urban areas as well as their tendency to interact with people (Himsworth *et al.* 2013b). Historically, rats have been associated with significant human disease (Bitam *et al.* 2010; Himsworth *et al.* 2013b), and they continue to be the source of a number of important pathogens (i.e., *Bartonella* spp., *Leptospira interrogans*, *Rickettsia typhi*, *Yersinia pestis* and Seoul Hantavirus) responsible for human morbidity and mortality in cities globally. In fact, rat-associated diseases are estimated to have killed more people in the last ten centuries than all of the wars combined (Nowak 1999).

Management of rat-associated health risks remains challenging because much of the focus has centred on detected disease in people. Yet, in North America, there are very few human cases of rat-associated illness (Vinetz *et al.* 1996; Comer *et al.* 2001; McVea *et al.* 2018), which can partly be attributed to under-detection as many such illnesses present with nonspecific symptoms. (i.e., chills, fever, headache rash etc. (Levett 2001; Adjemian *et al.* 2010; Billeter *et al.* 2014)). For example, leptospirosis, caused by the pathogenic bacterium *L. interrogans*, is estimated to affect one million people annually (Guerra 2009), but is commonly misdiagnosed as malaria, dengue, or other forms of illness (Costa *et al.* 2015a). Using detected disease in people to inform when and where to enact rat management is problematic because it leads to reactionary and ineffectual responses (Colvin and Jackson 1999; Meyer 2003; National Association of Country and City Health Officials 2015) which fail to address the underlying dynamics which promote pathogen

transmission to people. Instead, the One Health framework encourages a broader focus that also considers the factors that promote pathogen spread between rats and people within the local environment to inform mitigation efforts (Figure 1-1).



**Figure 1-1. A One-Health framework for assessing rat-associated health risks.** This framework considers the interconnectedness of human, animal, and environmental health in devising and deploying mitigation strategies.

### 1.3 THE VANCOUVER RAT PROJECT

Despite the fact that rats have lived alongside humans for centuries, the nuances of rat-associated health risks in cities remain surprisingly understudied. This paucity of information is particularly apparent in Canada, where, prior to the founding of the Vancouver Rat Project in 2011, there had not been a rigorous attempt to identify or evaluate rat-associated health risks in Canada's urban centres. Recognizing this important knowledge gap, the Vancouver Rat Project endeavoured to characterize the distribution and prevalence of rat-associated pathogens in Vancouver's Downtown Eastside (DTES), a disadvantaged urban neighbourhood where frequent rat-human interactions (McVea *et al.* 2018) could exacerbate rat-associated health risks. Given its novelty, the Vancouver Rat Project made a number of ground-breaking discoveries regarding how pathogens are distributed among rats, and how their prevalence relates to rat characteristics and environmental features (i.e., Himsworth *et al.* 2013a; 2014a; 2014c). However, as is typical of many foundational studies, the Vancouver Rat Project uncovered more questions than it had answers for.

Among the most striking findings derived from the Vancouver Rat Project was evidence that the prevalence of rat-associated pathogens varied significantly across fine spatial scales (i.e., by city block). For example, while rats carried the pathogenic bacterium *L. interrogans*, prevalence among rats varied from 0 – 66.7% by city block (Himsworth *et al.* 2013a). A similar pattern was evident for the bacterial pathogen *Bartonella tribocorum*, which ranged in prevalence from 0% – 60.5% by city block (Himsworth *et al.* 2015a). Although certain demographic characteristics such as rat weight or maturity were associated with infection status for rats, much of the variation in pathogen prevalence remained unexplained after controlling for factors such as season and morphometric/demographic characteristics. This suggested that other aspects of rat ecology,

particularly how rats interact with each other within the urban environment, might drive these patterns.

The Vancouver Rat Project also made important strides in characterizing human health risks. Interestingly, this work demonstrated that rats and people in this neighbourhood carried genetically similar isolates of the bacterial pathogen methicillin-resistant *Staphylococcus aureus* (MRSA) (Himsworth *et al.* 2014b). And although it remains unclear whether rats play a role in the transmission of this pathogen, the project demonstrated that people living in this neighbourhood have frequent interactions with rats suggesting that there are opportunities for pathogen spread (McVea *et al.* 2018). Ultimately, this underscored that there was an additional need to characterize the interactions between rats and people to better assess rat-associated health risks.

Ultimately, by largely focusing on rats and people independently, the Vancouver Rat Project revealed a need to shift focus from rats and people as separate entities to the interactions between them to better characterize rat-associated health risks.

#### **1.4 RAT – ENVIRONMENT INTERACTIONS**

Understanding the spatial dynamics of wildlife is critical to deciphering the ecology of the pathogens that they carry as well as the health risks that they pose. This is because the extent to which animals utilize the environment dictates the epidemiology of their associated pathogens (Volkova *et al.* 2010; Quixabeira-Santos *et al.* 2011; Guivier *et al.* 2011). Information on movement and contact among individuals is especially important for understanding rat-associated zoonotic spread because many of the pathogens carried by rats are transmitted through contact among individuals, either directly or indirectly through biting (Childs *et al.* 1998), exposure to urine and feces (Meerburg *et al.* 2009), or via arthropod ectoparasites (Bitam *et al.* 2010). Further, rats live in tight-knit social groups, with frequent contact among colony members and little overlap

between rats of neighbouring colonies (Calhoun 1963). Therefore, urban features which either promote or hinder rat movement and interactions among rat colonies are likely to impact pathogen spread, as well as determine where people are most likely to come into contact with rats and their pathogens. Given what is known about the ecology of urban rats, in combination with pathogen clustering evidenced in Vancouver's DTES, differences in pathogen prevalence among block-level rat populations may derive from connectivity of rats between city blocks.

Although there has been a global effort to identify the pathogens carried by rats (Himsworth *et al.* 2013b) there is very little data on how rats navigate the urban environment. This is due, in part, to the challenges associated with studying them (Parsons *et al.* 2017; Desvars-Larrive *et al.* 2018a) including their neophobic nature (Barnett 1963) and tendency to spend much of their time underground or hidden by vegetation (Schweinfurth 2020). Indeed, much of the baseline knowledge about urban rat movement ecology was sourced from just a few studies performed in New York and Baltimore nearly 60 years ago (Calhoun 1948; Davis 1953a; Davis and Christian 1956; Calhoun 1963). There are, however, a number of ways to track rat movement including direct observation, capture-mark-recapture methods (CMR; which involve capturing, tagging, and recapturing rats), and genomics-based approaches which infer movement distances based on the relative locations of closely related individuals to each other. As I have previously published a review paper on urban rat movement, I include detailed information about the application of these tools and what is known about urban rat movement in Chapter 2. Ultimately, an understanding of rat spatial ecology is paramount to informing efforts aimed at mitigating rat-associated health risks. This is because information on rat movement can be used to scale rat management practices to encompass the extent to which rats move.

## **1.5 RAT – HUMAN INTERACTIONS**

Although the focus on rat-associated health risks has almost exclusively focused on the pathogens carried by rats (Himsworth *et al.* 2013b), in North America, there are very few published cases of infection in people (i.e., Vinetz *et al.* 1996; Comer *et al.* 2001; McVea *et al.* 2018). Using human disease as the sole marker for determining whether rat infestations require control is problematic because without evidence of disease in people, municipalities may underestimate the negative impacts of rats and place less value on proactive mitigation and control efforts. Indeed, recent research demonstrates that rat infestations can also impact the mental health of those that live with them (German and Latkin 2016). Specifically, the awareness of rats in and around the home can serve as a chronic stressor, affecting both the mental and physical health of residents (German and Latkin 2016; Lam *et al.* 2018). These issues may be exacerbated in disadvantaged urban neighbourhoods as factors associated with poverty are thought to promote rat infestations and rat-human contact (Feng and Himsworth 2014). Although overlooked, this is an important component of the One Health framework because it more holistically evaluates human health outcomes in relation to the intersection of people, wildlife, and the environment. Further, an understanding of how people come into contact with rats can clarify the events which bring rats and people into close association and can thus highlight opportunities for preventing these interactions.

## **1.6 KNOWLEDGE GAPS, AIMS, AND APPROACHES**

It is clear that the implementation of a One Health framework to assess and address rat-associated health risks requires robust information not only on disease in rats and people, but also on the interactions between rats and their environment, and the interactions between rats and people. Building on the original work of the Vancouver Rat Project, I have identified two important

knowledge gaps to be addressed in this thesis: 1) a lack of information on urban rat movement ecology and its relation to pathogen distributions; and 2) a paucity of data on how living with rats affects the mental health of those that live with them. In this thesis, I take an interdisciplinary approach to build an understanding of how the ecology of urban rats, and their interactions with people, intersect to affect human health in Vancouver's DTES.

In **Chapter 2**, I aimed to build a baseline understanding of rat movement. To do this, I collated and synthesized the published literature detailing rat movement in urban settings. This review was used to inform fieldwork performed as part of this thesis by identifying important considerations for studying rat movement, such as rat trappability and appropriate study methods.

In **Chapters 3 – 5**, I endeavored to describe rat movement patterns in Vancouver's DTES in relation to distributions of pathogen prevalence previously described in this population (Himsworth *et al.* 2013a; 2014d; 2015a). Based on the literature review in Chapter 2, I first evaluated whether certain rat characteristics influenced their trappability. I determined this as an important first step because differences in trappability could bias movement estimates toward more robust data for those individuals more likely to re-enter traps. To evaluate trappability, in **Chapter 3** I designed an eight-month intensive capture-mark-recapture study in Vancouver's DTES. This study focused on the trapping, tagging, and recapture of rats where I collected information on trap location, rat demographics and morphometrics. As part of this work I also collected blood, urine, and fecal samples to test for zoonotic pathogens. I used statistical analyses to determine whether rat trappability was influenced by rat demographic characteristics and infection status.

Further informed by the literature review in Chapter 2, I aimed to use two complementary methods to describe rat movement. In **Chapter 4**, I evaluated the utility of using Global Positioning System (GPS) tags to track movement by tagging a subset of rats and observing the

duration of tag attachment. In **Chapter 5**, I utilized epidemiological data and rat tissue samples previously collected in the first phase of the Vancouver Rat Project. I performed genomics-based analyses to identify closely related rats (i.e., parent-offspring and sibling pairs) to infer distances travelled by relatives. These movement events were then compared to patterns of pathogen prevalence for three pathogenic bacteria carried by rats (*L. interrogans*, *B. tribocorum*, and *Clostridium difficile*) to elucidate the role of rat movement ecology in the clustering of these pathogens.

To address the role of rat-human interactions in human health outcomes, in **Chapter 6**, I explored the scope of health effects associated with rats. To do this, I interviewed residents of Vancouver's DTES to record their experiences living with rats and the impacts of those experiences on their physical and mental health. Using these interviews, I documented the extent to which people in this neighbourhood interacted with rats as well as the frequency and circumstances of these interactions. I draw on these experiences to illustrate what these scenarios suggest about the broader impacts of rats on the health of urban residents.

Finally, in **Chapter 7** I synthesize the findings of my research to make recommendations regarding how municipalities can use this information to mitigate rat-associated impacts in cities. More broadly, I discuss possible ways in which a One Health framework can be applied to health issues associated with urban rats and wildlife generally.

# CHAPTER 2: RATS ABOUT TOWN: A SYSTEMATIC REVIEW OF RAT MOVEMENT IN URBAN ECOSYSTEMS

## 2.1 SYNOPSIS

Norway and black rats (*Rattus norvegicus* and *Rattus rattus*) are ubiquitous urban pests, inhabiting cities worldwide. Despite their close association with people, urban rats remain difficult to control. This can be partly attributed to a general lack of information on basic rat ecology to inform management efforts. In this systematic review and narrative synthesis, we collate the published literature to provide a comprehensive description of what is known about urban rat movement, including information on home range, site fidelity, dispersal, movement patterns, barriers to, and factors impacting, movement. We also discuss the methodologies used to track and infer rat movement, as well as the advantages and limitations of employing these techniques. Our review suggests that the distances travelled by urban rats are location-specific, determined by both local resource availability and barriers to movement such as roadways. Although roads may impede rat movement, genetic techniques suggest that rats traverse roadways more often than revealed by capture-based tools, while long-distance dispersal events by either natural migration or facilitated by humans (i.e., as stowaways in transport vehicles) can maintain connectivity among distant populations. Because rat movement patterns are related to the transmission of rat-associated pathogens and the success of rodent control programs, these results have implications for city planners, pest control efforts, and public health. Therefore, we emphasize the importance of understanding local rat movement patterns in order to devise and deploy efficient and effective rat mitigation initiatives in urban centers.

## 2.2 INTRODUCTION

The presence of urban Norway and black rats (*Rattus norvegicus* and *Rattus rattus*) is an important and growing issue in cities globally due to their associated health and economic impacts (Feng and Himsworth 2014). For example, rats pose a risk to public health as they are the source of a variety of zoonotic pathogens (disease-causing microbes transmissible from rats to people, e.g., *Leptospira interrogans*) responsible for significant human morbidity and mortality (Himsworth *et al.* 2013b). Infestations can also serve as a chronic stressor, impacting both the mental and physical health of residents (German and Latkin 2016; Lam *et al.* 2018). Rats also damage urban infrastructure (due to chewing and burrowing activities) and contaminate foodstuffs. Finally, infestations can result in substantial economic losses, both directly (i.e., costs associated with rat control), and indirectly (i.e., costs associated with mitigating and repairing rat-associated damage) (Pimentel *et al.* 2005; Almeida *et al.* 2013). Given rapid urbanization, these issues are likely to increase in future; 55% of the world's population resides in cities, with a projected increase to 68% by 2050. Much of this growth will occur in developing regions (United Nations 2018) where rat-associated risks are higher due to issues of inadequate housing, infrastructure, and sanitation (Himsworth *et al.* 2013b). Further, a lack of effective tools to address rat infestations (Parsons *et al.* 2017) underscores the importance of re-thinking our current approaches to rat control.

To monitor and mitigate the impact of rats, an understanding of their spatial ecology is paramount. For example, the ways in which animals navigate and interact with the environment dictates both the epidemiology of the pathogens they carry (Volkova *et al.* 2010; Quixabeira-Santos *et al.* 2011; Guivier *et al.* 2011) as well as the scale at which pest control efforts will have the greatest success (Bomford and O'Brien 1995; Robertson and Gemmell 2004; Adams *et al.* 2014). One of the most significant remaining knowledge gaps relevant to describing the spatial

ecology of urban rats is information regarding the extent of their home range (Desvars-Larrive *et al.* 2018a). The home range represents the area frequented by an individual (Davis *et al.* 1948) and typically encompasses areas used for food acquisition, mating, and rearing young (Burt 1943). However, as individuals differentially use areas of their home range according to factors such as age, sex, population density, season, and environmental variability (Wolff 1985; Cederlund and Sand 1994; Wiktander *et al.* 2001; Dahle and Swenson 2003; Kjellander *et al.* 2004; Börger *et al.* 2006; Safi *et al.* 2007), or may even migrate to new home ranges (Burt 1943), information on home range size alone may underestimate the true area traversed by rats.

Beyond home range size, spatial ecology requires an understanding of the detailed movements of rats within cities. This includes information on dispersal distances (i.e., movement away from the natal or home area) (Drickamer 1987), and how features of, or changes to, the urban environment impact movement. For example, a meta-analysis found that terrestrial mammals residing in cities travelled shorter distances than did their non-urban counterparts (Tucker *et al.* 2018). This reduced structural connectivity may result from the varied quality and size of habitat patches in cities (Dickman and Doncaster 1987), as well as the physical barriers posed by roadways (Rondinini and Doncaster 2002). However, as rats can occupy habitats with a diverse set of characteristics (Himsworth *et al.* 2014c) they may exhibit greater structural connectivity than other urban wildlife.

The objective of this review is to summarize, compare, and evaluate the published literature detailing the movement patterns of urban Norway and black rats. We describe the tools that have been used for studying urban rat movement as well as the challenges of employing these techniques. Finally, we describe how information regarding the spatial ecology of rats may be of

relevance to different stakeholders and identify remaining gaps in knowledge to be addressed in future ecological research.

## **2.3 METHODS**

### **SEARCH STRATEGY**

From May 2018 – July 2018 we performed systematic searches following the approach outlined by (Moher *et al.* 2009). Our search included the databases: Web of Science CORE, CAB Direct, JSTOR, Medline, and Zoological Record. We used keyword combinations pertaining to the following concepts: Rats (*Rattus norvegicus*”, “Norway rat\*”, “brown rat\*”, “*Rattus rattus*”, “black rat\*”, “roof rat\*”), movement (dispersal, emigration, expansion, immigration, migration, movement, boundaries, distribution, domain, “home range\*”, “home area\*”, “site fidelity”, territory, zone) and the urban environment (urban, city, cities, municipal, suburban, residential, metropolis, metropolitan). The groups of keywords within each concept were combined using the Boolean operator ‘OR’ and concepts were combined using ‘AND’ (see Supplemental Table S2-1). We included literature from the earliest cut-off date for each database.

### **STUDY SELECTION**

Titles and abstracts were screened for eligibility using the abstract screener function in METAGEAR (Lajeunesse 2016). This package presents paper titles and abstracts in a graphical user interface for reviewer coding for inclusion or exclusion. Thirty percent of papers were screened by two authors (KAB and MJL) to ensure screening consistency. Articles deemed eligible in the first round of screening were reviewed in full by both KAB and MJL. Papers were excluded if they focused on rural rat populations, global rat migration patterns, or did not measure aspects of rat

movement (either directly or indirectly). Literature in languages other than English were excluded. Additional sources were added through citation searching.

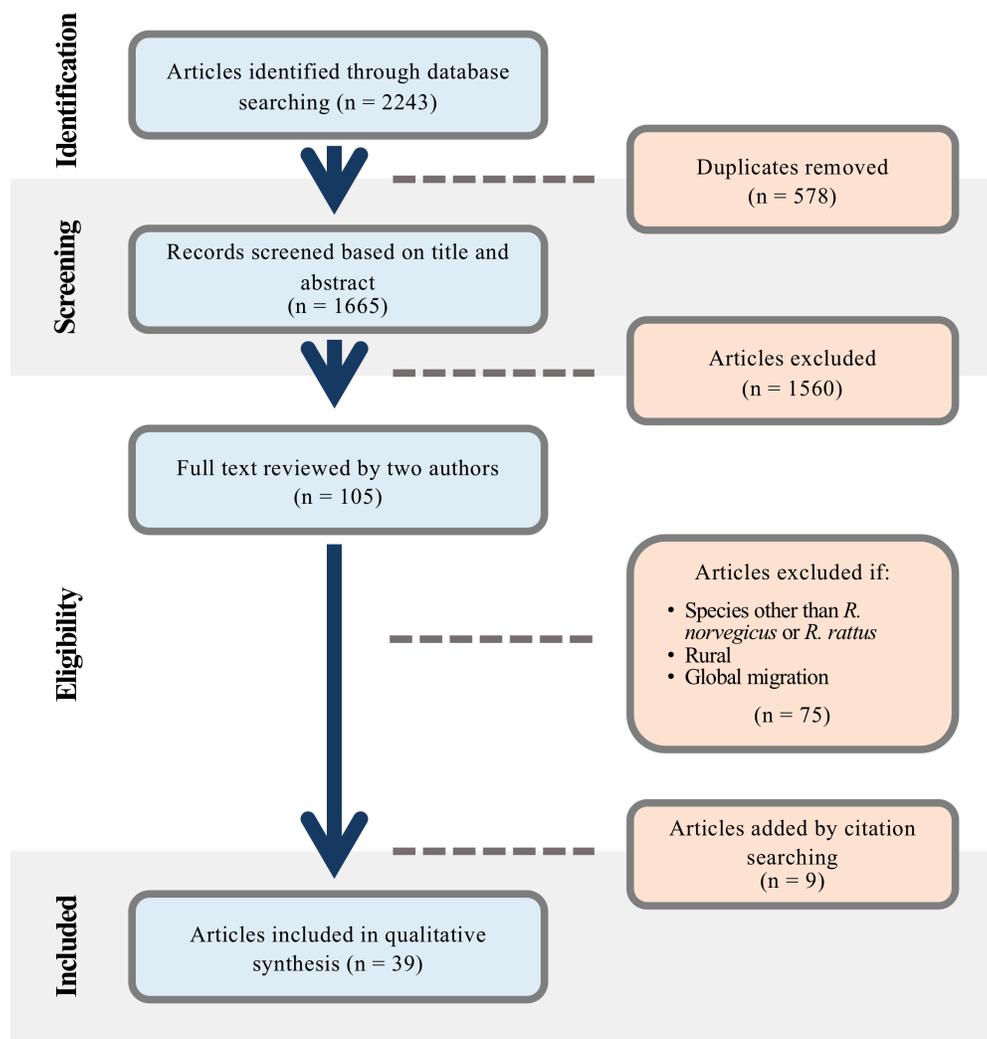
## **DATA COLLECTION AND ANALYSIS**

Included papers were grouped by trapping methodology (i.e., continuous tracking, capture-mark-recapture, genetic techniques, and proxy methods). The content of each paper was summarized using a matrix method (Garrard 2013) in which a number of categories relevant to describing the study characteristics (i.e., study location, study scale, species studied, sample size, methods used) and rat movement (i.e., home range, dispersal, areas and extent of movement, factors impacting movement, other relevant findings) were determined *a priori*. Each paper was reviewed and summarized according to these categories, and we compared information within each category across studies. Findings were synthesized using a narrative synthesis methodology which involves summarizing the findings of multiple works in text format (Arai *et al.* 2007). The following synthesis pertains to Norway and black rat movement patterns in urban ecosystems and is reviewed within seven themes derived during the synthesis: study design, home range, site fidelity, dispersal, movement patterns, barriers to movement, and factors impacting movement.

## **2.4 RESULTS**

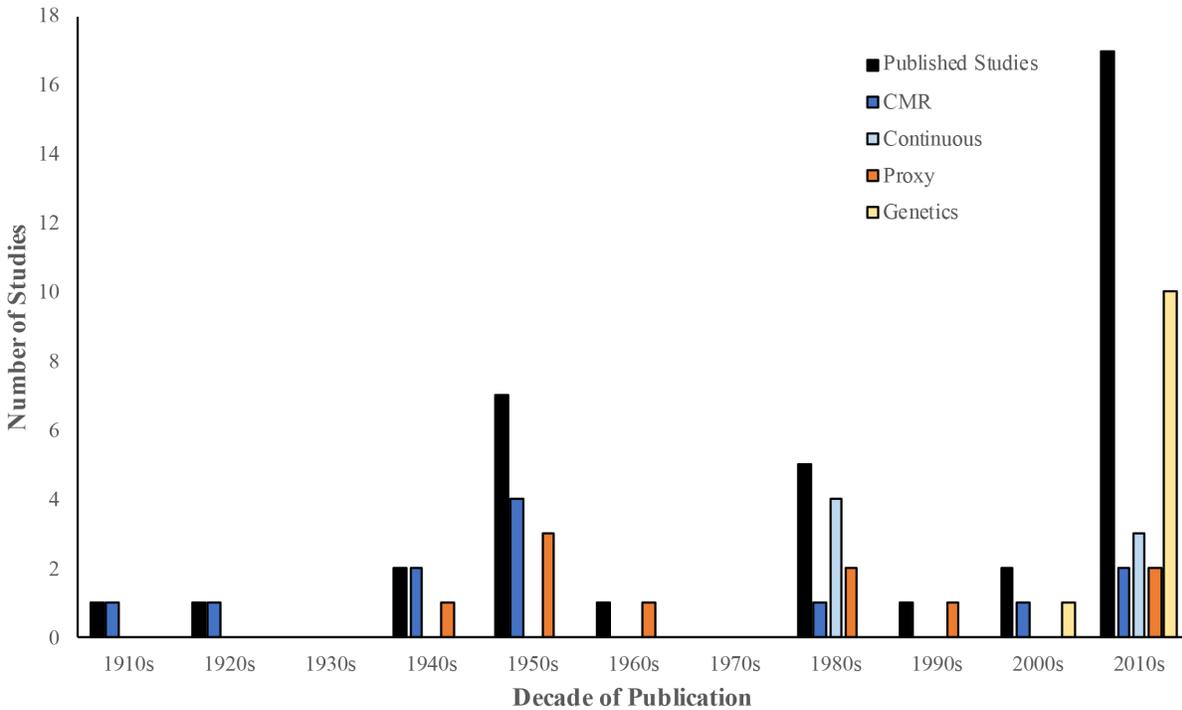
### **STUDY SELECTION AND CHARACTERISTICS**

Our initial search resulted in 1665 sources, 105 of which were reviewed in full (Figure 2-1). Of the final group of 39 papers, two were extensions of other included studies that contained additional relevant information. Therefore, we reviewed 37 unique studies examining the movements of Norway rats (N = 30), black rats (N = 6), or both (N = 1).



**Figure 2-1: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow chart depicting the screening process of articles included in the narrative synthesis.**

Although published research on rat movement occurs as early as 1915, nearly half (48.6%; N = 18) of included studies were published in the past decade (Figure 2-2), and approximately half (51.4%; N = 19) were conducted in North America (Supplemental Table S2-2). See Supplemental Table S2-3 for details of the included studies.



**Figure 2-2: The number of unique published studies (N = 37) included in the review by decade of publication.** Within each decade, the number of studies employing direct (capture-mark-recapture (CMR) and continuous tracking), and indirect methods (proxy measures and genetics-based tools) to assess rat movement are indicated.

## STUDY DESIGN

In general, all studies sought to describe urban rat ecology, but most (56.8%; N = 21) explicitly mentioned using this information to inform pest control. Both direct and indirect methods were employed in the study of rat movement (Figure 2-2). Direct measures included capture-mark-recapture (CMR; N = 12) and continuous tracking (e.g., direct observation, radio-tracking, and Global Positioning Systems (GPS); N = 7). Indirectly, movement was assessed through proxy measures of rat movement (e.g., track pads, rat tracks in snowfall, bait uptake, and feces marked with bait-specific dye; N = 11) and population genetics-based techniques (N = 11). In some instances (N = 3), multiple methods were employed. See Box 2-1 for an overview of these tools.

**Box 2-1: An overview of methods commonly used for studying urban rat movement, their benefits, and limitations**

**Direct Measures:** To quantify the movements of urban rats, many studies rely on trapping-based techniques. **Capture-mark-recapture (CMR)** methods involve trapping and tagging individuals (e.g., with numbered ear tags or Passive Integrated Transponder (PIT) tags) for future identification. Following tagging, animals are released at their original point of capture and are later recaptured. Movement is determined by measuring the distances between the traps in which rats are caught, or in the case of PIT tags, by the distances between sensor stations through which rats pass (Parsons *et al.* 2015). In this way, PIT tags are advantageous as they decrease handling-time of rats. Although these tools allow researchers to track large numbers of rats (e.g., 341 in Petrie (1923)), they are labor-intensive, rely heavily on trap placement, and yield fragmented data as they do not account for movement between capture points (Hayne 1949; Glass *et al.* 2016). Moreover, these techniques are hindered by the neophobic nature of rats, which can result in low recapture rates and trapping bias (Barnett 1963; Tanaka 1963; Taylor and Quay 1978).

To derive more complete descriptions of movement patterns, researchers have **directly observed** the behaviours of individual rats (Calhoun 1963; Takahashi and Lore 1980; Glass *et al.* 1989); but, this strategy is limited by the number of individuals which can be tracked at one time and is difficult when animals are not readily visible (Takahashi and Lore 1980). Two tools that combine trapping and observation are **Very-High-Frequency (VHF) radio-telemetry** and **Global Positioning System (GPS)** technologies which require affixing rats with tags that transmit movement data in real-time (VHF), or store location data in the tag for either future retrieval or remote download by the observer (GPS). Both VHF radio-telemetry and GPS-based tools allow for improved spatial resolution of rat movements, but until recently they have been hampered by tag size which is limited to 5% of the animal's weight to minimize negative tag-associated effects (Animal Care and Use Committee 1998). While sample sizes

for both methods tend to be smaller than for CMR (Tomkiewicz *et al.* 2010), GPS-based tools offer advantages over VHF radio-telemetry which requires close-range observation of the animal, potentially influencing natural behaviours (Cooke *et al.* 2004; Parsons *et al.* 2014). Further, radio-telemetry is challenging in cities where buildings and other structures can interfere with radio signals (LaPoint *et al.* 2015). Yet, while GPS-based tools may be more beneficial for these reasons, they remain difficult to deploy on urban rats due to issues of tag removal and tag-satellite line-of-sight obstruction (Byers *et al.* 2017). Moreover, the costs of GPS tags over radio-telemetry may make this method prohibitive (Cagnacci *et al.* 2010).

**Indirect Measures:** Rat movements can also be inferred using indirect measures. Visibly observing the **tracks** made by rats (e.g., in snow) allows for estimates of space use (Davis *et al.* 1948), but is naturally limited by the availability of snow. When the environment is not suitable for observing tracks, researchers can deploy **track plates** which become marked with characteristic ‘rat signs’ when rats travel across them (Hacker *et al.* 2016). Rat movement may also be determined through **bait consumption**. This method is common among studies assessing re-infestation of areas where rat eradication efforts were previously enacted (Barnett *et al.* 1951; Barnett and Bathard 1953; Greaves *et al.* 1968; Andrews and Belknap 1983; Colvin *et al.* 1998). Bait that is **dyed** with a compound that colours rats’ feces can also be used to calculate the extent of space use around dyed-bait stations (Davis *et al.* 1948). While these methods are less time consuming to enact than the direct measures previously mentioned, they provide only minimal information on rat activity.

Recently, there has been an increase in the use of **population genetics**-based methods to infer rat movement (see Figure 2-2). These tools analyze differences among individuals at specific locations of the genome caused by genetic mutations. These mutations can result in single nucleotide polymorphisms (i.e., SNPs) (Richardson *et al.* 2017; Combs *et al.* 2018a; 2018b) or rearrangements resulting in different numbers of small repeating sequences (e.g., microsatellites) (Gardner-Santana *et al.* 2009; Kajdacs *et al.*

*al.* 2013). Using these tools, researchers can infer historical movements by identifying the distances between relatives (e.g., parents and offspring (Costa *et al.* 2016; Glass *et al.* 2016)), and identifying potential migrants (e.g., individuals genetically assigned to a population other than the one in which they were caught (Kajdacsi *et al.* 2013; Berthier *et al.* 2016; Desvars-Larrive *et al.* 2017)). These methods have the benefit of supporting large sample sizes (e.g., 1220 in Combs *et al.* (2018a), but they are limited to detecting first-generation migrants and movements during which rats mate and are reproductively successful, underestimating true levels of connectivity among populations (Richardson *et al.* 2017).

## HOME RANGE

For both Norway and black rats (hereafter termed “rats” when referencing both species), the home range size and shape is determined by access to feeding and harborage sites (Davis *et al.* 1948; Recht 1982; Low *et al.* 2013) as well as access to mates (Low *et al.* 2013; Glass *et al.* 2016). These associations lead to irregularly shaped home ranges with individuals often moving along narrow pathways connecting harborage and food sources (Davis *et al.* 1948; Recht 1982; 1983). The presence of conspecifics may also influence home range size, as some individuals have been found to avoid the home ranges of other rats (Low *et al.* 2013; Oyedele *et al.* 2015). Beyond the value of regular access to resources, an intimate familiarity with the features of the home range may serve as a protective measure for rats. For example, individuals within their home range have been recorded entering areas of cover (e.g., a rat hole) more rapidly than those in areas outside of their home range (Davis *et al.* 1948). This is further evidenced by rats’ neophobic behaviours towards new and/or introduced features such as traps (Barnett 1963).

Rats are familiar with the extent of their home range (Recht 1982; 1983), but usage is concentrated within a fraction of this area (Low *et al.* 2013; Oyedele *et al.* 2015). Termed the “core home range”, this region represents the space where an animal spends 50% of its time (Downs and

Horner 2008). The two studies which calculated core home range size for urban rats estimated its size as 11% of the total home range for Norway rats (Oyedele *et al.* 2015), and approximately 31% of the space used for black rats (Low *et al.* 2013). Studies in both species have found that the core home range encompasses important food sources, the home burrow, and areas of dense vegetation (Davis *et al.* 1948; Recht 1982; 1983). However, rats will travel throughout the home range to occupy alternate burrows, particularly when their home burrow is disrupted (Recht 1982; 1983). In fact, rats have been found to switch the location and extent of their home range altogether (Davis *et al.* 1948; Low *et al.* 2013), signifying that the size, shape, usage, and location of the home range are flexible for individual rats and dependent on physical and environmental characteristics.

Home range size has also been found to vary by sex, with evidence that male Norway rats occupy larger home ranges than do females (Tanaka and Kawashima 1951; Oyedele *et al.* 2015). This may be due to differences in reproductive behaviour, whereby males increase their ranges to actively search for mates (Dowding and Murphy 1994). For example, in Norway rats, the area of the total and the core home range of males was approximately 13X and 5X larger than that of females, respectively (Oyedele *et al.* 2015). In black rats, the total and core home range area for males was 4X and 3.5X greater than for females, respectively (Low *et al.* 2013). Indeed, home ranges of male black rats have been shown to overlap with those of other males and females, whereas females had home ranges that were exclusive of each other (Low *et al.* 2013), further supporting the role of mate-searching in determining the extent of the home range.

Studies also indicate that home range size and shape vary by location (Davis *et al.* 1948; Recht 1982; 1983; Oyedele *et al.* 2015). For example, the home range for Norway rats in Baltimore, Maryland was 30 – 45m in diameter (Davis *et al.* 1948), and in George Town, Malaysia the average home range size was 130m<sup>2</sup> (Oyedele *et al.* 2015). Similarly, for black rats, home

range size did not exceed 30.5m in diameter in the City of Orange, California (Recht 1983) while on Christmas Island it was 5330m<sup>2</sup> (Low *et al.* 2013). As home ranges of urban rats are irregularly shaped (Davis *et al.* 1948; Recht 1982; 1983), and because home range estimates will vary depending on the methodology used (see Box 2-1) it is impossible to directly compare these measurements. However, studies in both Norway and black rats have suggested that differences in home range size between study sites may be due to differences in resource availability (Low *et al.* 2013; Oyedele *et al.* 2015).

#### **SITE FIDELITY**

Distances travelled by rats are dependent on the presence of harborage and food in the environment (Creel 1915; Petrie 1923; Davis *et al.* 1948; Heiberg *et al.* 2012). When these are readily available, rats display a strong site fidelity, rarely leaving their home area. For example, CMR studies in Norway rats have found that 27 – 63% of rats in residential areas were recaptured in the same location as their prior capture (King 1950; Tanaka and Kawashima 1951; Glass *et al.* 1989) although this was less common (e.g., 8% of rats) in urban parklands (Glass *et al.* 1989). Genetic results support these findings. For example, by DNA fingerprinting methods 95% (Gardner-Santana *et al.* 2009) and 97% (Glass *et al.* 2016) of rats were genetically assigned to the area of their capture (i.e., based on genetic similarity to other rats in the vicinity of their capture, they were more likely to have been born in the area in which they were caught than in another sampled site). Strong site fidelity was also revealed by Costa *et al.* (2016), who genotyped male rats as well as pregnant females and their offspring, and found that males with a high probability of siring offspring (>99%) were within 70m ± 58m of the pregnant female. Similarly, Richardson *et al.*

(2017) demonstrated that rat movement occurred mostly within the area (i.e., valley) from which rats were sampled. Estimates for site fidelity in urban black rats have not been documented.

Daily movements by rats are typically over short distances. For Norway rats, various CMR studies have documented typical movements ranging from 10m – 20m (Davis *et al.* 1948; Tanaka and Kawashima 1951; Glass *et al.* 1989; Parsons *et al.* 2015). In urban parklands, Norway rats have been recorded moving greater average distances of 25m (Glass *et al.* 1989). In comparison to CMR, genetic analyses have demonstrated that Norway rats move further still (e.g., 30 – 150m), approximately corresponding to the length of a city block (Gardner-Santana *et al.* 2009; Combs *et al.* 2018b). Interestingly, limited movement was supported by an analysis of the ectoparasite communities of urban Norway rats. In this study, Angley *et al.* (2018) found that rats located near each other geographically had more similar assemblages of ectoparasites than did rats located further apart. Because rat ectoparasites are transmitted among individuals via close contact, this implied that rats near each other came into contact with each other more frequently than those further apart.

In urban sewer systems, rats have been found to travel further distances day-to-day than their above ground counterparts. For example, in London, England, sewer rats moved up to 77m (Bentley *et al.* 1958) while in Copenhagen, Denmark, rats travelled up to 200m in a day (Heiberg *et al.* 2012), over 10X the distance recorded for surface populations. In this way, sewers may be more easily traversable, serving as conduits to movement. Interestingly, while daily distances travelled by rats are thought to be greater for males than females (Davis *et al.* 1948), this does not appear to be the case for sewer populations (Heiberg *et al.* 2012), suggesting that the environment is a strong determinant of distances travelled.

## DISPERSAL

Dispersal of rats away from their natal site is generally over short distances. For example, mean dispersal distances between parents and offspring have been recorded as 45m for Norway rats (Combs *et al.* 2018b) and 496m for black rats (Mangombi *et al.* 2016) while distances between putative parents (dams and sires of offspring) ranged from 0-353m for Norway rats (Costa *et al.* 2016; Glass *et al.* 2016). Genetic patterns of isolation by distance (whereby individuals are more closely related to rats in neighbouring areas than they are to individuals further away) corroborate these trends (Gardner-Santana *et al.* 2009; Mangombi *et al.* 2016; Combs *et al.* 2018a; 2018b). For example, in a multi-city comparison of Norway rat population genetic structures, rats were generally highly related to each other at distances within 500m (Combs *et al.* 2018a). However, evidence for isolation by distance has not been found by all studies (Kajdacsí *et al.* 2013; Berthier *et al.* 2016).

Less often, dispersal can occur over long distances. For example, dispersal distances have been recorded up to 11.5km for Norway rats (Gardner-Santana *et al.* 2009). Although such extended movements are infrequent (e.g., 19 of 230 black rats (8.2%) were classified as migrants in Sahel Niger (Berthier *et al.* 2016)), evidence of gene flow among Norway rat colonies from 1.5km to 3km apart suggests that connectivity among populations is maintained by immigration amongst colonies (Gardner-Santana *et al.* 2009; Combs *et al.* 2018a). This dispersal may be non-random, whereby individuals move among similar habitat types (e.g., residential areas vs mixed-use (Angley *et al.* 2018)) and may also be facilitated anthropogenically, such as by commercial transport along road networks (Berthier *et al.* 2016).

For rats, dispersal has been primarily associated with resource availability and competition, dominance hierarchies, and mating behaviour (Calhoun 1963; Glass *et al.* 1989). Specifically,

when feeding and harborage sites are scarce, rats may travel significant distances in search of resources. For example, when in an unfamiliar resource-poor area, Norway rats have been recorded traversing twice the distance as individuals in unfamiliar resource-rich locations (6km vs 3km (Creel 1915)). Mate-searching is also an important driver of dispersal, with rats (particularly males) extending their movements in search of mates (Davis *et al.* 1948; King 1950; Glass *et al.* 2016). Sex-biased dispersal has been documented in Norway rats where the majority of migrants are often reproductively mature males (Gardner-Santana *et al.* 2009; Kajdacs *et al.* 2013; Desvars-Larrive *et al.* 2018b). Sex-biased dispersal has been further evidenced by close proximity among related females caught at a fine spatial scale, suggesting that females moved shorter distances than males in the same population (Desvars-Larrive *et al.* 2017). While these patterns have not been observed in all studies (Gardner-Santana *et al.* 2009; Combs *et al.* 2018b) they align with foundational experimental research on Norway rats that found that mature male rats dispersed greater distances than adult females and juveniles (Calhoun 1963).

In cases where rats immigrate into stable populations, invading rats may be unable to successfully establish home ranges, necessitating extended movements of evicted rats. For instance, the introduction of 112 foreign rats into a city block resulted in the invaders being more likely to emigrate from the site of release than were resident rats in the same area (Calhoun 1948). Further, the immigration of large numbers of rats into a population may temporarily decrease the reproductive rate of the resident population (Davis and Christian 1956). Therefore, although dispersal can maintain connectivity among populations, not all immigration events are successful, and can, in some cases, disrupt the regular population dynamics of the resident population.

## MOVEMENT PATTERNS

Rats are generally found to be nocturnal (Recht 1982; 1983) with heightened activity two to three hours before sunrise and after sunset (Takahashi and Lore 1980; Recht 1983). However, rats may also be active during the day (Recht 1982). Indeed, Parsons *et al.* (2015) found that rats were active between 06:00 to 19:00 with declining activity in the late morning/early afternoon. These activity patterns have also been shown to differ between the sexes, with males generally active longer than females (Parsons *et al.* 2015), leaving their burrow one to two hours before females living in the same area (Oyedele *et al.* 2015). However, as rat activity varies by location, and across differing study methodologies, it is unclear how aspects of the environment and study design contribute to these differences in activity patterns.

During times of activity, rats generally traverse the same pathways (Recht 1982; 1983; Oyedele *et al.* 2015). However, they may use alternate routes to adapt to environmental change. For instance, Recht (1982) recorded Norway rats using alternate pathways both to obtain food left over from picnickers and to avoid people. Norway rats typically move along the ground through narrow runways (Davis *et al.* 1948), near to fences and other cover (Glass *et al.* 1989), while black rats utilize aerial features such as greenery, pipes, and wires (Worth 1950). Both species have been found to travel between adjacent buildings (Petrie *et al.* 1924; King 1950; Tanaka and Kawashima 1951; Recht 1982; 1983; Hacker *et al.* 2016). Indeed, Tanaka and Kawashima (1951) observed rats moving among three to four houses in a city block over the course of a single week. Additionally, rats may travel between surface and sewer locations (Colvin *et al.* 1998; Heiberg *et al.* 2012), but not in all cases (Gras *et al.* 2012). In contrast, rats do not appear to travel between adjacent, but separate, sewer systems (Heiberg *et al.* 2012).

## **BARRIERS TO MOVEMENT**

Landscape features such as roads, waterways, and ‘resource-deserts’ (areas with very limited resources) may impede the movement of rats throughout cities (Combs *et al.* 2018a). In general, roadways are reported as the most common barrier to rat movement (Petrie *et al.* 1924; Davis *et al.* 1948; King 1950; Worth 1950; Traweger and Slotta-Bachmayr 2005; Richardson *et al.* 2017). This is supported by findings that Norway rat home ranges rarely overlap with roads (Davis *et al.* 1948), and by few cases of rats moving among city blocks (Petrie 1923; Calhoun 1948; Davis *et al.* 1948; Emlen *et al.* 1949; Worth 1950). For example, of 146 black rats trapped in Egypt, only one moved between city blocks (Petrie 1923). Likewise, in a study which followed Norway rat tracks in fresh snowfall, (Davis *et al.* 1948) estimated the rate of road crossings to vary from one crossing every 66 days to one crossing a day, with the frequency of crossing reliant on resource availability.

The permeability of roadways is dependent on their width. While larger roadways have deterred movement more than smaller roadways (Petrie 1923), even the width of an alley may impede rats. For example, Davis *et al.* (1948) found that almost all dyed feces were located on the same side of the alley as bait stations. Although rats may avoid crossing alleys, they traverse them more frequently than roadways. An observation of rat movement found that rats crossed alleys 80X more often than they crossed roads (Glass *et al.* 1989). Given that rats may also move greater average distances in underground infrastructure such as sewers (Heiberg *et al.* 2012), barriers posed by roads may be overcome by alternate means of crossing heavily trafficked spaces.

While CMR studies suggest that movement among city blocks are infrequent, genetic analyses demonstrating gene flow reveal that movement is more frequent (Gardner-Santana *et al.* 2009; Glass *et al.* 2016; Mangombi *et al.* 2016; Combs *et al.* 2018b). For example, by analyzing

the genetics of pregnant females and their offspring, Glass *et al.* (2016) demonstrated that females mated most often with males trapped in alleys other than their own. The authors suggested that this pattern likely occurred through ‘mate chases’ in which groups of males left their home site to mate with females in neighbouring blocks (support for multiple paternity of litters is further supported by Costa *et al.* (2016)). In combination, these results indicate that roads are permeable to rat movement and that movement among blocks may be driven by mate searching (Glass *et al.* 2016) or resource availability (Davis *et al.* 1948).

### **FACTORS IMPACTING MOVEMENT**

Because rat movement patterns are dictated by features of the urban environment, changes in weather and anthropogenic habitat modification alter normal rat movement patterns. For example, Recht (1982) observed that Norway rats cease movement in rain, while black rats continue to forage (Recht 1983). Habitat modification can alter rat movement due to either the removal of areas of harborage and/or by blocking typical movement routes. For example, Recht (1982) found that habitat modification (e.g., trimming of vegetation, and removal of debris) resulted in increased Norway rat activity and exploration, larger home ranges, and movement into previously unvisited areas, while construction caused black rats to move to alternate burrows (Recht 1983).

Control methods (e.g., trapping and poisoning) can also promote rat movement, as individuals migrate to occupy and recolonize previously targeted sites. For example, Kajdacs *et al.* (2013) demonstrated that following control efforts, there was both population replacement (i.e., local rat reproduction by surviving rats) and recolonization due to the migration of individuals from surrounding areas. Rat migration may also play a role in the re-infestation of urban sewers systems. For example, following rodent reductions of up to 88% (as indicated by bait uptake), rat

populations increased from 3% - 20% per week (Barnett and Bathard 1953; Bentley *et al.* 1959; Greaves *et al.* 1968). This increase was attributed in part to rat immigration from within the same sewer system (Greaves *et al.* 1968) and from an influx of surface populations (Barnett and Bathard 1953). Such population rebounds can be rapid, occurring in as little as four weeks post-eradication efforts (Hacker *et al.* 2016).

## **2.5 DISCUSSION**

Overall this synthesis highlighted a number of important characteristics of urban rat movement. Specifically, rat movement is dependent on the distribution and availability of important resources such as food and harborage and is limited by the barriers posed by features including roads and waterways. While roads may relegate individuals to home ranges corresponding to the limits of a city block, recent studies suggest that rats cross city streets more often than previously estimated. Further, normal movement patterns may be altered due to environmental change, prompting rats to move greater distances still. These findings have several important implications for city planners, pest control professionals, and public health officials seeking to monitor and mitigate the economic and public health impacts posed by urban rats. However, despite increased scientific attention to describing urban rat ecology in the past decade, this review reveals that the specific details of their spatial ecology remain largely undescribed.

### **IMPLICATIONS FOR CITY PLANNERS**

This review illustrates that features of the urban environment influence the spatial ecology of rats. Because city planners determine and design many aspects of cities, they have the potential to create spaces less prone to rat infestation. For example, as features such as urban parkland may be more

easily traversed by rats (Glass *et al.* 1989), approaches to reduce waste and improve infrastructure/building conditions in and around these areas may lower rats' ability to infest surrounding regions. However, while our review suggests that parkland and sewer systems may facilitate rat movement, the specific landscape features and socioeconomic attributes which determine the connectivity of rat populations within cities are still poorly understood (LaPoint *et al.* 2015). Indeed, the only multi-city comparison of urban rat population structure found that the local environment is a strong determinant of rat movement (Combs *et al.* 2018a). Therefore, it is becoming increasingly important to identify both common features among cities which influence rat movement as well as local features, which can be used by city planners to target and predict areas prone to rat infestation and re-infestation. Targeting these features is particularly important in under-served and marginalized communities where residents are at heightened risk of exposure to large numbers of rats and their associated health and economic impacts (Himsworth *et al.* 2013b; Costa *et al.* 2015a).

Urban centers are continuously expanding and undergoing dramatic habitat modification (Grimm *et al.* 2008). These issues are enhanced in rapidly urbanizing under-resourced settings (United Nations 2018) where unplanned urban development and land use changes (e.g., Chitrakar *et al.* 2016; Pawe and Saikia 2018) pose additional challenges. Our review suggests that habitat disturbance can instigate long distance movements by rats; this is particularly relevant to city planners as ubiquitous activities such as demolition and construction may both create an environment suitable for rat harborage (e.g., open soil and shelter from equipment) (Colvin and Jackson 1999) as well as drive rats from disturbed sites to surrounding areas (Richter 1968; Battersby *et al.* 2002). To pre-empt the potential for rat colonization and migration, city planners should consider employing Integrated Pest Management approaches to proactively decrease

habitat suitability and migration risks. Integrated Pest Management is a multi-faceted approach which incorporates long-term planning goals, data management, as well as partnership among governments, private pest control companies and communities (Colvin and Jackson 1999). Such an approach may include implementing policies that require the eradication of rats prior to the demolition of a building to minimize the efflux of rats and the degree of subsequent colonization. This requires coordination among developers and private pest control companies to identify areas for control, enact control efforts, and monitor the success of the control campaign. For regions where development is primarily undertaken by urban dwellers as opposed to municipalities (i.e., in urban slums), city planners might instead focus on educating communities about the importance of undertaking pest control before and during construction, as well as providing resources such as traps or deploying private pest control companies to areas with ongoing development. In tandem, actions to reduce food sources and harborage sites in adjacent city blocks or homes can also decrease their attractiveness to rats and their ability to support rat population growth. These initiatives also require community involvement and educational programs to inform residents about the ways to properly dispose of food waste and remove potential harborage sites (Colvin *et al.* 1998). Although Integrated Pest Management approaches require sustained and significant investment (i.e., in time and personnel), reactive approaches which fail to address the underlying features that promote rat abundance and facilitate rat movement are likely to remain ineffective.

### **IMPLICATIONS FOR PEST CONTROL**

It is necessary for control methods to account for rat movement patterns. Studies have demonstrated that control campaigns aimed at culling rats alone can be compromised by rapid population rebounds due to reproduction by surviving rats (Barnett and Bathard 1953; Hacker *et*

*al.* 2016), and/or immigration of individuals from surrounding areas (Kajdacsi *et al.* 2013). Given that rats may cross roads for resources and mating (Davis *et al.* 1948; Glass *et al.* 2016), our review suggests that limiting the scale of control to a single property or city block is likely to be ineffective due to reinvasion of the targeted site. Instead, efforts should focus on effectively identifying and targeting areas at the scale of “eradication units”. These areas represent the spatial scale at which rats are interconnected, allowing for recolonization following a control intervention (Abdelkrim *et al.* 2007). For example, in Salvador, Brazil where the majority of Norway rat movement was found to occur within a valley, targeting rat populations at the level of the valley might be appropriate (Richardson *et al.* 2017). In contrast, a study evaluating the genetic signatures of black rat populations before and after an eradication campaign on four islets in the French Caribbean, found that control efforts would need to extend to surrounding islands to minimize the potential for re-invasion (Abdelkrim *et al.* 2007). Because the extent of movement varies by location (Combs *et al.* 2018a), deriving specific recommendations as to the scale of pest control efforts is difficult. Yet, to design effective control strategies, research that quantifies the contribution of landscape attributes to rat migration is necessary to help pest control professionals define the scale of control and prevention approaches. Further, to support the integration of scientific knowledge into actionable information for pest control professionals, it is necessary that projects evaluate how scaling control efforts to the level of local rat movement (i.e., eradication units) compares to traditional pest control efforts.

An understanding of rat movement is not only necessary for more effectively implementing current pest control practices, but it is also important in developing and deploying future pest control innovations. For example, gene drive technologies have received increasing attention for their potential pest control applications. Gene drive technologies involve genetically engineering

individuals so that sets of genes are disseminated within populations through sexual reproduction. For pests, genes which lower the fertility and fecundity of individuals are of particular interest (Moro *et al.* 2018). Because the spread of these traits throughout a population is reliant on interactions among individuals, understanding local rat movement ecology will be necessary to inform the implementation of these technologies in these species.

### **IMPLICATIONS FOR PUBLIC HEALTH**

Our review supports the long-held position that much of rats' activities remain within the confines of a single city block. Because many of the pathogens carried by rats are transmitted through close contact among conspecifics (Childs *et al.* 1998; Himsworth *et al.* 2013b) this limited movement implies that most transmission events are also restricted to within-block populations. These findings support prior research by Himsworth *et al.* which demonstrated significant heterogeneity in pathogen prevalence across adjacent city blocks (Himsworth *et al.* 2013a; 2014d; 2015a), such that some blocks had many infected rats and other blocks had very few. Similar findings have been demonstrated in Salvador, Brazil, where shedding of the pathogen *L. interrogans* by Norway rats varied significantly by location (Costa *et al.* 2015b). If limited movement allows for the clustering of pathogens, then the risk of encountering an infected rat may be site specific. In tandem with these results, our review suggests that activities that disrupt rat colonies could increase movement within and between blocks. Evidence suggests that when rats migrate to surrounding colonies, they fight (Calhoun 1948), and as aggressive behaviours are the primary mode of transmission of some pathogens (e.g., *Streptobacillus monilliformis*, and Seoul hantavirus (Himsworth *et al.* 2013b)), migration events could promote disease spread. Indeed, Lee *et al.* (2018) demonstrated that employing lethal control techniques may increase pathogen prevalence among remaining rats. This

increase could be due, in part, to the effects of pest control on rat movement, and underscores the potential role of methods which reduce rat population size without prompting migration (e.g., rat birth control, gene drive technologies). Therefore, to monitor and mitigate the potential health risks posed by rats, public health officials require information on the distribution of rat-associated pathogens, the role of movement in the transmission of pathogens among urban rats, and how different approaches to pest control can minimize these risks.

## **LIMITATIONS**

Although one of the aims of this review was to compare and contrast data across study locations, deriving quantitative estimates of urban rat movement patterns is difficult due to the limited number of studies evaluating urban rat movement, and an over-representation of research in developed countries (Supplementary Table S2-2). These limitations are compounded by differences between, and limitations of, the included studies. First, rat movement estimates have been derived using various methods which have a suite of limitations (see Box 2-1). These limitations highlight the challenges of studying the movements of not only rats (Parsons *et al.* 2017; Desvars-Larrive *et al.* 2018a), but urban wildlife in general (LaPoint *et al.* 2015). Second, even among studies which employ similar techniques to measure movement (i.e., CMR), researchers have used a variety of models for calculating home range size (Low *et al.* 2013; Oyedele *et al.* 2015). In tandem, these differences limit the ability to make direct comparisons. Yet, these issues emphasize the importance of employing multiple tools to address methodological limitations (e.g., combining continuous tracking and genetics-based methods) and utilizing either multiple or standardized calculation methods to estimate movement parameters to foster comparability amongst studies.

## **CONCLUSIONS**

Overall, this review highlights a number of important features with regards to rat movement and underscores their significance for stakeholders addressing urban rat infestations. Despite the information synthesized in this review, a number of important questions remain (Table 2-1). To address these knowledge gaps, we suggest that future research prioritize collaborative, multi-jurisdictional research which incorporates multiple methods and standardized approaches to measure rat movement.

**Table 2-1: Conclusions from a review of the published literature describing Norway and black rat (*Rattus norvegicus* and *Rattus rattus*) movement in urban centers**

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*Knowledge gained from this review*

- Urban rat movement is dependent on access to important resources (i.e., food and harborage)
- Rat movement is impeded by barriers such as roads and waterways
- Population genetics-based tools demonstrate that rats may cross roads more often than previously estimated using trapping-based techniques
- Long-distance dispersal events are infrequent but can occur over a distance of several kilometres, facilitating connectivity among distant populations
- Rat immigration is not always successful, with some migrating individuals being evicted by resident populations
- Rats may change their home range and natural movement patterns in response to environmental change and anthropogenic habitat modification

*Remaining knowledge gaps*

- How do specific environmental and socioeconomic features of the urban environment promote or hinder rat movement?
  - Why do rats disperse? Is there a consistent answer or variety of reasons for dispersal?
  - What is the dispersal kernel (i.e., the distribution of dispersal distances) of rats?
  - How does habitat disturbance (e.g., demolition) affect rat movement, and how do proactive approaches to rat control minimize these effects?
  - How do pest control initiatives which are scaled to the level of rat movement (e.g., eradication units) compare to traditional pest control approaches?
  - How can information on rat movement be used to inform innovative pest control technologies?
  - What is the role of rat movement in the transmission of rat-associated pathogens among populations, and how does this affect pathogen prevalence?
-

## CHAPTER 3: RAT IN A CAGE: TRAPPABILITY OF URBAN NORWAY

### RATS (*RATTUS NORVEGICUS*)

#### 3.1 SYNOPSIS

Understanding the local ecology of urban Norway rats (*Rattus norvegicus*) is necessary to inform effective rat mitigation strategies. While capture-mark-recapture (CMR) methods can be used to acquire such ecological information (e.g., abundance, movement patterns, and habitat use), these techniques assume that all individuals of the study population are equally trappable. To test whether urban rats adhere to this assumption, we conducted a four-week CMR study in an urban neighbourhood of Vancouver, Canada, to evaluate whether rat characteristics (i.e., age, sex, size, wound status, and infection with the pathogen *Leptospira* spp.) were associated with trappability. We found that the majority of rats entered traps in the first two weeks of trapping, and that larger rats were caught earlier in the trapping period. However, smaller rats were recaptured more often than were larger rats, suggesting that prior capture affects the ability to recapture urban Norway rats. This highlights the need for CMR studies to account for size and prior capture when interpreting data.

#### 3.2 INTRODUCTION

Norway rats (*Rattus norvegicus*) are infamous urban exploiters, thriving in cities worldwide (Feng and Himsforth 2014). Consequences of infestations can be severe. First, they are economically costly, estimated to account for over 19 billion dollars in damages annually in the United States through their consumption and contamination of food products alone (Pimentel *et al.* 2000). At the regional level, an estimate by the province of Alberta, Canada projected that rats would cost

up to 42.5 million dollars annually in the absence of their current rodent control program (McClay *et al.* 2004). Second, rats place considerable pressures on ecosystems, contributing to global biodiversity loss both directly (e.g., through predation) and indirectly (e.g., through habitat modification and species displacement) (Townsend *et al.* 2006; Jones *et al.* 2008a; Doherty *et al.* 2016). Third, rats pose a health risk to human populations, harboring numerous zoonotic pathogens (those transmissible between animals and people) responsible for human morbidity and mortality in cities globally (Himsworth *et al.* 2013b).

An understanding of urban rat ecology is the cornerstone of any attempt to understand rats and rat-associated issues. To gain this knowledge, ecological methods such as capture-mark-recapture (CMR) can be used to estimate population characteristics like abundance and density (Wilson *et al.* 2007; Robinson *et al.* 2009; Sarmiento *et al.* 2009), demographic characteristics (Votier *et al.* 2005; Lachish *et al.* 2007; Graham *et al.* 2013), and movement patterns (Beirincx *et al.* 2006; Lagrange *et al.* 2014; Tuckey *et al.* 2017). However, traditional CMR techniques generally assume that all individuals are equally trappable over time (Krebs and Boonstra 1984; Conroy and Carroll 2009; Lindberg 2012), an assumption which has not held in other species (e.g., Carter *et al.* 2012; Byrne *et al.* 2012; Camacho *et al.* 2017).

Although several models have been developed to address unequal detection of individuals within a population (reviewed by Gimenez *et al.* (2018)), selecting and properly parameterizing an appropriate model is improved by information on trappability. Indeed, Abadi *et al.* (2013) stated that CMR models should incorporate animal characteristics that affect the probability of capture (e.g., sex, age) as covariates. When these covariates vary with time, termed ‘states’ (e.g., reproductive status, or disease status), multi-state CMR models can be employed, which allow for individuals to transition among states (Gimenez *et al.* 2018). Further, where states relating to

capture probability (i.e., trap aware or trap unaware) are affected by events (e.g., captured or not captured) multi-event models (an expansion of multi-state models) (Pradel 2005) can be used to more broadly reflect individual heterogeneity (Pradel and Sanz-Aguilar 2012). Finally, when heterogeneity is not fully captured by covariates and states, individual heterogeneity can be modelled as individual random effects (Abadi *et al.* 2013). Therefore, it is important to understand the extent of capture heterogeneity within a population to first determine whether to incorporate it into CMR models (Ford *et al.* 2012), and second to identify an appropriate model and parameters.

The extent to which urban rats adhere to the assumption of equal trappability is largely unknown. Studies of their forest-dwelling conspecifics suggest that trap-related factors such as bait type (Laurance 1992), trap type (Blackwell *et al.* 2002), and odors from previous occupants (e.g., predators and conspecifics) (Tobin *et al.* 1995; Parsons *et al.* 2015) may influence which individuals enter traps (i.e., trappability). Beyond trap-related effects - which can be controlled for through thoughtful study design (Williams *et al.* 2002) - trappability may vary with rat characteristics. For example, two capture-removal studies found that larger, sexually mature rats were more likely to enter traps early in a trapping period (Davis and Emlen 1956; Himsworth *et al.* 2014a), countering assumptions of equal trappability. If the assumptions of CMR are not met, then this may lead to significant errors in the interpretation of the resulting data. For example, given that *Leptospira* spp., a zoonotic bacterial pathogen shed in rat urine, is more prevalent among larger, sexually mature rats (Himsworth *et al.* 2013a; Minter *et al.* 2017), the tendency for larger, sexually mature rats to enter traps earlier than other members of the population may result in inflated prevalence estimates for *Leptospira* spp.

Trappability may also be impacted by prior capture. Marked individuals can become “trap shy”, whereby individuals avoid traps that they have been caught in previously (Evans 1951;

Tanaka 1963; King *et al.* 2003; Linhart *et al.* 2012), or “trap-happy”, resulting in numerous recapture events (Morris 1955; Geis 1955; Tanaka 1963; Gurnell 1982). Although both Norway and black rats (*Rattus rattus*) may display neophobic behaviours (Barnett 1963; Clapperton 2006), to our knowledge there has been only one other study to date which assessed how prior capture influences the trappability of Norway rats, and this study was performed in a rural setting (Tanaka 1963).

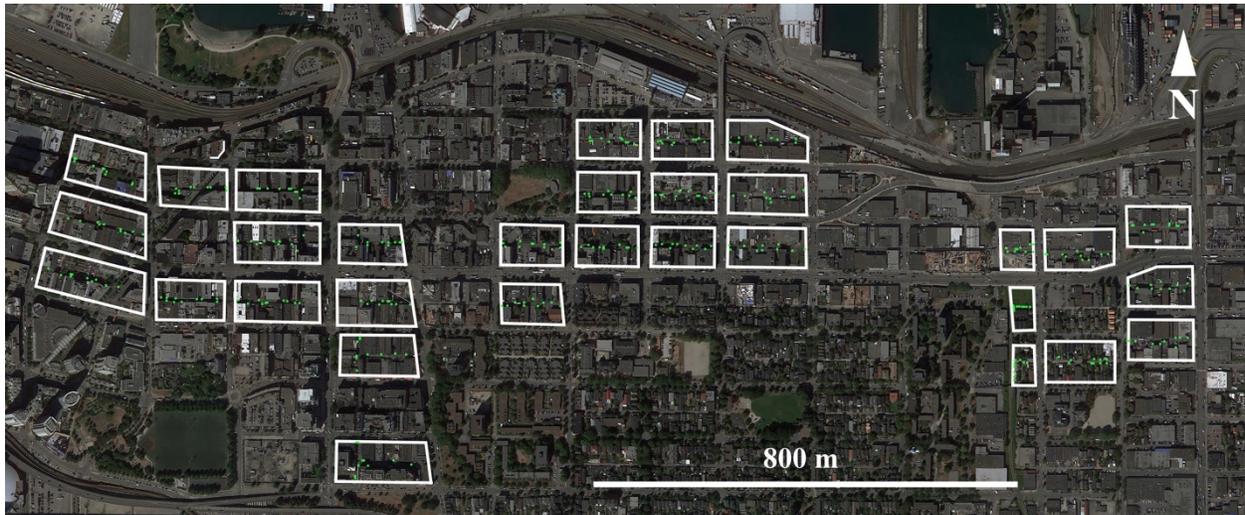
The overarching objective of this study was to test the assumption of equal trappability of urban Norway rats. Specifically, we evaluated whether rat characteristics (i.e., age, sex, size, wound status, and infection with the pathogen *Leptospira* spp.) and prior capture were associated with trappability. This information will be valuable for future studies aimed at understanding rat ecology and rat-related issues (e.g., rat control, rat-associated public health risks, etc.).

### **3.3 METHODS**

#### **TRAPPING**

Trapping was carried out in an urban neighbourhood in Vancouver, British Columbia, Canada. Rats were trapped from June 2016 - January 2017 in 31 proximal city blocks (Figure 3-1) which were selected as part of a larger CMR study (e.g., Byers *et al.* 2017; Lee *et al.* 2018; Donovan *et al.* 2018). Briefly, ten Tomahawk Rigid Traps (Tomahawk Live Traps, Hazelhurst, USA) were deployed in each city block. These traps were placed inside stainless-steel trap covers to prevent vandalism (Integrated Pest Supplies Ltd, New Westminster, Canada) and were chained to immovable objects along the length of the alleyway that bisected each city-block. To acclimatize rats to traps, traps were pre-baited for one week and fixed in an open position (Barnett 1963). Bait consisted of peanut butter mixed with oats, and Hydrogel (ClearH2O, Westbrook, USA) was

provided as a water source. Where possible, traps were placed against vertical surfaces in the path of potential rat runways (Himsworth *et al.* 2014a).



**Figure 3-1: Map of study sites in Vancouver, BC, Canada.** Within each of the 31 city blocks where rats were trapped, green circles indicate the positions of the 10 traps placed in each block. Images provided through Google Earth Professional (<https://www.google.com/earth/versions/#download-pro>).

Following pre-baiting, active trapping commenced and continued for four weeks. Traps were set each evening by 1600 hours and checked each morning by 0700 hours. Traps were set five days a week, and fixed open and baited on the sixth and seventh day. Traps were disinfected using 10% bleach immediately following any period of pre-baiting (i.e., prior to active capture) as well as following any time a rat was captured to prevent the potential effect of odor on rat trappability (bleach and other disinfectants have been shown not to impact the trappability of various species of small mammals (van Horn and Douglass 2000; Wilson and Mabry 2010)) and the unintended transmission of pathogens among rats (Health Canada 2001).

## **SAMPLING**

Trapped rats were transported to the back of a mobile laboratory-van, where each individually-caged animal was placed above a disinfected plastic tray and covered with a blanket to minimize stress. Urine was collected directly from the tray using a sterile syringe and was stored at -80°C until it was tested for *Leptospira* spp.. Subsequently, rats were transferred into an inhalation induction chamber (Kent Scientific, Torrington, USA) and anesthetized with 5% isoflurane in oxygen using an isoflurane vaporizer (Associated Respiratory Veterinary Services, Lacombe, Canada). Anesthesia was maintained throughout sampling.

For each rat the following data were collected: body weight (grams), total length (nose-to-tip of tail in centimeters), sexual maturity (males with scrotal testes and females with a perforate vagina were considered mature), sex (male or female), and the presence/absence of bite wounds (presence determined as per Himsworth *et al.* (2014e)). Each rat was given a uniquely numbered laser-etched ear-tag (Kent Scientific, Torrington, USA) for identification upon recapture. Rats were allowed to recover fully from anesthesia (15-30 minutes) before being released at the exact location of their capture.

Occasionally there were too many rats caught for the field team to process. In those cases, rats that had not been processed by 1600 hours were counted but released without collection of additional data or sampling. The order in which rats were sampled was randomized by city-block each day.

## **LEPTOSPIRA SPP. TESTING**

Starting urine volumes ranged between 20 – 200µL and all were volume corrected to 200µL using sterile, 1X Phosphate Buffer Solution buffer, pH 7.4. Nucleic acid extraction and amplification of

the LipL32 gene (encodes an outer membrane lipoprotein virulence factor (Stoddard *et al.* 2009) of pathogenic *Leptospira* species) was performed by real-time PCR (Life Technologies) as outlined in Lee *et al.* (2018). Samples were classified as negative (cycle threshold [Ct])  $\geq 40$ , suspect positive (Ct = 37–39.99), or positive (Ct  $\leq 36.99$ ). Any sample within the suspect range was retested three times.

## STATISTICS

### TRAP SUCCESS

To determine trap success, we divided the total number of rats caught by the total trap effort and adjusted according to Nelson and Clark (1973). This method accounts for the capture of non-target species and accidental trap activation by subtracting half a trapping unit from the total trap effort for each sprung trap.

### TRAPPABILITY

Linear regression was used to characterize the association between trap day (i.e., the day during the trapping period in which a rat was first captured, with “Day 1” being the first day of active trapping in any given city block) and the following covariates: sex, sexual maturity, weight, total length, bite wound presence, *Leptospira* spp. status, and season of capture (summer: June-August; and fall: September-November). Bivariable linear regression was used to individually examine the relationships between trap day and each characteristic and all covariates that were associated with trap day with a  $p < 0.10$  were carried forward into a multivariable model. A backwards selection process was used to select the multivariable model with the lowest Akaike Information Criterion (AIC) to balance and compare relative model fit and parsimony. As weight and length were

collinear (Spearman's  $Rho = 0.93$ ,  $p < 10^{-15}$ ), they were considered in separate competing models. Model assumptions were assessed in both the bivariable comparisons and in the final multivariable model. Biologically plausible interactions were assessed in the final model (i.e., between: weight and bite wounds; weight and sexual maturity; weight and sex).

#### RETRAPPABILITY

Logistic regression was used to characterize the association between the aforementioned covariates and whether a rat was recaptured (yes/no) within seven days of their initial capture. A seven-day recapture window was chosen to ensure that every rat had an equal opportunity to be recaptured regardless of whether it was caught at the beginning or at the end of the trapping period. Note that 114 of 147 (78%) recaptured rats in the larger CMR study were recaptured within seven days of initial capture. Bivariable and multivariable modelling was carried out as described above; however, weight and length were dichotomized around their medians because they were not linearly associated with the log odds of the outcome. Biologically plausible interactions were assessed in the final model (i.e., between: weight and bite wounds; weight and sexual maturity; weight and sex).

#### EFFECT OF THE CITY BLOCK

To assess whether there was clustering of explanatory variables associated with the outcome by city-block, we compared the final multivariable model to the same model while including a random effect for the city-block, for both the *trappability model* (mixed effects linear regression) and the *retrappability model* (mixed effects logistic regression).

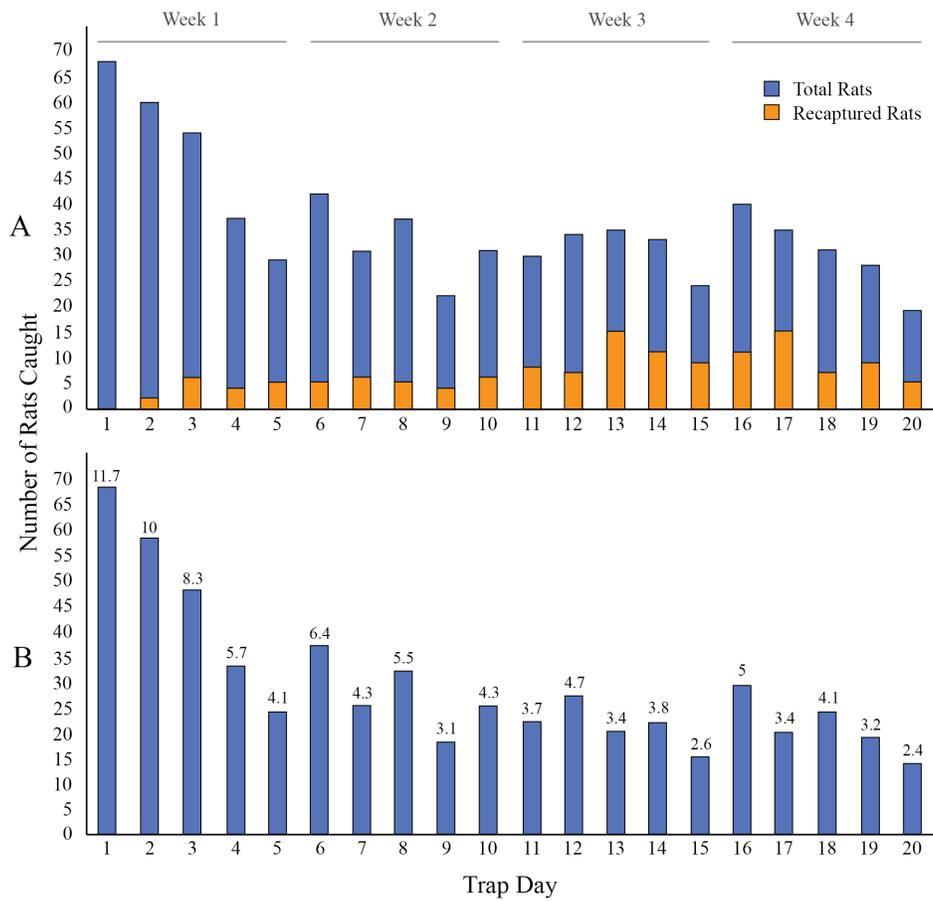
All analyses were carried out using R Studio version 1.1.456 (Boston, USA). Regression was performed using the stats (R Core Team, 2018) and lme4 (Bates *et al.* 2015) packages.

### **3.4 RESULTS**

Altogether, 580 individual Norway rats were captured over 20 trap days with an overall trap success of 14%. Of the 580 Norway rats caught, 231 (39.8%) were caught in week one, 137 (23.6%) in week two, 106 (18.3%) in week three, and 106 (18.3%) in week four (Figure 3-2). Data were not collected for 195 rats (unmarked) because there were too many rats for the field team to process in one day. An additional six rats had missing data for one or more variables under consideration. A total of 379 rats were included in subsequent analyses.

#### **TRAPPABILITY**

Among the 379 rats included for consideration, 195 (51%) were male (106 mature, 89 immature) and 184 (49%) were female (101 mature, 83 immature). The median weight and length of rats included in the trappability model were 111g and 30.5cm respectively. Urine was sampled from 335 individuals of which 39 (12%) were positive for *Leptospira* spp. (see Table S3-1).



**Figure 3-2: Norway rats caught each day over 20 days in 31 city blocks of Vancouver, Canada.** A) The number of rats caught each day, including rats caught only once (blue) and rats that were recaptured (orange), for a total of 720 rat capture events. B) The number of new rats caught each day (i.e., without recaptured rats). The percentage of rats caught out of the total number of individual rats (N = 580) is displayed on the top of each bar for each trap day (e.g., 11.7% of individuals were caught on day one).

**Table 3-1:** Descriptive statistics of captured urban Norway rats (*Rattus norvegicus*)

Covariate	Levels	Not Recaptured Total Rats =324 N (%Total)	Recaptured Total Rats =55 <sup>a</sup> N (%Total)	Total Total Rats=379 N (%Total)
Sex	Female	158 (49)	26 (47)	184 (49)
	Male	166 (51)	29 (53)	195 (51)
Sexual Maturity	Immature	139 (43)	33 (60)	172 (45)
	Mature	185 (57)	22 (40)	207 (55)
Dichotomous Weight	<111	153 (47)	36 (65)	189 (50)
	>=111g	171 (53)	19 (35)	190 (50)
Dichotomous Length	<30.5cm	151 (47)	35 (64)	186 (49)
	>=30.5cm	173 (53)	20 (36)	193 (51)
Wound Presence	None	250 (77)	43 (78)	293 (77)
	Present	74 (23)	12 (22)	86 (23)
Season	Summer (Jun-Aug)	131 (40)	22 (40)	153 (40)
	Fall (Sep-Nov)	193 (60)	33 (60)	226 (60)
<i>Leptospira</i> Status	Negative	248 (88) <sup>b</sup>	48 (92) <sup>b</sup>	296 (88) <sup>b</sup>
	Positive	35 (12) <sup>b</sup>	4 (8) <sup>b</sup>	39 (12) <sup>b</sup>

<sup>a</sup> Only considered rats within the seven-week window for recapture (N = 281)

<sup>b</sup> Urine was not collected from all rats included in this analysis (N<sub>total</sub>=335, N<sub>not recaptured</sub>=283, N<sub>recaptured</sub>=52)

Upon bivariable linear regression (Table 3-2), weight (p-value < 0.01), length (p-value < 0.01), and wound presence (p-value < 0.001) were significantly (p < 0.05) associated with trap day. However, in the final multivariable model, only weight (beta<sub>adj</sub> = -0.0091, 95% CI = (-0.015,-0.0036), p-value = 0.00134) was retained, although length was roughly equivalent in that it explained approximately the same amount of the variation in trap day (R<sup>2</sup><sub>length</sub> = 0.026; R<sup>2</sup><sub>weight</sub> = 0.027) (Supplementary Figure 3-1). In this model, heavier rats were more likely to be caught earlier in the trapping period. No interactions that were assessed were statistically significant in the final model.

**Table 3-2:** Unadjusted (bivariable) and adjusted (multivariable) linear regression of each rat characteristic against the outcome of trap day; N = 379

Covariate	Categories	Unadjusted <sup>a</sup>				Adjusted <sup>b</sup>			
		Estimate <sup>c</sup>	SE <sup>d</sup>	p-value	95% CI	Estimate	SE	p-value	95% CI
Sex	Female	Ref <sup>e</sup>	Ref	Ref	Ref	-	-	-	-
	Male	0.016	0.56	0.98	(-1.08,1.11)	-	-	-	-
Sexual Maturity	Immature	Ref	Ref	Ref	Ref	-	-	-	-
	Mature	-0.90	0.56	0.11	(-1.99,0.20)	-	-	-	-
Weight	Continuous	-0.0091	0.0028	0.0013	(-0.015,-0.0036)	-0.0091	0.0028	0.0013	(-0.015,-0.0036)
Length	Continuous	-0.12	0.038	0.0016	(-0.20,-0.047)	-	-	-	-
Wound Presence	None	Ref	Ref	Ref	Ref	-	-	-	-
	Present	-1.73	0.66	0.0091	(-3.03,-0.43)	-	-	-	-
Season	Summer (June-Aug)	Ref	Ref	Ref	Ref	-	-	-	-
	Fall (Sep- Nov)	0.50	0.57	0.38	(-0.62,1.62)	-	-	-	-
<i>Leptospira</i> Status	Negative	Ref	Ref	Ref	Ref	-	-	-	-
	Positive	-1.52	0.92	0.101	(-3.34,0.30)	-	-	-	-

R<sup>2</sup> for final model = 0.027

<sup>a</sup> Bivariable linear regression

<sup>b</sup> Multivariable linear regression

<sup>c</sup> Estimated effect of the given variable for a 1-day increase in trap day

<sup>d</sup> Standard error

<sup>e</sup> Reference category

## RETRAPPABILITY

In the first three weeks of trapping, 281 rats were released. Twenty-three rats were not released because they died either prior to or following anesthesia. While the cause of death for these individuals is unknown, some of these rats showed signs of rodenticide poisoning (i.e., bleeding from nose and mouth), malnutrition, and significant wounding (i.e., large open wounds). Indeed, rodenticide application was common in the study area and therefore it is highly probable that many of the captured rats had previously consumed rodenticides.

Seventy-three (26%) rats were recaptured, and 55 (75%) of these individuals were recaptured within seven days of their initial capture. Of these, 46 were recaptured once, seven were recaptured twice (six immature and one mature rat), and two were recaptured three times (both immature rats). Twenty-nine (53%) recaptured rats were male (13 mature, 16 immature) and 26 (45%) were female (9 mature, 17 immature) (Table 3-1). The median weight and length of rats included in the retrappability model were 80g and 27cm respectively. Four of the recaptured rats (8%) tested positive for *Leptospira* spp. (Table 3-1).

Upon bivariable logistic regression (Table 3-3), the odds of being recaptured were significantly lower for rats that were mature ( $p < 0.01$ ), that weighed 111g or more ( $p < 0.001$ ), and that were 30.5cm or more in total length ( $p < 0.01$ ). In the final multivariable model, only dichotomous weight was retained; however, while weight alone was the best predictor of whether a rat would be recaptured, the model containing length was roughly equivalent ( $AIC_{\text{weight}} = 269.26$ ,  $AIC_{\text{length}} = 271.34$ ). In this final model, larger rats were significantly less likely to be recaptured with rats heavier than the median weight having 0.34 times the odds of being recaptured as compared to rats less than the median weight (95% CI = (0.18,0.62). No interactions that were assessed were statistically significant in the final model.

**Table 3-3:** Unadjusted (bivariable) and adjusted (multivariable) logistic regression of each rat characteristic against the outcome of binary recapture (yes/no). The seven-day recapture window includes rats caught for the first time in the first three weeks of trapping; N = 281

Covariate	Categories	Unadjusted <sup>a</sup>				Adjusted <sup>b</sup>			
		OR <sup>c</sup>	SE <sup>d</sup>	p-value	95% CI	OR	SE	p-value	95% CI
Sex	Female	Ref <sup>e</sup>	Ref	Ref	Ref	-	-	-	-
	Male	1.20	0.30	0.55	(0.66,2.20)	-	-	-	-
Sexual Maturity	Immature	Ref	Ref	Ref	Ref	-	-	-	-
	Mature	0.37	0.31	0.0014	(0.20,0.68)	-	-	-	-
Weight	<111g	Ref	Ref	Ref	Ref	-	-	-	-
	>=111g	0.34	0.32	0.00054	(0.18,0.62)	0.34	0.32	0.00054	(0.18,0.62)
Length	<30.5cm	Ref	Ref	Ref	Ref	-	-	-	-
	>=30.5cm	0.37	0.31	0.0015	(0.20,0.68)	-	-	-	-
Wound Presence	None	Ref	Ref	Ref	Ref	-	-	-	-
	Present	0.76	0.36	0.43	(0.36,1.49)	-	-	-	-
Season	Summer (June-Aug)	Ref	Ref	Ref	Ref	-	-	-	-
	Fall (Sep- Nov)	1.13	0.39	0.69	(0.62,2.08)	-	-	-	-
<i>Leptospira</i> Status	Negative	Ref	Ref	Ref	Ref	-	-	-	-
	Positive	0.47	0.55	0.18	(0.14,1.26)	-	-	-	-

<sup>a</sup> Bivariable logistic regression

<sup>b</sup> Multivariable logistic regression

<sup>c</sup> Odds ratio

<sup>d</sup> Standard error

<sup>e</sup> Reference category

## EFFECT OF THE CITY BLOCK

In the *Trappability Model*, adding the random effect of the block did not substantially change the effect of weight on trap day ( $\beta_{\text{adj}} = -0.009$ , 95% CI = (-0.15,-0.0031), p-value < 0.01). However, the variance associated with the effect of the block was 2.14 and the relative fit of the model increased slightly ( $\text{AIC}_{\text{no random effect}} = 2350.9$ ,  $\text{AIC}_{\text{random effect included}} = 2344.6$ ; see Supplementary Figure 3-2). Similarly, in the *Retrappability Model*, adding the random effect of the block did not impact the effect of weight on recapture ( $\text{OR}_{\text{adj}} = 0.34$ , 95% CI = (0.18,0.62), p-value < 0.001). Further, the variance associated with the effect of the block was 0 and the relative fit of the model decreased with the addition of the random effect ( $\text{AIC}_{\text{no random effect}} = 269.26$ ,  $\text{AIC}_{\text{random effect included}} = 271.3$ ).

## 3.5 DISCUSSION

Understanding the characteristics that influence urban rat trappability is essential to inform the design and interpretation of capture-based programs seeking to describe local rat ecology. We found that the number of rats captured decreased over the trapping period and that larger rats were more likely to enter traps earlier in the trapping period and were less likely to be recaptured than were smaller rats. Together, these results suggest that urban Norway rats do not follow the assumption of equal trappability, and that CMR studies may be biased toward obtaining more robust capture histories for smaller individuals than larger individuals. Therefore, studies modelling CMR data for rats should consider distinct probabilities of capture based on characteristics such as size and sexual maturity as well as differential impacts of prior capture on individual trappability.

## **TRAPPING PERIOD**

Trapping duration is an important component of CMR studies. Insufficient trapping periods may result in low sample sizes and thus affect accurate estimates of population characteristics (Olsen 1975; Burke *et al.* 1995). However, extending trapping duration can be prohibitive due to equipment and labour costs. In this study, we found that trap success was greatest in the first week of trapping, with pronounced declines in rat numbers following the first day. These results are similar to a previous study which found that the greatest number of rats (22.2%) were caught on the first day of a 12-day trapping period (Himsworth *et al.* 2014a). Decreasing numbers of trapped rats using CMR could demonstrate that the proportion of “trap shy” individuals increases over the trapping period (Tanaka 1963). Our results suggest that trapping initiatives may benefit from maximizing their efforts in the first week of trapping and highlights the importance of understanding how certain methods could increase trap success in that period (e.g., pre-baiting).

## **TRAPPABILITY**

Larger rats were more likely to enter traps early in the trapping period (Supplementary Figure 3-1). These results align with previous trap-removal studies which found that larger, sexually mature rats were more likely to enter traps in the first few days of trapping than were smaller, sexually immature rats (Davis and Emlen 1956; Himsworth *et al.* 2014a). This is important because it suggests that short-term trapping-based studies seeking to describe local rat population ecology may be biased towards oversampling larger individuals. This is particularly problematic for studies evaluating the disease ecology and population health risks associated with urban rats because a number of zoonotic pathogens are associated with rat size (Glass *et al.* 1988; Himsworth *et al.* 2013a; 2014d). It is interesting therefore, that our study found no association between trappability

and carriage of *Leptospira* spp., even without controlling for characteristics such as weight. This suggests that carriage of *Leptospira* spp. may not be associated with the probability of capture. Finally, trappability was affected by some unmeasured block-level characteristic (e.g., resource availability). While our analysis was concerned with assessing the characteristics of individuals that entered traps earlier vs later in a trapping period, it could also be that block-level characteristics influence the tendency of rats to enter traps.

### **RETRAPPABILITY**

While the number of new rats captured decreased with time, the number of recaptured individuals increased in the latter half of the trapping period. This is unsurprising, as the number of marked individuals available for recapture increases with the number of individuals marked. In this study, smaller rats were more likely to be recaptured than larger rats. This is important because it suggests that prior capture may differentially affect trappability. Differences in aversion between smaller and larger rats may be due to differential access to resources (Feng and Himsforth 2014) whereby smaller, less dominant individuals are relegated to resources associated with increased risk (e.g., bait in traps). Indeed, experimental studies have demonstrated that adolescent rats (up to 60 days of age) display greater risk-taking behaviours than adults (Imhof *et al.* 1993). In addition to size, sexual maturity was associated with odds of recapture in the bivariable but not the multivariable model, suggesting that size likely represents more than just sexual maturity and that smaller, mature rats also have a decreased odds of recapture. This could be due to the relationship between an individual's body mass and their position within the social hierarchy of their colony, or as a general indicator of malnourishment, both of which could influence the results of CMR studies. Unlike with trappability, there did not appear to be an influence of block-level characteristics on

retrappability. This may be due in part to dominance characteristics of rats which dictate rat interactions (Barnett 1958). Dominance interactions may influence the tendency for subordinate rats to re-enter traps regardless of block-level characteristics. Finally, while there was no association between *Leptospira* spp. and retrappability, it is difficult to draw definitive conclusions given its overall low prevalence combined with the limited sample size for the recapture analysis.

## LIMITATIONS

One potential limitation of the retrappability model is the restriction of designating rats as “recaught” only if they were recaught within seven days of their initial capture. This seven-day window was used in order to allow all rats an equal time to reenter traps. Although an initial assessment of the larger CMR dataset indicated that the majority of individuals were recaught within seven days, it could be that this timeframe biased our sample of recaught rats. For example, it is possible that larger rats require more time to overcome acquired trap shyness, and thus may be more likely to re-enter traps after seven days of capture. However, an analysis of the rats caught outside of the seven-day window demonstrated that these rats were on average 138g (N = 16), within the weight range assigned to “smaller rats”. Additionally, while our study found that 12% of rats were positive for *Leptospira* spp., it is possible that this is an underestimate of the actual number of infected rats as previous studies in other species found intermittent or decreasing shedding of *Leptospira* over time (Leonard *et al.* 1992; Rocha *et al.* 2017). However, in a study which evaluated *Leptospira* shedding by Norway rats over two months in Salvador, Brazil, the bacteria was shed consistently over time (Costa *et al.* 2015b), and therefore the extent to which variations in shedding affects our study is unclear. Finally, as there may be many rats in an area

which never enter traps, it is important to note that our study can only make inferences on the “trappable” population of Norway rats, and may not be reflective of the entire population.

## **CONCLUSIONS**

Overall, our study demonstrates that: 1) trap success is greatest at the start of a trapping period; 2) larger rats are more likely to enter traps early in the trapping period compared to smaller rats; and 3) smaller rats are more likely to reenter traps than larger rats. This is important because it indicates that urban Norway rats violate the assumption of equal trappability inherent to traditional CMR methods. We suggest that studies employing these methods consider rat characteristics as well as the impact of capture during study design, CMR model selection, and data interpretation.

# **CHAPTER 4: A NOVEL METHOD FOR AFFIXING GLOBAL POSITIONING SYSTEM (GPS) TAGS TO URBAN NORWAY RATS (*RATTUS NORVEGICUS*): FEASIBILITY, HEALTH IMPACTS, AND POTENTIAL FOR TRACKING MOVEMENT**

## **4.1 SYNOPSIS**

Despite the ubiquity of rats, we lack an understanding of how they move within the urban environment. Traditional tools for studying rat movement, such as capture-mark-recapture, are time-intensive and provide coarse movement estimates. Alternative methods, such as continuous tracking by radio-telemetry are difficult to employ in cities where buildings may obstruct radio signals. Global Positioning System (GPS) tags are a promising alternative for resolving fine-scale movement patterns. To test the utility of GPS tracking for urban rats, we affixed tags to 14 sexually mature Norway rats (*Rattus norvegicus*) in Vancouver, Canada, using veterinary adhesive and absorbable sutures. Six GPS tags had remote-download capabilities, and eight stored location data downloadable upon tag recovery. We did not acquire location data from either tag type. While the data receiver successfully recognized five of six remote-download tags, these tags had not stored any locations. Further, of the three recaptured rats (21.4%), all had dislodged tags, although there were no observable adverse health effects from tag attachment. Given low recapture success, our results suggest that remote-download technologies offer greater potential for data recovery. That remote-download tags did not record locations could be due to obstruction of tag line-of-sight with a satellite either through rat ecology (e.g., burrowing), and/or removal in obstructed areas. Future technological advancements, such as surgically implantable tags that hinder removal, may improve

the potential use of GPS tags to track urban rat movement. This information is essential to develop effective rat control strategies and mitigate future rat-related public health concerns.

## **4.2 INTRODUCTION**

Norway rats (*Rattus norvegicus*) are ubiquitous urban pests (Aplin *et al.* 2003), noteworthy for both their propensity for close association with people and their ability to carry numerous zoonotic pathogens (those that are transmissible between animals and people) (Himsworth *et al.* 2013b). Developing a comprehensive understanding of rat ecology is important for several reasons. First, certain aspects of rat ecology can impact the efficacy of rat control interventions. For example, following site-specific population reduction (i.e., through trapping or poisoning), rats will commonly immigrate from surrounding areas, re-infesting the targeted site (Barnett and Bathard 1953; Greaves *et al.* 1968). In concert with a high fecundity (Feng and Himsworth 2014), rat populations can quickly rebound (Barnett and Bathard 1953; Bentley *et al.* 1959), reaching their prior population size in as little as four weeks following control efforts (Hacker *et al.* 2016). Second, rat ecology is an important determinant of the epidemiology of zoonotic pathogens within rat populations and the risk of rat-to-human disease transmission (Himsworth *et al.* 2013b). Studies have shown that, in the absence of anthropogenic disturbances, rat colonies form ‘self-containing units’, where a colony with a high pathogen prevalence can exist alongside one that is free of that pathogen, likely due to minimal contact among colonies (Himsworth *et al.* 2013a; 2015a). This underscores the importance of understanding rat ecology when devising effective management programs.

Movement patterns are a key characteristic of rat ecology, yet remain poorly understood (Feng and Himsworth 2014). This paucity of data is not unique to rats, as the movements of urban

animals, in general, are rarely studied (LaPoint *et al.* 2015). Traditional methods for studying movement such as capture-mark-recapture (CMR) are time-intensive and yield fragmented data, failing to account for fine-scale movements between capture points. These limitations are compounded by the neophobic nature of urban rats (Barnett 1963), which presents a barrier to performing accurate trapping-based studies by adding significant trapping-bias. Alternatives to CMR include Remote Frequency Identification (RFID), and Very High Frequency (VHF) radio-telemetry. Remote Frequency Identification serves as a bar-code for micro-chipped animals, identifying individuals as they pass near a sensor (Parsons *et al.* 2015). Similar to CMR, RFID necessitates luring animals to scanning stations, which is challenging, may artifactually alter natural movement patterns, and fails to account for movement patterns between scanning stations. Very High Frequency radio-telemetry can be used to track continuous movements; however, tags that transmit location data continuously require close-range observation of tagged animals, which may influence their behaviour (Parsons *et al.* 2014). Additionally, radio-telemetry is challenging to perform in the urban environment, particularly with species that dwell underground and/or within structures that can interfere with radio signals (LaPoint *et al.* 2015).

Many of the aforementioned limitations can be minimized through the use of Global Positioning System (GPS)-based tools. Such tools provide greater spatial resolution, are less time-intensive than other tracking methods, are less prone to signal interference, and do not require frequent recapture or close monitoring of the animal (LaPoint *et al.* 2015). This makes GPS particularly promising for studying urban wildlife. While GPS devices have been used effectively to track movements of larger animals (e.g., Douglas-Hamilton *et al.* 2005; Newman *et al.* 2009; Parsons *et al.* 2014), trade-offs between battery size (tags should weigh less than 5% of an animal's body weight (Animal Care and Use Committee 1998)) and the number of locations a tag can

acquire has hindered their use on small animals. Recently, miniaturization of tags and batteries have facilitated their use on smaller animals such as big brown bats (*Eptesicus fuscus*), hoary bats (*Lasiurus cinereus*) (Castle *et al.* 2015), pigeons (*Columbia livia*) (Rose *et al.* 2006), pygmy rabbits (*Brachylagus idahoensis*) (McMahon *et al.* 2017), and grey squirrels (*Sciurus carolinensis*) (Stevenson *et al.* 2013). Further, while traditional GPS tags log data on board and require tag recovery (Cagnacci *et al.* 2010), advancements in remote-download technologies minimize the necessity to recapture animals to recover data. Therefore, remote-download tools are particularly useful when recapture rates are low, hindering tag retrieval. While these developments are promising, there have not been any studies evaluating the potential use of GPS tags to track urban rats.

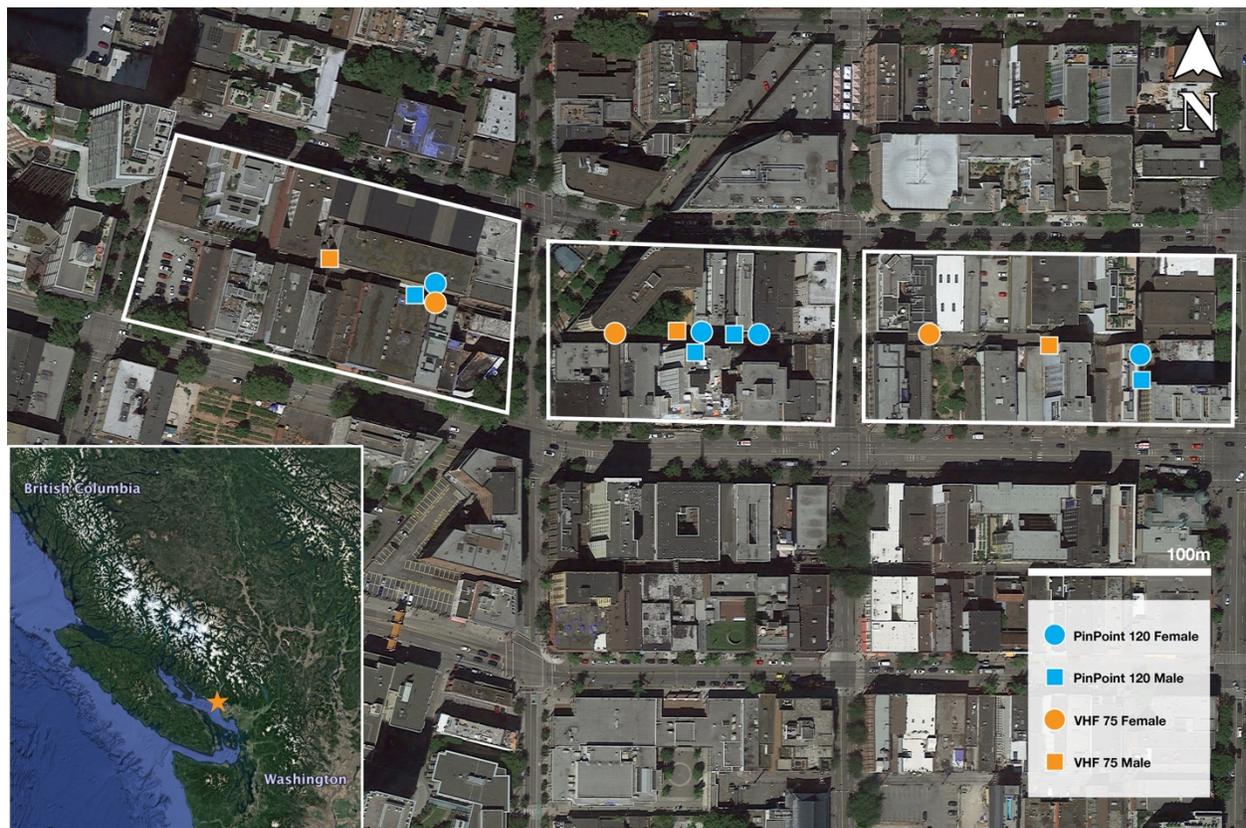
We tested the efficacy of GPS tags to track movements of Norway rats in an urban setting. To address this aim, we endeavored to assess the: 1) feasibility of attaching lightweight GPS tags (< 5g) to urban Norway rats; 2) impact of GPS tag attachment on rat health (as determined by weight loss and/or signs of trauma or infection at the suture site upon recapture); and 3) potential for tracking rat movement using remote-download and store-on-board GPS technology.

## **4.3 METHODS**

### **STUDY AREA AND TRAPPING METHODOLOGY**

This study was performed as part of an eight-month CMR project evaluating urban rat ecology and disease transmission. This study occurred over eight weeks from 21 September 2016 – 23 October 2016, and 31 November 2016 – 18 December 2016. For the purposes of this project, we focused on three contiguous city-blocks covering approximately 4.5ha in the Downtown Eastside neighbourhood of Vancouver, Canada (N49°17'/W123°6') (Figure 4-1). Within these blocks, 10

traps for rats (Tomahawk Live Trap, Hazelhurst, WI) were placed in the alleyway of each block (total traps = 30). Traps were covered in stainless steel covers (Integrated Pest Supplies Ltd., New Westminster, BC) to minimize vandalism and contact between rats and people. Traps were locked to immovable objects and, where possible, were evenly spaced throughout the length of the alley and placed near buildings or fences to align with rats' preference to run alongside vertical surfaces (Barnett 1963).



**Figure 4-1: Map of the three-block study site (each outlined region is a single city-block) in Vancouver's Downtown Eastside (N49°17'/W123°6').** Spatial distribution of sexually mature Norway rats (*Rattus norvegicus*) affixed with Global Positioning System tags are indicated by sex and tag type (PinPoint 120 tags which store data (N = 8) and VHF 75 tags with remote-download capabilities (N = 6)). Map created using Google Earth Professional.

Traps were fixed in an open position with bait for one week prior to trapping (pre-baiting) to allow rats to become acclimatized to traps and minimize avoidance behaviours (Barnett 1963).

We used a combination of peanut butter and oats as bait, and HydroGel® as a water source (ClearH<sub>2</sub>O, Westbrook, ME). Following pre-baiting, active trapping continued for four weeks. Six weeks following the first trapping effort, we performed another week of pre-baiting and two weeks of active trapping. Traps were set at 1600 hours and checked at 0700 hours five days a week.

After capture, each rat was transferred to a rodent inhalation induction chamber (Kent Scientific, Torrington, CT) using rodent handling gloves (Integrated Pest Supplies Ltd., New Westminster, BC). Using an isoflurane vaporizer (Associated Respiratory Veterinary Services, Lacombe, AB), rats were administered 5% isoflurane in oxygen until they reached a plane of anesthesia in which the individual no longer illustrated a righting reflex. Rats were placed on a sanitized and covered surgical table on top of a heating pad. We maintained anesthesia at 1 – 5% isoflurane in oxygen using a large rat nose cone (Kent Scientific, Torrington, CT) and monitored respiratory rate and response to stimuli throughout the procedure. For each rat, we recorded sex (male or female), sexual maturity (males with scrotal testes and females with a perforate vagina were considered mature), weight (grams), and we gave each individual a uniquely labeled laser-etched ear tag (Kent Scientific, Chicago, MI) for future identification.

#### **TAG DESCRIPTION AND SCHEDULE**

We used two types of GPS tags for tracking rat movement: programmable GPS tags with VHF transmitters and remote-download capability (Pinpoint VHF 75), and store-on-board GPS tags without VHF transmitters (Pinpoint 120) (Lotek Wireless, Newmarket, ON). Pinpoint VHF 75 tags weighed 3.5g and were 25 x 14 x 7mm in size with a 50mm caudally-directed GPS antenna and 180mm VHF antenna. Pinpoint 120 tags weighed 4.8g and were 30 x 15 x 10mm in size with a caudally-directed 50mm GPS antenna.

Rats have been documented in some settings to demonstrate peak activity approximately near dawn and dusk (Feng and Himsworth 2014; Oyedele *et al.* 2015) with less activity during mid-day (Parsons *et al.* 2015). To confirm that rats in our study site were active during these times, we observed rats using direct sight in the morning (0300 – 0700 hours) and evening (1800 – 2300 hours) prior to tag deployment. Accordingly, we scheduled tags one hour before dawn, and two hours after dusk. To maximize battery life, tags were programmed to take a GPS location (fix) every 30 minutes for a total of six fixes each day.

### **TAG ATTACHMENT**

As this study occurred in conjunction with a larger CMR study, the first seven male and female rats (N = 14) captured that were sexually mature and weighed over 100g rats were identified as candidates for GPS tag attachment. Rats under 100g were measured (as indicated above), given an ear tag for identification and re-released. A weight of > 100g was used to ensure that tags constituted less than 5% of each rat's body weight (Animal Care and Use Committee 1998). We selected an equal number of males and females to account for potential sex-biased dispersal, and tagged an equal number of males and females from each block (Figure 4-1). For suture insertion, a 2 x 2cm area behind the scapulae was shaved and a sterilized sanitary drape was placed over top of the rat's body, exposing the dorsum. This area was sanitized using a chlorhexidine aseptic soap and prepped with a local anesthetic (0.25% bupivacaine).

As there are no published studies outlining GPS tag attachment for rats, we modified a suturing protocol used for bats (Castle *et al.* 2015). Tags were affixed to the skin using Ethicon PDSII (polydioxanone) sutures size 3-0 (Ethicon Inc., Cincinnati, OH) with a factory-attached reverse cutting needle; sutures were absorbable within 182-238 days in tissue (Ethicon product

insert), which exceeded the timeline of this study. To attach the tag, we tunneled sutures through the subcutaneous space under the skin. Two sutures were placed on each lateral side of the tag from the caudal to cranial space, and two sutures were placed medially at the caudal and cranial ends of the tag. Sutures were secured on the top surface of the tag. Prior to tightening the sutures, Vetbond™ Tissue Adhesive was placed on the ventral side of the tag against the skin, and slight pressure was applied to the tag for up to five minutes, or until the adhesive dried completely (Figure 4-2).



**Figure 4-2: Norway rat (*Rattus norvegicus*) with a Global Positioning System tag.** The tag is affixed behind the scapulae using monofilament, synthetic, absorbable sutures and Vetbond™ Tissue Adhesive. This rat has recovered from anesthesia and is ready for re-release.

Following tag attachment, rats were briefly administered 100% oxygen, and returned to their cage where they were kept warm throughout recovery. Approximately 15 – 30 minutes following tag attachment, rats were re-released to their site of capture (see Figure 4-1 for capture locations).

## **RECAPTURE AND DATA DOWNLOAD**

We attempted recapture of rats five days a week for four weeks in September - October, and again for two weeks in December. Upon recapture, rats were anesthetized, weighed, inspected for signs of injury or adverse tag-related effects, and re-released at their site of capture. To remotely-download data from the PinPoint VHF 75 tags, we walked each of the three alleys with a VHF remote command unit (Lotek Wireless, Newmarket, ON) in hand between 0600 – 0700 five days a week.

## **4.4 RESULTS AND DISCUSSION**

### **CHARACTERISTICS OF TAGGED RATS**

The average weight of tagged rats (N = 14) was 252.14g (range: 124 – 380g) and did not differ between the sexes (Student's t-test,  $t_{12} = 0.81$ ,  $P = 0.44$ ). Tags attached to adult Norway rats weighed between 1.1 – 3.9% total body mass (Table 4-1).

**Table 4-1:** Sex and weight of sexually mature Norway rats (*Rattus norvegicus*) affixed with remote-download (PinPoint VHF 75) and store-on-board (Pin Point 120) Global Positioning System tags

Tag ID	Date Attached	Rat Sex (M/F)	Rat Mass (g)	Tag Mass (g)	Tag % Body Mass
PinPoint VHF 75 Tags					
VHF 175	28.9.2016	M	263	3.5	1.3%
VHF 176	28.9.2016	F	303	3.5	1.2%
VHF 177	28.9.2016	M	303	3.5	1.2%
VHF 178	2.10.2016	F	324	3.5	1.1%
VHF 179	6.10.2016	M	300	3.5	1.2%
VHF 180	8.10.2016	F	248	3.5	1.4%
PinPoint 120 Tags					
PP120 1476	29.9.2016	F	143	4.8	3.4%
PP120 1477	30.9.2016	M	380	4.8	1.3%
PP120 1478	2.10.2016	M	303	4.8	1.6%
PP120 1479	30.9.2016	M	124	4.8	3.9%
PP120 1480	1.10.2016	M	208	4.8	2.3%
PP120 1481	8.10.2016	F	227	4.8	2.1%
PP120 1482	5.10.2016	F	136	4.8	3.5%
PP120 1483	7-10-2016	F	266	4.8	1.8%

#### FEASIBILITY OF ATTACHING TAGS TO URBAN NORWAY RATS

In comparison to traditional CMR techniques and VHF radio-telemetry, GPS tags collect fine-scale movement data (LaPoint *et al.* 2015), are less time-intensive, and require fewer recaptures (Parsons *et al.* 2014). However, while CMR and VHF-radio-telemetry can be performed without anesthetic, tag attachment in our study required a surgical intervention, involving anesthesia and appropriate training in suturing techniques. Therefore, for each tagged rat, the time from capture to re-release took up to one and a half hours, for anesthesia (15 – 30 minutes), tag attachment (15 – 30 minutes) and recovery from anesthesia (15 – 30 minutes). Tag attachment, requiring at least 45 minutes per rat and specialized anesthetic equipment, was feasible from a research standpoint,

but may not be practical for pest control professionals seeking to understand their local rat populations due to equipment and labour costs.

### IMPACTS OF GPS TAG ATTACHMENT ON RAT HEALTH

Among the recaptured rats (N = 3), tag attachment did not have any apparent adverse health effects. There were no indications of skin trauma or infection, though one individual demonstrated light scabbing at the suture site (Table 4-2). All recaptured rats demonstrated weight loss from 1.0 – 17.0g (Table 4-2), well within the range of loss amongst non-tagged recaptured rats that were a part of the larger disease transmission study (4 – 95g, unpublished). Indeed, it is difficult to determine whether this degree of weight loss is uncommon as many contemporary studies on urban rats in similar inner-city settings use trap-removal techniques instead of CMR (Himsworth *et al.* 2014a; Panti-May *et al.* 2016).

**Table 4-2:** Date of recapture and change in weight of Norway rats (*Rattus norvegicus*) affixed with Global Positioning System tags

Tag ID	Date Recovered	Days Post-Attachment	Weight Change (g)	Appearance of GPS Attachment Site
VHF 178	16.10.2016	14	-17	Some light scabbing at sutures, no sign of infection
VHF 179	15.10.2016	9	-1	Suture sites healed, no sign of skin irritation
PP120 1480	19.10.2016	18	-2	Suture sites healed, no sign of skin irritation

We were unable to account for the overall effect of tag attachment on rat health as we could not quantify or compare the mortality rate of tagged rats to non-tagged rats. It is possible that capture (Shanker 2000) and tag attachment (Theuerkauf *et al.* 2007) resulted in increased mortality due to heightened stress and/or behavioural modifications (Walker *et al.* 2012). Although, for rats,

the effects of handling are more pronounced with repeated recapture over time (Shanker 2000), and tag weights < 4.5% body weight have been assumed not to result in additional mortality (Taylor 1978). Furthermore, because urban rats have a short life span (90% live less than one year (Davis 1953b)) due to environmental factors such as anticoagulant poisoning, vehicle collision, and predation (Taylor 1978), it is difficult to assess the impact that tags had on mortality. However, the observed recapture rate of 21.4% (3 of 14) aligns with the overall 20% recapture rate of untagged rats in this study (unpublished). Thus, tag attachment did not appear to result in additional mortality that would have been evident through reduced recapture success in the tagged population.

#### **POTENTIAL FOR TRACKING RAT MOVEMENT**

We were unable to obtain any movement data from the deployed tags. This may be attributed to a combination of a low recapture rate, the inability of remote-download tags to log location data, and post-release removal of GPS tags.

Low recapture rates highlight the necessity of using remote-download tools, which obtain data without recapturing tagged animals. The low recapture rate (21.4%) in our study hindered the potential to retrieve store-on-board tags (Table 4-2). This corresponds with low recapture rates in other studies (Glass *et al.* 1988), and may be due to rats' learned-aversion behaviours (Taylor *et al.* 1974) which make them difficult to capture and recapture (Clapperton 2006).

To overcome the issue of low recapture rates, we deployed six remote-download tags. Five of the six remote-download tags were able to communicate with the VHF receiver, but none were able to obtain satellite signals. Each attempt to connect with satellite signals lasted 70 seconds before terminating. Failed location attempts are often attributed to decreased line-of-sight between

satellites and GPS tags, and may be influenced by topographical features, vegetation and/or animal behaviours (Rempel *et al.* 1995; Frair *et al.* 2010; Moriarty and Epps 2015) that limit the degree of sky cover (Rose *et al.* 2005; Adams *et al.* 2013). In this regard, certain urban environments may be suboptimal for satellite acquisition due to obstruction caused by dumpsters or building overhangs. These limitations may be particularly pronounced in species, such as Norway rats (Cavia *et al.* 2009; Feng and Himsworth 2014), that occupy burrows or inhabit buildings (D'Eon and Delparte 2005; McMahan *et al.* 2017). For these reasons, we think it is likely that the ecology of Norway rats interferes with the effective use of GPS tags in urban settings. These technologies may be more successful in other urban exploiter species, such as black rats (*Rattus rattus*) which nest on rooftops and commonly move along fences and telephone wires (Worth 1950). This could make black rats a better target for GPS tag attachment, as they may be less prone to satellite line-of-site obstruction.

Of the three recaptured rats, none retained their GPS tags, illustrating that the performance of both types of tags was hindered by removal. The fact that the combined use of sutures and veterinary adhesive was insufficient for attachment of GPS tags is likely due to rat ecology. The tendency of Norway rats to travel through narrow spaces (Davis *et al.* 1948) could have led to dislodgement of tags through repeated wear on sutures. Additionally, tags may have been destroyed by chewing of antennae, as has been documented in black rats and Polynesian rats (*Rattus exulans*) (Theuerkauf *et al.* 2007). As Norway rats nest and groom with conspecifics (Barnett and Spencer 1951), there may be opportunities for conspecifics to remove tags. Given the potential for tag dislodgement occurring in as little as nine days post tag deployment (Table 4-2), scheduling a greater number of fixes over a shorter period might increase the likelihood of obtaining information on movement but may be negated by rapid tag damage and removal.

## CONCLUSIONS

Understanding urban rat movement is increasingly important for control efforts given rapid urbanization worldwide (Himsworth *et al.* 2013b; United Nations 2014) and the rising risk of rat-associated zoonoses in urban centers (Himsworth *et al.* 2013b). Current methods for studying rat movement patterns are hindered by resources and logistical complications of urban ecological studies (Parsons *et al.* 2015). Despite advancements in GPS technologies, we have demonstrated that GPS tags are challenging to deploy on urban Norway rats due to feasibility of attachment. However, we have shown that, given low recapture rates of rats, tags with remote-download technologies offer a greater potential for future use, allowing for recovery of data without rat recapture. Future technological advancements, such as surgically implantable GPS tags, may help to address issues with tag removal. As the probability of removal is likely to increase with time, we suggest maximizing the number of fixes attempted within a shorter period of time than was used here, to increase the likelihood of improving tag line-of-sight, instead of fewer fixes over an extended period of time. These modifications in GPS tag attachment and scheduling have the potential to greatly improve our ability to use these tools to understand local rat movement patterns. Lacking this technology, current programs aimed at understanding rat movement may benefit from incorporating multiple methods to resolve movement patterns. For example, despite the coarse movement estimates provided through CMR techniques, combining CMR with genetic information, which is capable of inferring historical movement of populations (Gardner-Santana *et al.* 2009; Kajdacsí *et al.* 2013; Mangombi *et al.* 2016; Richardson *et al.* 2017), may improve our understanding of local rat movement patterns in heterogeneous urban landscapes. This information can be used to better describe disease transmission among rat populations and to devise and deploy effective rodent-control programs.

# CHAPTER 5: USING GENETIC RELATEDNESS TO UNDERSTAND HETEROGENEOUS DISTRIBUTIONS OF URBAN RAT-ASSOCIATED PATHOGENS

## 5.1 SYNOPSIS

Urban Norway rats (*Rattus norvegicus*) carry several pathogens transmissible to people. However, pathogen prevalence can vary across fine spatial scales (i.e., by city block). Using a population genomics approach, we sought to describe rat movement patterns across an urban landscape, and to evaluate whether these patterns align with pathogen distributions. We genotyped 605 rats from a single neighbourhood in Vancouver, Canada and used 1,495 genome-wide single nucleotide polymorphisms to identify parent-offspring and sibling relationships using pedigree analysis. We resolved 1,246 pairs of relatives, of which only 1% of pairs were captured in different city blocks. Relatives were primarily caught within 33m of each other leading to a highly leptokurtic distribution of dispersal distances. Using binomial generalized linear mixed models we evaluated whether family relationships influenced rat pathogen status with the bacterial pathogens *Leptospira interrogans*, *Bartonella tribocorum*., and *Clostridium difficile*, and found that an individual's pathogen status was not predicted any better by including disease status of related rats. The spatial clustering of related rats and their pathogens lends support to the hypothesis that spatially restricted movement promotes the heterogeneous patterns of pathogen prevalence evidenced in this population. Our findings also highlight the utility of evolutionary tools to understand movement and rat-associated health risks in urban landscapes.

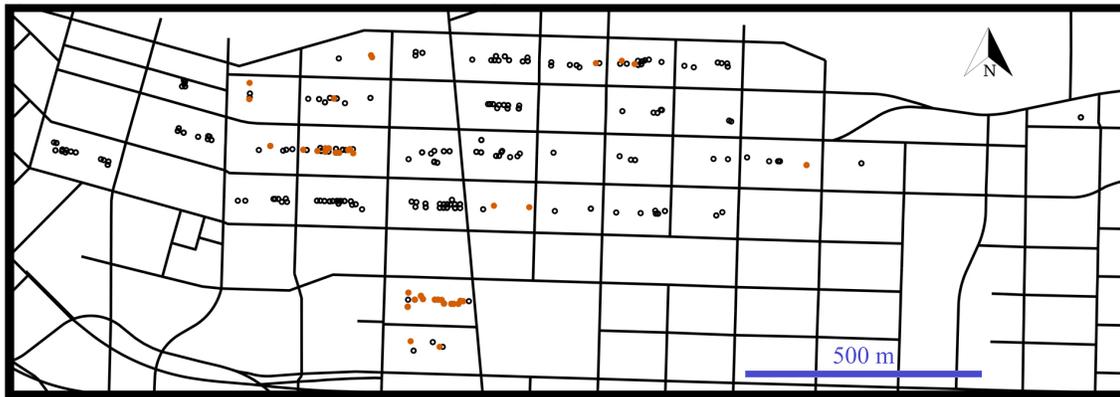
## 5.2 INTRODUCTION

Norway rats (*Rattus norvegicus*) are carriers of a number of ‘zoonotic’ pathogens (those transmissible between animals and humans) responsible for significant morbidity and mortality in cities globally (Himsworth *et al.* 2014c). For example, the rat-associated pathogen *Leptospira interrogans* affects approximately one million people annually and can result in kidney failure or pulmonary hemorrhage (Guerra 2009; Costa *et al.* 2015a). Urban rats serve as reservoirs for numerous important pathogens including *Yersinia pestis*, *Bartonella* spp., *Rickettsia typhi* and Seoul hantavirus (Easterbrook *et al.* 2008; Himsworth *et al.* 2013b; Firth *et al.* 2014; Pépin 2016). In addition, rats can carry human-associated pathogens such as methicillin-resistant *Staphylococcus aureus* (MRSA) (Himsworth *et al.* 2014b), and *Clostridium difficile* (Himsworth *et al.* 2014d), although whether their carriage contributes to human transmission is unknown. Rat-associated pathogens are spread among rats and to people in various ways, including through direct contact with rats, via disease vectors (i.e., fleas and lice), and through environmental contamination with rat urine and/or feces (Himsworth *et al.* 2013b). Understanding rat-pathogen dynamics is an increasingly important issue internationally given the global distribution of rats (Long 2003) and rapid urbanization and densification (United Nations 2018) which is likely to intensify rat-associated impacts worldwide (Himsworth *et al.* 2013b).

The prevalence of rat-associated pathogens is often spatially heterogeneous and may be driven by rat dispersal globally and locally. Differences in disease prevalence at regional scales (i.e., by city) are well established (Ellis *et al.* 1999; Peterson *et al.* 2017; Kosoy and Bai 2019) and may arise through founder events, such that pathogen presence is dependent on the disease status of the individuals first introduced to an area. Indeed, the current global distribution of Norway rats has been attributed to multiple introduction events, thought to have been facilitated by human

migration (Feng and Himsworth 2014; Puckett *et al.* 2016). Patterns of heterogeneous pathogen prevalence are also evident at fine spatial scales (i.e., by city block) (Anglely *et al.* 2018). For example, in Vancouver, Canada, the prevalence of the bacterial pathogen *L. interrogans* ranged from 0 – 66% by city block (Himsworth *et al.* 2015a) (Figure 5-1A). Comparatively, the prevalence of *Bartonella* spp. varied from 10 – 85% by trapping location in New York City, and 0 – 97% in New Orleans (Peterson *et al.* 2017). Similar to global movement patterns, at local scales pathogen distributions may be driven by rat dispersal and connectivity across the landscape. Urban rats typically exhibit strong philopatry, remaining near their natal colony and occupying small home ranges about the size of a city block (reviewed in Byers *et al.* (2019b)). This behavioural tendency to occupy small territories, in conjunction with barriers to rat dispersal, can result in genetic discontinuities of rats across the landscape (Brouat *et al.* 2013; Kajdacs *et al.* 2013; Combs *et al.* 2018a) thus potentially limiting the spread of pathogens. Indeed, such restricted connectivity has been linked to decreased spread of feline immunodeficiency virus among bobcats (*Lynx rufus*) (Kozakiewicz *et al.* 2020) and rabies virus among raccoons (*Procyon lotor*) (Biek *et al.* 2007). Additionally, increased contact among closely related individuals may promote unequal transmission, such that relatives are more likely to share pathogens than non-relatives (Root *et al.* 2004; Grear *et al.* 2010). Although rat dispersal and family relationships may be important drivers of pathogen distributions, they remain understudied.

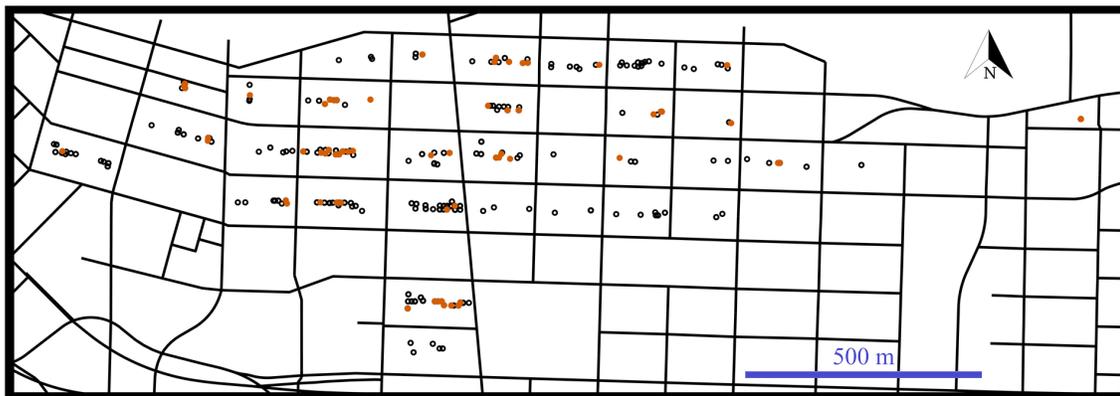
(a) *Leptospira interrogans*



(b) *Bartonella tribocorum*



(c) *Clostridium difficile*



Longitude

Pathogen Status ● Positive ○ Negative

**Figure 5-1: Spatial distribution of Norway rats (*Rattus norvegicus*) carrying zoonotic pathogens across Vancouver's Downtown Eastside neighbourhood.** Rats were tested for carriage with: A) *Leptospira interrogans* of which 11% (60/535) tested positive; B) *Bartonella tribocorum* of which 26% (90/349) tested positive; and C) *Clostridium difficile* of which 13% (80/605) tested positive.

A lack of information regarding urban rat movement ecology is largely due to the challenges of tracking rats in real-time. Traditional ecological approaches such as capture and recapture of marked individuals are labour and time-intensive (Conroy and Carroll 2009) and unequal trappability can bias movement estimates towards “trap-happy” individuals (Byers *et al.* 2019c). While other tools such as Global Positioning System tags enable fine-scale monitoring over time, they remain difficult to deploy on urban rats due to issues of tag obstruction and tag removal (Byers *et al.* 2017). Population genetic methods afford an alternative to traditional approaches by identifying closely related individuals, with accuracy improving with an increased number of genetic markers (Premachandra *et al.* 2019; Foroughirad *et al.* 2019). The relative locations of related individuals can be used to infer movement events. In fact, genetic approaches tend to reveal greater travel distances than suggested through traditional methods (Byers *et al.* 2019b), although these patterns vary by location and sampling effort (Combs *et al.* 2018a). For example, genetic approaches have identified rat movement distances of up to 11.5km in Baltimore, Maryland (Gardner-Santana *et al.* 2009) and up to 536m in New York City (Combs *et al.* 2018b) although average movements are typically within 30 – 150m (Gardner-Santana *et al.* 2009; Combs *et al.* 2018b). Genomics-based approaches have also demonstrated that differences in movement can vary by sex, with males travelling further afield than females (Kajdacsí *et al.* 2013; Desvars-Larrive *et al.* 2017) in search of mates (Glass *et al.* 2016). Together, these findings suggest that patterns of relatedness vary over space and that genetic methods can provide valuable insight into movement events involved in pathogen spread or clustering.

In this study we combine previously published disease (Himsworth *et al.* 2013a; 2014d; 2015a) and population genomic data (Combs *et al.* 2018a) from rats in Vancouver, Canada to explore the role of fine-scale genetic structure and movement in the distribution of rat-associated

pathogens. Previously, our team demonstrated that pathogen prevalence in this population varied significantly by city block (Himsworth *et al.* 2013a; 2015a) (Figure 5-1), and we found that genetic structuring varied across fine spatial scales, with some genetic clusters spanning one or several city blocks (Combs *et al.* 2018a). Here, we combine these data sets and use a genomics-based pedigree inference approach to: a) identify closely related individuals and infer movement events; b) compare patterns of relatedness and movement to prevalence data for pathogenic bacteria carried by rats; and c) explore the impact of family membership on an individuals' pathogen status. We hypothesised that first- and second-order relatives would reside within the same city block, and that these patterns of relatedness would align with the spatial clustering of pathogens. Further, we chose to evaluate rat-relatedness in relation to three pathogens of public health concern (*L. interrogans*, *Bartonella tribocorum*, and *C. difficile*) as we hypothesized that family membership would contribute to pathogen status for pathogens transmitted through close contact (*L. interrogans* and *B. tribocorum*) but not for those environmentally-acquired (*C. difficile*). Together, information from this study can be applied to urban rat management strategies aimed at mitigating human health risks.

## 5.3 METHODS

### STUDY SITE

Rats were trapped in the Downtown Eastside (DTES) neighbourhood of Vancouver, Canada, an area where rats are abundant (Himsworth *et al.* 2014a) and there is considerable contact between residents and rats (Byers *et al.* 2019a), which makes it of particular concern for rat-associated zoonoses. Vancouver has a moderate oceanic climate, an annual mean temperature of 11°C, and annual precipitation of 1,588mm. The study site encompassed 43 contiguous city blocks and one

site at the adjacent international shipping port on the neighbourhood's northern border (N49° 17' / W123° 6'). The neighbourhood is densely populated with approximately 18,500 people (City of Vancouver 2014) and is comprised of residential, commercial, and industrial buildings, many of which are in disrepair (Smith 2000).

## TRAPPING

Rats were trapped as part of a long-term study evaluating rat disease ecology; detailed trapping methods have been published elsewhere (Himsworth *et al.* 2013a). In brief, rats were trapped from September 2011 – August 2012. Each city block and the international port site was assigned randomly to a 3-week study period during the 1 year of trapping. We used Tomahawk Rigid Traps (Tomahawk Live Trap, Hazelhurst, USA) which were set in the alleyway bisecting each city block. Traps were pre-baited for one week prior to two weeks of active trapping. We recorded the date and location of each trapped rat.

Prior to euthanasia, we collected blood via intracardiac puncture under isoflurane anaesthesia. Rats were humanely euthanized via intracardiac injection with pentobarbital. At the international shipping port, rats were trapped by a collaborating pest control professional using lethal snap traps. All rats underwent a complete necropsy, with aseptic collection of the kidney, liver, and colon. Samples were stored at -80°C prior to pathogen testing and DNA sequencing. We collected morphological data including: sex, sexual maturity (scrotal testes for males, perforate vagina for females), weight (grams), and pregnancy.

For subsequent analyses, we used the von Bertalanffy (1938) growth curve equation to infer rat age in days from rat weight. This equation accounts for the non-linear relationship between weight and age (Calhoun 1963) and has been used previously to model rat age curves

(Minter *et al.* 2017; 2019). Specifically:  $\text{weight} = a[1 - \exp\{-r(\text{age} - c)\}]$ , where “a” represents the asymptote, “r” represents the constant growth rate and “c” represents the age at which maximum growth occurs. We used parameters derived from Calhoun (1963) as in Minter *et al.* (2019), and for pregnant females, we adjusted weight by the average difference between pregnant and non-pregnant, sexually mature females (Minter *et al.* 2017).

## DISEASE TESTING

All pathogen testing was completed as part of a broader epidemiological study evaluating the prevalence of rat-associated pathogens in the DTES. For this study, we included rats that were tested for the bacterial pathogens *L. interrogans*, *B. tribocorum*, and *C. difficile*.

For *L. interrogans*, DNA was extracted from rat kidney and analyzed using a real-time PCR (Life Technologies) that targets a 242 bp fragment of the LipL32 gene of pathogenic *Leptospira* species (Stoddard *et al.* 2009) as outlined in Himsworth *et al.* (2013a).

For *B. tribocorum*, blood clots were cultured at the Bartonella and Rodent-Borne Disease Laboratory, Centers for Disease Control and Prevention, Fort Collins, CO as outlined by Himsworth *et al.* (2015a). *Bartonella* spp. were identified based on colony morphology and confirmed by PCR amplification of the citrate synthase gene (*gtlA*) (Ying *et al.* 2002; Bai *et al.* 2007).

For *C. difficile*, colon contents were cultured and identified as outlined in Himsworth *et al.* (2014d). Identification of *C. difficile* was made using colony morphology and odor, Gram staining, and the presence of L-proline aminopeptidase activity (Remel Inc., Lenexa, Kansas, USA).

## GENETIC SEQUENCING

We used a genome-wide single nucleotide polymorphism (SNP) dataset acquired through double digest restriction site associated DNA sequencing (ddRADSeq) of DNA from rat liver samples. In brief, Combs *et al.* (2018a) used Stacks v. 1.35 (Catchen *et al.* 2013) to demultiplex sequencing reads and align them to the RNOR v.6.0 reference genome for *R. norvegicus* (Gibbs *et al.* 2004). Using these previously published reference-aligned reads, Combs *et al.* (2018a) identified SNPs using the *pstacks*, *cstacks*, and *sstacks* pipeline from STACKS v1.35, retaining only a single SNP per RADtag. Using this dataset, we then further filtered SNPs based on coverage, removing sites with <20x and >50x coverage using VCFtools (Danecek *et al.* 2011). We used PLINK 1.9 (Chang *et al.* 2015) to prune SNPs on the basis of linkage disequilibrium. Sliding windows of 50 SNPs (with a step of 5) were thinned using a variance inflation factor of 2. Autosomal SNPs with a minor allele frequency >5% that were called in >85% of individuals were retained for further analysis. SNPs with excessive heterozygosity (>80%) were removed in PLINK 1.9. Our filtering criteria resulted in 1,495 SNPs genotyped in 605 individuals.

## PEDIGREE INFERENCE

We identified related rats by running parentage assignment using the *Sequoia* v. 1.3.3 (Huisman 2017) package in R (RStudio Team). *Sequoia* was developed for use with SNP data and is robust to unsampled individuals. Data incorporated into the parentage analysis also include the animal's sex and birth year. Birth year is used to assist in distinguishing among relationships such as parent-offspring and full-sibling pairs (Huisman 2017). Given the rapid reproductive rate of rats (Feng and Himsworth 2014) and that urban rats often live less than one year (Davis 1953b), we defined birth years as follows: first we estimated each rat's birth date by subtracting their computed age in

days from the date of trapping. Second, based on the distribution of ages, we estimated that rats in this population reached sexual maturity at as early as 39 days as there was a division in the distribution of weights of mature and sexually immature rats at 110g (Supplementary Figure S5-1). Although previous estimates suggest that rats reach sexual maturity within 45 – 75 days for females and 45 – 95 days for males (Calhoun 1963), time to maturity can vary based on resource availability (MacDonald *et al.* 1999). Finally, we calculated the number of days from the earliest estimated birth date to the latest estimated birth date and separated this time frame into 11, 39-day intervals designated as “birth years”. Using these life history data, we identified first-order (parent-offspring and full-sibling) and second-order (half-sibling) relationships.

#### **INFERRING GEOGRAPHIC AND GENETIC DISTANCES BETWEEN RELATIVES AND BY SEX**

To characterize distances travelled, we calculated the pairwise Euclidian distance between each member of a set of relatives and categorized distances within relationship type (i.e., parent-offspring, full-sibling, half-sibling). We mapped relationships spatially to visualize patterns of relatedness and to identify instances where relatives were located within the same city block and in different blocks. Mapping was performed using `ggplot2` in R using open-source shape files (<https://vancouver.ca/your-government/open-data-catalogue.aspx>) to create maps.

To identify evidence of sex-biased dispersal we created correlograms comparing matrices of geographic and genetic distances between pairs of male and female rats separately. Correlograms identify the extent of isolation-by-distance (i.e., spatial autocorrelation) for pairs of individuals at different distance classes, where variation between sexes indicate differences in dispersal intensity or mechanism (Banks and Peakall 2012). We used the `ecodist` package in R, specifying distance classes of 50m and using 1000 permutations (Goslee and Urban 2007).

## GENETIC RELATEDNESS AND PATHOGEN STATUS

We used binomial generalized linear mixed models to evaluate whether rat family relationships influenced rat disease status. We designated a ‘family’ as a group of full-siblings as we hypothesized that full-siblings would be most likely to have been in close proximity through nest-sharing. This designation also prevented rat membership in multiple families (i.e., as would have occurred by including half-siblings). For each pathogen (*L. interrogans*, *B. tribocorum*, or *C. difficile*), we created a model where the response variable was rat infection status (positive or negative), and we included rat morphometrics and capture characteristics as covariates if they were previously identified as predictors of pathogen status in this population (Himsworth *et al.* 2013a; 2014d; 2015a). As these pathogens were previously found to vary in prevalence by city block, we included city block of capture as a random effect in all models. To test whether ‘family’ improved model fit, we included ‘family’ as a random effect nested within city block and compared the relative fit of models with and without ‘family’ using Akaike Information Criterion (AIC). Models were considered to be similarly supported if the difference between their AIC values was  $\leq 2$  (Burnham and Anderson 2002). Modeling was performed using the package lme4 in R.

## 5.4 RESULTS

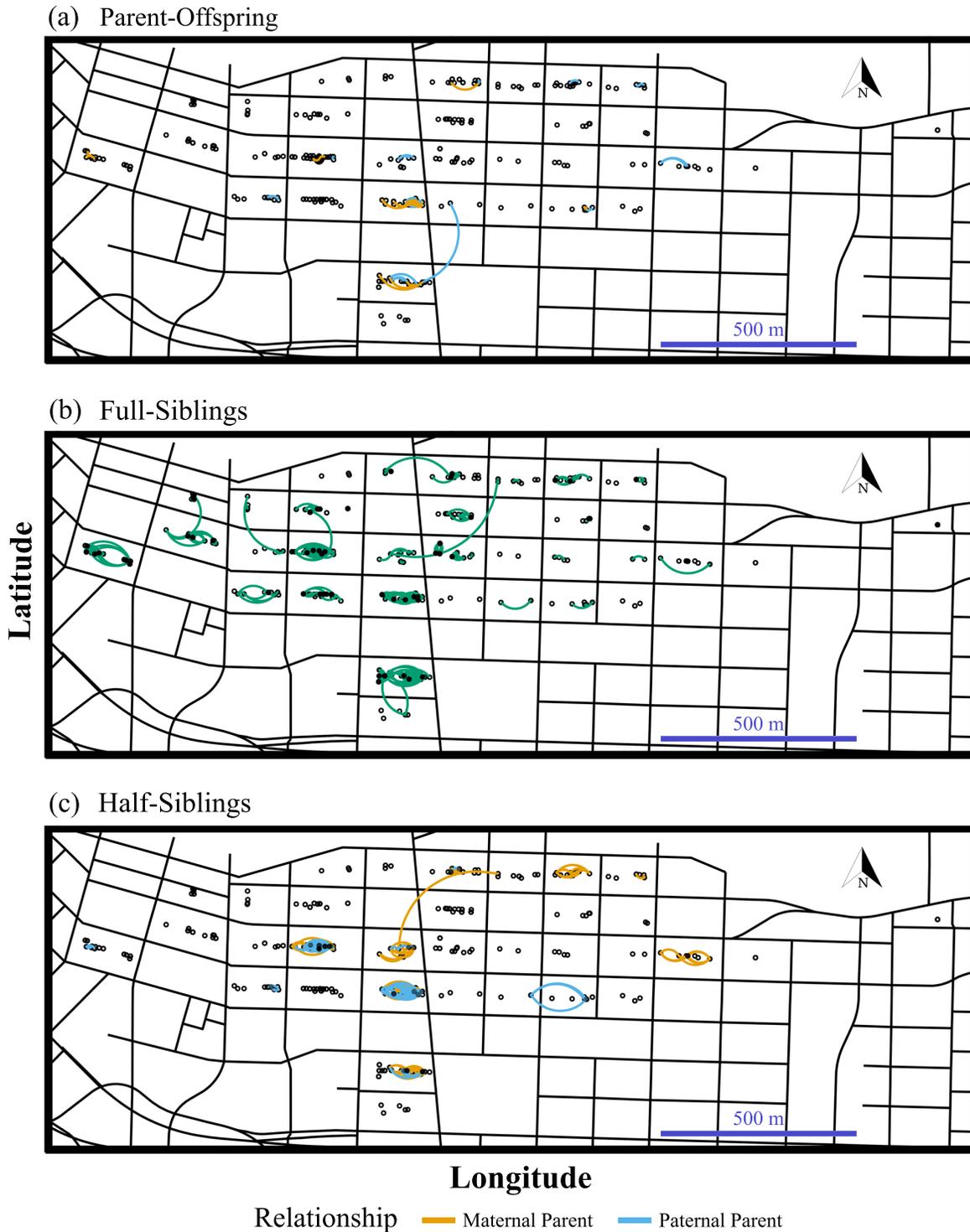
### POPULATION CHARACTERISTICS

A total of 685 Norway rats were trapped over the course of one year. Following filtering of genetic data, we retained 605 rats, of which 332 (55%) were male (192 mature, 139 immature, one unknown), 261 (43%) were female (129 mature, 132 immature), and 12 (2%) were of unknown sex and maturity. The number of rats tested for each rat-associated pathogen varied. For *L. interrogans*, 535 rats were tested of which 60 (11%) were positive. For *B. tribocorum*, 349 rats

were tested of which 90 (26%) were positive. For *C. difficile*, all 605 rats were tested, of which 80 (13%) were positive.

### **PEDIGREE INFERENCE**

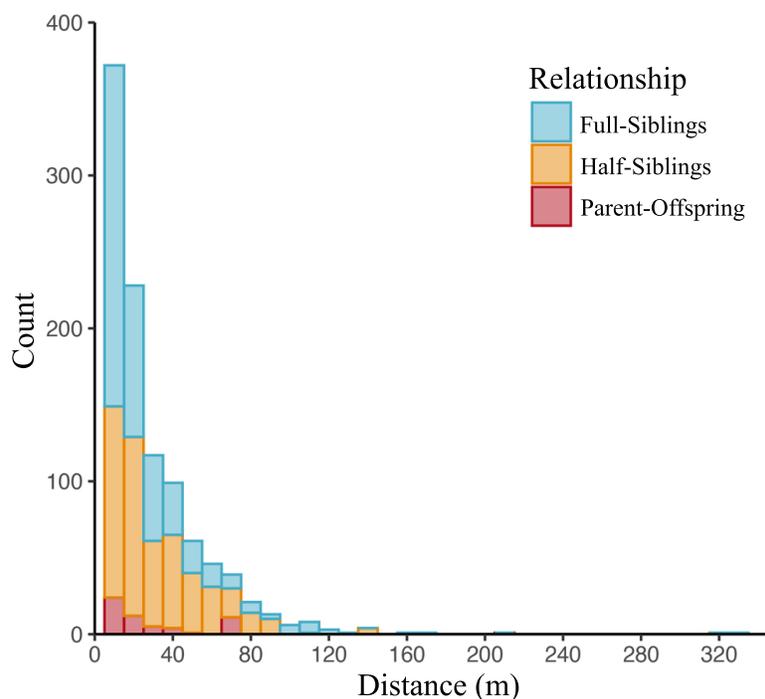
Among the 605 genotyped rats included in the parentage analysis, we resolved a total of 1,246 pairs of relatives (Figure 5-2), 713 of which were first-order and 533 of which were second-order relatives. Of the first-order relatives, we identified 68 parent-offspring pairs, including 11 dams assigned to 29 offspring and 20 sires assigned to 39 offspring (Figure 5-2A). Further, 72% (442/605) of rats were paired with at least one full-sibling (Figure 5-2B). We identified 645 full-sibling pairs which were grouped into 155 distinct full-sibling ‘families’. These full-sibling ‘families’ included anywhere from 2 – 16 individuals (median = 2 individuals per family). Regarding second-order relatives, we identified 533 half-sibling pairs which included 314 pairs sharing a dam and 219 pairs sharing a sire (Figure 5-2C)



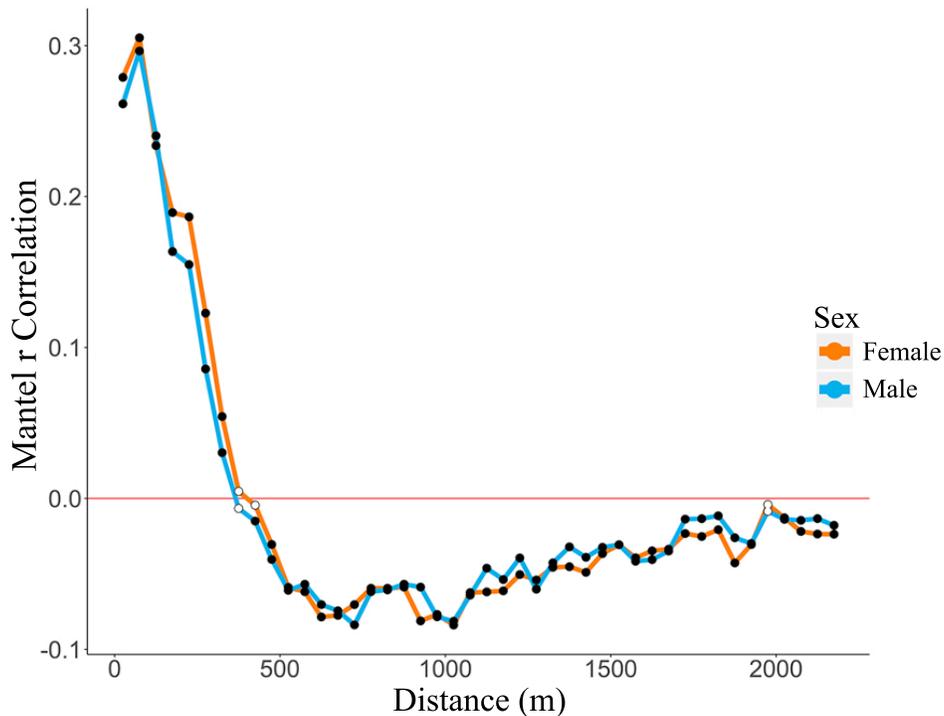
**Figure 5-2: Distribution of pairs of related Norway rats (*Rattus norvegicus*) across Vancouver's Downtown Eastside neighbourhood.** Of 1,246 related pairs, we resolved: A) 68 parent-offspring pairs; B) 645 full-sibling pairs; and C) 533 half-sibling pairs. Thirteen pairs were associated across city blocks. Relatives captured in the same trap are identified with (●), and relatives trapped in different locations are connected by a curved line.

## GEOGRAPHIC AND GENETIC DISTANCES BETWEEN RELATIVES AND BY SEX

Figure 5-2 illustrates that the majority of rats were caught within the same city block as their relative. Of the 1,246 related pairs, 1% (13/1,246) were captured in different city blocks. Distances between related pairs ranged from 0 – 330m, with 25% of relatives caught within 7m, 50% within 16m, and 75% within 33m (Figure 5-3). Full-siblings were caught in closest proximity to each other with a median distance of 10m between pairs, while parent-offspring (median = 15.4m) and half-siblings (median = 22.5m) were caught further apart. In our analysis of isolation-by-distance, we did not find any evidence that distance between pairs differed by sex. Patterns of isolation-by-distance were similar for both sexes across all distance classes (Figure 5-4).



**Figure 5-3: Distances between capture points of related rats.** Of 1,246 pairs of related rats, 75% of individuals were caught within 33m of their relative, with 24 pairs of rats captured more than 100m apart.



**Figure 5-4: Correlogram of genetic and geographic distance for pairs of rats.** The Mantel r correlation is the strength of correlation between genetic and geographic distance between pairs of male (N = 332) and female (N = 261) rats. Correlation values are denoted within each distance class of 50m.

#### GENETIC RELATEDNESS AND PATHOGEN STATUS

Modelling was informed by previous work on this population of rats. Specifically, we included covariates identified as informative predictors of rat pathogen status such as: rat weight in the *L. interrogans* model (Himsworth *et al.* 2013a); sexual maturity and season in the *B. tribocorum* model (Himsworth *et al.* 2015a); and weight in the *C. difficile* model (Himsworth *et al.* 2014d). Table 5-1 depicts the parameters for the best fitting model for each disease. Incorporating ‘family’ into infection models did not improve model fit. For all pathogens, models run with and without ‘family’ as a random effect were within 2 AIC (Table 5-1).

**Table 5-1:** Comparison of models containing predictors of pathogen status with and without ‘family’ membership included as a random factor.

Model		Model Includes ‘Family’ Random Effect			Model Excludes ‘Family’ Random Effect		Model Comparison
Pathogen	Covariates	AIC	Family Variance (Std Dev)	Block Variance (Std Dev)	AIC	Block Variance (Std Dev)	$\Delta$ AIC
<i>Leptospira interrogans</i>	Weight	219.3	0.00 (0.00)	4.99 (2.26)	217.3	4.99 (2.24)	2
<i>Bartonella tribocorum</i>	Maturity Season	323.2	0.42 (0.65)	1.19 (1.09)	322	1.08 (1.04)	1.2
<i>Clostridium difficile</i>	Weight	452.9	0.52 (0.72)	0.56 (0.75)	452.8	0.56 (0.75)	0.1

At the level of the block, we identified 8 pairs of blocks that shared a pair of relatives (Figure 5-2). Cases where both pairs of blocks share pathogen status (i.e., both blocks either possessed affected rats or did not) were greatest for *L. interrogans* (7/8 block pairs shared pathogen status), followed by *B. tribocorum* (6/8 pairs of blocks shared pathogen status), and *C. difficile* (5/8 blocks shared pathogen status).

## 5.5 DISCUSSION

Understanding how rats move and interact within the urban environment is integral to informing control efforts aimed at mitigating rat-associated impacts like the spread of zoonotic diseases. Our study is the largest parentage-based analysis of wild rats to date and reveals fine-scale spatial clustering of closely related individuals within 33m of each other, with most relatives located within the same city block. These patterns of relatedness suggest very little movement and interaction of rats between neighbouring city blocks which may restrict opportunities for pathogen spread.

The distinct clustering of close relatives evidenced in this study may be attributed to a combination of social and environmental barriers to movement. Urban rats are territorial (Barnett 1963), occupying home ranges as small as 30 – 45m in diameter (Davis *et al.* 1948; Davis 1953a) which is approximately 1/3 the length of city blocks in this study. Rats often stay within their home range (Gardner-Santana *et al.* 2009; Glass *et al.* 2016), and while they may extend their home range in relation to resource availability (Davis *et al.* 1948) the abundance of food and areas to burrow in the DTES (Himsworth *et al.* 2014c) may minimize the need for rats to venture beyond their natal block. It is also important to note that immigrating to a new colony can have other social consequences. The territoriality of Norway rats can impede the successful integration of unknown

individuals as they are often ejected by resident rats (Calhoun 1948). Although previous work suggests that some males will travel to neighbouring blocks to mate with females of a different colony (Glass *et al.* 2016), males will also breed with related females. For example, in Salvador, Brazil, females were more related to the sires of their offspring than would be expected (Costa *et al.* 2016). Therefore, it is possible that the high population density of rats in this neighbourhood may limit the need of males to travel in search of mates. Indeed, we identified only one instance where a sire was captured in a different block than its offspring, and just 1% of relatives were caught in different city blocks. And while this result strongly suggests that movement among city blocks is infrequent, it is important to note that this may be an underestimate of rat movement as blocks were trapped at different times. This difference in trapping periods could bias estimates toward finding more relatives within blocks than between blocks, particularly when adjacent city blocks were trapped at separate times. However, of the eight pairs of blocks sharing relatives in this study, five were trapped during different time periods (ranging from one to eight months apart). Indeed, the study site included a total of 17 pairs of adjacent blocks that were trapped contemporaneously, and only three of these pairs shared cross-block relatives. These patterns suggest that, although movement among city blocks may be more frequent than can be captured by this study, the majority of relatives remain within the same city block.

For all inferred movement events, it is impossible to say which individual in a pair moved, or whether gene flow is due to movement of a parent not sampled in this study. However, our results suggest that males and females contribute similarly to gene flow, with little evidence for sex-biased dispersal. These findings align with studies in Baltimore and New York City, USA (Gardner-Santana *et al.* 2009; Combs *et al.* 2018b), although sex-biased dispersal has been reported in both Salvador, Brazil and Hauts-de-Seine, France (Kajdacs *et al.* 2013; Desvars-

Larrive *et al.* 2018a). Beyond social barriers, environmental features may also impede rat movement. Landscape features such as high-traffic roadways, waterways, and areas with fewer resources have been found to align with restricted gene flow, suggesting that these environmental characteristics can pose a barrier to movement (Richardson *et al.* 2017; Combs *et al.* 2018a). In fact, Combs *et al.* (2018a) indicated that roadways in this study were likely barriers to dispersal, although in some non-urban contexts roads may facilitate movement (Berthier *et al.* 2016). Overall, the minimal connectivity of rats among city blocks explains the high levels of inbreeding previously reported in this population ( $F_{IS}$  ranging from 0.06 – 0.28) (Combs *et al.* 2018a). As urban centers densify and land use changes (i.e., through emphasis on “greening” city spaces (Goddard *et al.* 2010; Lovell and Taylor 2013)) these patterns are likely to change in response to altered segregation of rat colonies with implications for pathogen spread.

The patterns of limited connectivity among city blocks in Vancouver align with heterogeneous patterns of pathogen prevalence (Himsworth *et al.* 2013a; 2015a). We find that in instances where there were cross-block relatives, these pairs of blocks often shared pathogen status (i.e., blocks either both had affected rats, or they did not). These patterns were most striking for *L. interrogans* and *B. tribocorum* where seven of eight pairs of connected blocks and six of eight pairs of connected blocks shared pathogen status respectively. Connectivity through movement may allow for the spread of some pathogens due to aggressive interactions between the immigrating individual and members of the established colony (Calhoun 1948). These interactions would be particularly important for facilitating transmission of pathogens such as *L. interrogans* and *B. tribocorum*, as they are transmitted through contact with rats and their parasites. However, it is difficult to ascertain whether these patterns are driven by rat movement, particularly given a limited sample size from which to draw firm conclusions.

Within city blocks, fine spatial structuring appears to be less important in determining pathogen status than block-level associations. As full-siblings share a nest until they begin free-roaming at as early as 25 days old (Calhoun 1963), we hypothesized that full-siblings would be more likely to share pathogen status. However, membership in a full-sibling ‘family’ did not appear to explain pathogen status. While this result was expected for *C. difficile*, a pathogen thought to be transmitted among rats through environmental contamination (Himsworth *et al.* 2014d), this result was unexpected for *B. tribocorum* and *L. interrogans* carriage. Specifically, because *B. tribocorum* is transmitted among rats through contact with their fleas, which reside both on rats and in their nests (Krasnov *et al.* 2004), where rats regularly maintain close physical contact (Barnett 1963), we expected family membership to account for some of the variation in *B. tribocorum* status. However, as multiple paternity is common in Norway rats (Costa *et al.* 2016; Glass *et al.* 2016), individuals are also likely to share the nest with half-siblings. Therefore, a more extensive designation of ‘family’ which includes half-siblings may better elucidate the role of nest-sharing in *B. tribocorum* status. We also hypothesized that ‘family’ would in part explain *L. interrogans* carriage as it is transmitted through contact with affected rat urine (Costa *et al.* 2015a) and may also be transmitted through social interactions such as biting (Minter *et al.* 2019). As previous work suggests that most rats in this area acquire *L. interrogans* after leaving the nest (Minter *et al.* 2019), contact with urine-contaminated water in alleyways may be a more important source of infection than contact with urine near the nest. Further, as biting often occurs through fighting and contests for dominance (Barnett 1963), it is possible that these interactions occur at a similar frequency among closely and more distantly-related rats. To ascertain the social interactions of urban rats, further rat behavioural work is necessary, with the last in-depth studies on urban rat behaviour occurring over 50 years ago (i.e., Davis and Christian 1956; Calhoun 1963).

Overall, our results suggest that block-level associations are more powerful for explaining patterns of pathogen prevalence than are closer full-sibling relationships, however a more extensive consideration of how rats interact with each other within and between colonies is needed to resolve these dynamics.

The relationship between rat genetic structure and pathogen prevalence provides an opportunity for pest control professionals seeking to mitigate rat-associated health risks. First, the clustering of close relatives within city blocks, suggests that, in the short term, the ‘city block’ may serve as an appropriate eradication unit with barriers such as roadways serving as natural borders to management (Combs *et al.* 2019). Second, the highly heterogeneous distributions of rat-associated pathogens such as *L. interrogans* and *B. tribocorum* can allow management approaches to prioritize blocks with high pathogen prevalence. Such targeting can be used to address disease prevention. However, it is important to note that even within a neighbourhood, connectivity among city blocks can vary. Indeed, we find more inferred movement events in the northern area of the study site, while previous work has demonstrated that genetic clusters of closely-related individuals can span several city blocks (Combs *et al.* 2018a). Further, underground infrastructure such as sewers may provide opportunities for movement among blocks otherwise segregated by roadways, and therefore these avenues of connectivity and pathogen spread must also be considered. The potential for the reinvasion of managed blocks (Davis 1953b; Hansen *et al.* 2020) in combination with population rebounds attributed to the survival and reproduction of rats following an eradication campaign (Barnett and Bathard 1953; Hacker *et al.* 2016), necessitates more broadly applied, long-term approaches to address neighbourhood-level infestation. To support long-term population reduction, an increasing number of studies articulate

the need to target the underlying habitat features which promote rat infestations such as access to food and areas to burrow (Singleton *et al.* 1999; Lambert *et al.* 2008; Corrigan 2011).

## **CONCLUSIONS**

Despite their infamy as long-distance travellers, we contribute to the growing evidence that urban Norway rat movement is highly localized. We demonstrate that even within city blocks, related rats are aggregated often within 33m. These clusters of closely-related individuals align with heterogenous patterns of pathogen prevalence, particularly for pathogens transmitted through close contact with rat excreta and ectoparasites such as *L. interrogans* and *B. tribocorum*. Management approaches, particularly those facing resource limitation, may benefit from targeting city blocks with high pathogen prevalence in order to address the most pertinent public health issues. In instances where the scope of management efforts is applied to at least the level of the city block, it may minimize pathogen spread among remaining rats and between blocks.

# **CHAPTER 6: “THEY’RE ALWAYS THERE”: RESIDENT EXPERIENCES OF LIVING WITH RATS IN A DISADVANTAGED URBAN NEIGHBOURHOOD**

## **6.1 SYNOPSIS**

The presence of urban rats in the neighbourhood environment may negatively impact the physical and mental health of residents. Our study sought to describe the experiences with, perceptions of, and feelings towards rats and rat control efforts among a group of disadvantaged urban residents in Vancouver, Canada. Semi-structured interviews were held with 20 members of the Vancouver Area Network of Drug Users (VANDU) recruited by VANDU staff. Interviews were audio recorded, transcribed, and analyzed using thematic analysis. Participants reported daily sightings of rats and close contact during encounters. Participants generally disliked encountering rats, raising issues of health and safety for themselves and the community due to the belief that rats carry disease. Fear of rats was common, and in some cases resulted in avoidance of rats. Effects of rats on participants were particularly pronounced for those living with rats in the home or for homeless participants who described impacts on sleep due to the sounds made by rats. Although rats were viewed as more problematic in their neighbourhood than elsewhere in Vancouver, participants believed there to be a lack of neighbourhood-level control initiatives that angered and disheartened participants. In combination with other community-level concerns (e.g., housing quality and availability), the presence of rats was viewed by some to align with a general disregard for the community and its residents. This study suggests that the presence of rats in urban centres may have several consequences for the physical and mental health of residents living in close contact with them. These effects may be exacerbated with continued contact with rats and when

residents perceive a lack of initiative to control rats in their neighbourhood. As such, research and policies aimed at mitigating the health risks posed by rats should extend beyond disease-related risk and incorporate diverse health outcomes.

## 6.2 INTRODUCTION

Neighbourhood environments are comprised of a constellation of features that influence the mental health of residents (Diez Roux and Mair 2010; Gong *et al.* 2016). For example, aspects of the built environment such as traffic level (Gee and Takeuchi 2004; Yang and Matthews 2010), green space availability (Maas *et al.* 2009; Pope *et al.* 2015; Ward Thompson *et al.* 2016), and architecture (Weich *et al.* 2002) have been linked to psychological distress (Gong *et al.* 2016).

Despite the ubiquity of rats (*Rattus* spp.) in urban settings (Himsworth *et al.* 2013b) their impacts on the mental health and well-being of urban residents has been understudied (Lam *et al.* 2018). Rats are a potentially important neighbourhood stressor in communities where aging infrastructure, high human population density, and low socioeconomic status allow for rat populations to flourish (Davis and Fales 1949; Clinton 1969; Childs *et al.* 1998; Vadell *et al.* 2010; Jassat *et al.* 2013; German and Latkin 2016) due to the availability of harbourage and food sources (Davis 1953b; Easterbrook *et al.* 2005; Feng and Himsworth 2014).

Rats may affect the health outcomes of residents through a number of pathways. First, rats can represent neighbourhood disorder and deterioration. Prior work has demonstrated that the perception of an area as disordered or decayed (e.g., graffiti, litter, broken glass, building abandonment, proximity to noxious land uses, and perceived violence and safety) may cause distress (Downey and van Willigen 2005; Mair *et al.* 2010; Wilson-Genderson and Pruchno 2013), and has been connected to feelings of anger, anxiety, depression, fear, powerlessness, and poorer

quality of life (Perkins and Taylor 1996; Ross 2000; Downey and van Willigen 2005; Yen *et al.* 2006; Gary *et al.* 2007; Ross and Mirowsky 2009). Indeed, work around rat-associated psychological health impacts supports the link between mental health outcomes and rat presence (Zahner *et al.* 1985; Bachelder *et al.* 2016). Because rats are more prevalent in under-resourced areas (Himsworth *et al.* 2013b) where mental health effects are already particularly pronounced (Weich *et al.* 2002; Galea *et al.* 2005), rat infestations may contribute to issues of “environmental injustice” because of greater health burdens among disadvantaged populations (Mohai *et al.* 2009).

Second, residents may view rats negatively due to health and safety concerns (Panti-May *et al.* 2017). Rat presence is often synonymous with disease due to rats’ carriage of numerous pathogens transmissible to people (Himsworth *et al.* 2013b). Perceived rat-associated health risks may negatively impact mental health outcomes during or following interactions with rats. For example, residents who saw rats daily were more likely to report symptoms of depression (German and Latkin 2016), while rat exposure in the home has been linked to physiological symptoms of poor mental health (e.g., headaches, dizziness, sweating, and upset stomach) (Zahner *et al.* 1985). This suggests that the negative effects of rat presence may be intensified for those who regularly interact with rats.

Third, because the roles of tenants and landlords in the eradication of pests are often unclear (Marshall and Murphy 2003; Bryks 2011; Harrison 2018), individuals who view rat control as the landlord’s responsibility may be more likely to view rats and rat infestations as environmental hazards (i.e., threats to health and quality of life due to human action) (Masuda *et al.* 2008). Because harmful environmental features are recognized determinants of mental wellbeing (National Collaborating Centre for Environmental Health and Determinants of Health 2017) rats viewed within this context may contribute to negative mental health outcomes. Compounding this

interaction, perceived inaction by landlords to address tenant complaints may result in increased stress (Bachelder *et al.* 2016). Together, these works suggest that contact with rats in the home environment may adversely affect the mental health of residents, and that these effects can be mitigated or amplified by the actions taken by those deemed responsible (e.g., landlords, governments, or communities).

To date, there has been only one study to evaluate the impact of urban rats on psychological health (German and Latkin 2016). Aligning with the potential pathways through which rats may affect resident health, this quantitative study demonstrated that rat exposure may act both as an independent stressor, and as a reminder of other community-level stressors, contributing to and exacerbating perceptions of neighbourhood disorder (German and Latkin 2016). While this work has been formative in our understanding of the relationship between rats and psychological health, it does not address the breadth or extent of issues associated with rats and their impact on residents.

The aim of this qualitative study was to elicit descriptions of living with rats and to understand how these experiences affect the health and wellbeing of residents in Vancouver's Downtown Eastside (DTES), an area where residents frequently encounter rats (McVea *et al.* 2018). Regarded as Canada's most impoverished urban neighbourhood, approximately one in every 18 people are homeless (Swanson *et al.* 2018), and many residents live in low-income housing such as Single Room Occupancy (SRO) units (Smith 2000). In addition, there is a significant population of individuals who, due to the criminalization and law enforcement of drug use, are forced to use injection and non-injection drugs in "riskier" areas (Small *et al.* 2006), potentially increasing their interactions with and exposure to rats (McVea *et al.* 2018). In taking a qualitative approach, we sought to describe experiences with and perceptions of rats and rat control efforts among DTES residents. Through closer attention to the experiences of disadvantaged urban

residents, it is possible to obtain a more comprehensive understanding of the effects of rats on health (both physical and psychological), which in turn will aid in devising appropriate initiatives to improve efforts to mitigate these impacts.

### **6.3 METHODS**

This is an exploratory descriptive study (Sandelowski 2000) using individual interviews to elicit and describe the experiences of DTES residents with rats. Because of the close contact between DTES residents and rats, this area has been the site of considerable urban research evaluating urban rat ecology (e.g., Himsworth *et al.* 2014a; Byers *et al.* 2017) and health risks posed by rat-associated-zoonoses (e.g., Himsworth *et al.* 2014b; Lee *et al.* 2018; Donovan *et al.* 2018). The impetus for this study came from discussions with DTES community members while conducting field research on rat ecology in the area from July 2016 – January 2017. The enthusiasm with which residents shared their interactions with and feelings about rats highlighted a gap in knowledge around the potential consequences of living in close contact with rats.

To conduct this study, we collaborated with the Vancouver Area Network of Drug Users (VANDU), an internationally-recognized user-run organization that serves as a trusted community institution with over 2000 members (Kerr *et al.* 2006). Although VANDU's mission is centered around improving the lives of those individuals who use drugs, members may or may not use illicit drugs (Kerr *et al.* 2006). We chose to recruit participants through VANDU because: 1) VANDU has extensive experience collaborating in community-engaged research (Jozaghi *et al.* 2018); and 2) because many of its members reside in Vancouver's DTES and may have a greater exposure to rats due to issues of housing availability and quality in the DTES (Smith 2000; Jozaghi *et al.* 2018) in comparison to a population with stable housing. Team members (KAB and CGH) have worked

with VANDU on urban rat research since 2010 and have maintained ongoing communication with the Board of Directors to disseminate findings to its members. Prior to beginning the study, we met with the president of VANDU and one board-appointed member to discuss the study and seek permission to hold interviews on the premises. A pilot interview was performed with a member of VANDU to assess and inform the accessibility and appropriateness of the language and content of interview questions.

In August 2017 we held face to face interviews with 20 individuals recruited by VANDU staff. All participants in this convenience sample were members of VANDU and recruited on VANDU premises. Information about the study was provided to recruiters and made available to participants prior to the interview. Inclusion criteria was current residency in the DTES and English proficiency. Interviews were conducted in a private office at VANDU by KAB and LR. Participants provided written informed consent prior to interviews and received a \$10 CAD honorarium. At the start of the interview, participants were assigned a pseudonym for anonymity and were asked for their age and years of residence in the DTES. A semi-structured interview guide (Supplementary File S6-1) was used to promote discussion around participants' experiences with rats. Some questions were predetermined (e.g., we asked participants to describe the frequency with which they encountered rats) while others developed during interviews to explore new ideas as they arose with each participant (e.g., in instances where participants mentioned avoiding rats, we asked participants to describe these aversion techniques). Interviews were audio recorded and lasted approximately 25 minutes. Field notes were kept by the interviewer (KAB) to reflect on interviews following their completion.

The aims of this exploratory study were to elicit and describe the experiences of DTES residents with rats, and not to build a theory to explain these experiences. Theory-building requires

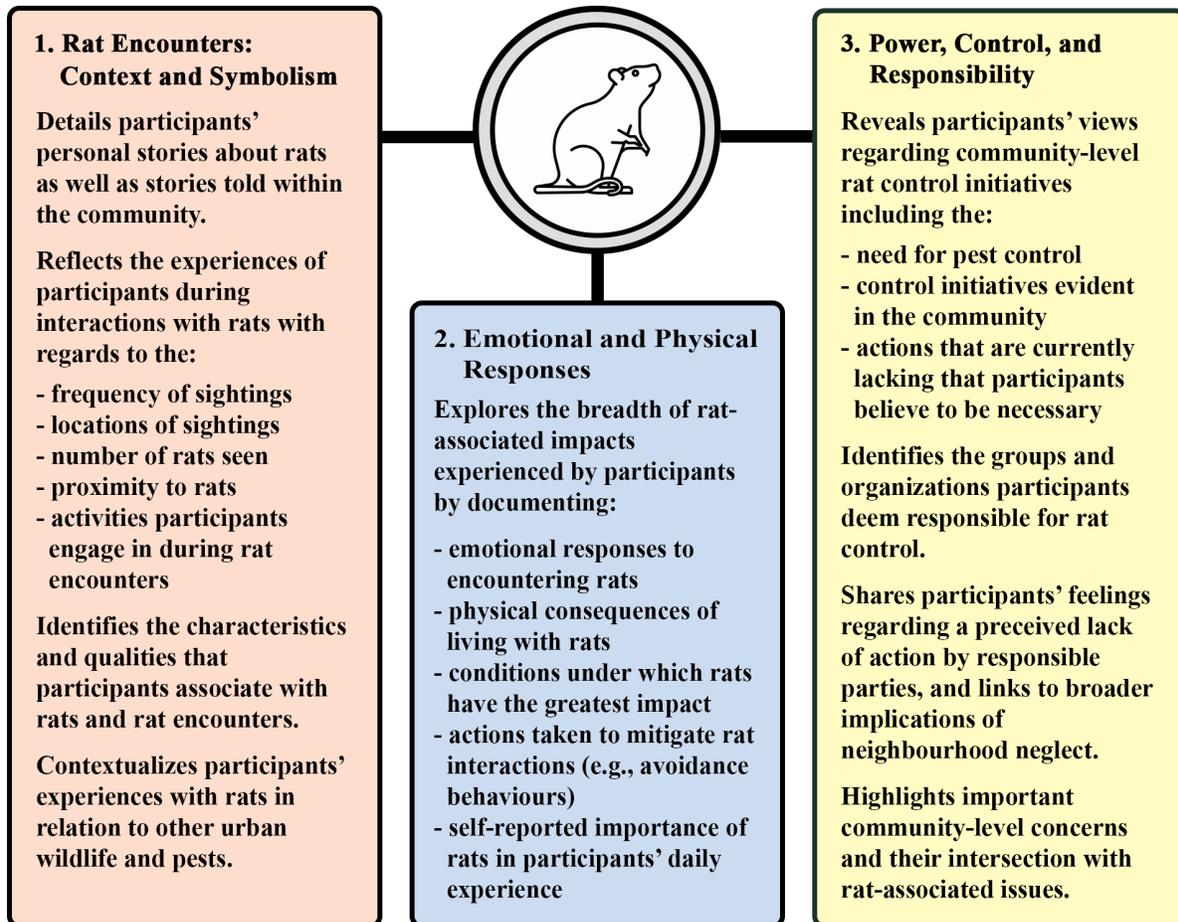
a grounding of good descriptive work in order to identify and saturate the categories relevant to the theory with data (Sandelowski 2000). Thus, we followed the descriptive qualitative content approach outlined by Sandelowski (2000). The lead researcher (KAB) transcribed interviews verbatim, and transcription accuracy was assessed by LR. All transcriptions were read by KAB to conceptualize emerging themes relevant to the overarching objective. Analysis was undertaken using a “thematic framework” (Nowell *et al.* 2017). A preliminary coding framework was developed by KAB and SMC for thematic analysis of transcripts. Some *a priori* codes were derived from the pre-determined interview questions (e.g., timing and locations of rat encounters), and others were identified *in vivo* by reading through a subset of three interviews as well as field notes (e.g., activities of participants during encounters). Codes were adopted according to their relevance to the research aims and participants’ emphasis and tendency to discuss certain topics. Interviews were coded manually, and the thematic framework was revised as the analysis proceeded. Themes were developed in two ways: *a priori* based on the interview guide (e.g., the main theme of “Rat Encounters” was predetermined as describing these experiences was a central aim of the study); and *in vivo* by identifying recurring ideas relevant to the research question (e.g., one subtheme that emerged was “People Affected by Rat Encounters” as participants often mentioned that they believed certain individuals to be particularly affected by rats). Codes were grouped into main themes and subthemes that were summarized in concept maps reflecting the content of each interview; maps were then compared to derive a composite map inclusive of all themes and subthemes. Preliminary findings were presented to VANDU’s Board of Directors for member checking of the interpretation of the findings. The Board enthusiastically supported the results, and there were no modifications to the themes and subthemes presented.

## **6.4 RESULTS**

### **SAMPLE CHARACTERISTICS**

We interviewed 20 participants (five females and fifteen males). The median age of participants was 52.5 years (range: 39 – 69) and the median length of residency in the DTES was 12.5 years (range: 2 – 53). One participant identified as homeless, and one participant had been homeless previously. Ten participants explicitly mentioned living with rats, either in their home at the time of the interview (N = 1), in their home in the past (N = 7), or while homeless (N = 2). Throughout the results, participants are identified by gender (M for male, and F for female). Participants who identified as homeless when discussing their experiences with rats are indicated with H.

The results are presented according to three themes: Rat Encounters: Context and Symbolism; Emotional and Physical Responses; and Power, Control, and Responsibility. Figure 6-1 demonstrates a visual representation of the thematic structure.



**Figure 6-1: Thematic structure detailing the experiences of residents living with rats.** The chief areas of description and analysis are summarized within each of the three themes: Rat Encounters: Context and Symbolism; Emotional and Physical Responses; and Power, Control, and Responsibility. Rat by Jake Dunham, available through the Noun Project.

**RAT ENCOUNTERS: CONTEXT AND SYMBOLISM: “EVERY DAY I GO OUT I SEE A RAT, IT’S A GUARANTEE”**

Most participants reported encountering rats daily or almost daily and described seeing anywhere from two to “hundreds” of rats regularly. Sightings were routinely in the early morning or at night, although participants were adamant that rats could be encountered at all hours. Some vigorously described the heightened sense of rat presence or abundance as troublesome.

“If you could count every goddamn rat that goes by there’re probably more fuckin’ rats around than people around the streets.” – Owen (M)

Vancouver was thought to have more rats than other Canadian cities where participants had lived (e.g., Winnipeg and Edmonton). This was attributed to an abundance of resources available to rats, specifically access to food from markets and food waste from restaurants. The warmer climate was also thought to be more hospitable to rats than other colder Canadian cities. Several participants believed that rat encounters were more frequent than approximately five to ten years prior. Participants attributed this increase to rats’ rapid reproductive rate and subsequent population growth. Only one participant believed there to be fewer rats than in the past.

“They multiply like crazy. That’s why there needs to be a handle on them. There needs to be a population control. Umm, otherwise they’ll run us over and out of town. Well, it could happen.” – Ernest (M)

Rats were considered to be “part of the DTES” due to their constant presence and prevalence. The ubiquity of rats was emphasized by almost half of participants and was particularly felt among women who stated that rats could be encountered “everywhere” in the DTES. For some, they symbolized “bad human rights”; for others, they were associated with issues of personal safety and neighbourhood disorder. Indeed, one participant indicated that the more often they saw rats, the “more dirty” they considered the city to be.

“Everything that’s in a horror movie is down here. It’s just so weird, you know?”

And rats – it’s interesting. They just fit right in.” – Noreen (F)

Sightings occurred in alleys, public parks, and buildings, with participants recounting stories of rats in their residence or in the residence of friends. Encounters also occurred at a local community garden and soup kitchen where participants had volunteered. However, interactions were most common in alleys, near to dumpsters, with one participant stating that rats could be seen near every dumpster in an alley. In part, it was this proximity to refuse that led participants to associate rats with garbage and being “dirty”, although this perception was also attributed to their appearance, and the smell associated with their presence.

“They’re dirty little creatures... Uhh well, they get in the garbage and everything eh? So, I don’t really care for critters like that.” – Hugh (M)

Encounters commonly occurred while walking in alleys, and some came into contact with rats while drinking alcohol or using drugs. While participants did not recount personal experiences of injecting drugs in the presence of rats, one participant felt that encountering rats was “probably a regular thing for injection users”.

“It just depends when I go hang around and go with my buddies, smoke up ‘n that, walk around with them, that’s the only time I guess I see the rats.” – Owen (M)

The most striking and recurring description of rat encounters was the proximity of rats to people and the lack of “personal boundaries”. Participants perceived rats to be “bold” and/or not “afraid of humans”, and this tendency to approach residents was viewed as bothersome and elicited fear in some participants. Other participants shared stories about encounters with rats that were vivid in detail and almost humorous in their characterizations of how the rats interacted with humans.

“I had one I was sitting on (street), there was a bag of bagels, and these bagels were like, multigrain, stale [pause] heavy, heavy things and it come out of this hole right beside me, like two inches from my body, I recognized that it was there immediately, the presence of it was so massive, and I glanced down... He crawled into this bag of bagels and with these freakin’ teeth that musta been huge, he chomped down onto this bagel, picked it up, backed out of this bag of bagels, turned around and went back in the wall. The whole time rubbing against my thigh, without an issue – without an issue. They’re just nuts.” – Ima (M, H)

The uneasiness ascribed to the proximity of rats was often linked to the belief that “bacteria” or “parasites” could be transmitted from rats to people through close contact. Despite a dearth of specific disease knowledge based in academic terms, participants were universally afraid of rat-associated diseases based on their perceived severity. Indeed, disease carriage and the risk of disease transmission to people was mentioned by nearly all participants. Although the majority were unsure of which diseases rats carried, five participants correctly cited plague and one suggested both *Escherichia coli* and *Salmonella* spp., that have been reported in rat feces (Himsworth *et al.* 2015b). Other diseases mentioned by participants, but that are not recognized

rat-associated zoonoses, were rabies, malaria, and scurvy (Himsworth *et al.* 2013b). Although some participants indicated that they could not recall the disease name, they believed that the illness would present with flu-like symptoms. One participant directly linked the presence of rats to their own poor physical health.

“And they affect your breathing ‘cuz they’re shitting everywhere ‘n it gives ya flu-like symptoms right?” – Fred (M)

Rat bites were consistently cited as a route of disease transmission, either by infection with rat-associated pathogens or due to the introduction of bacteria from the environment into the wound. Participants also believed that they could contract a rat-associated illness through a scratch, contact with the rat’s fur, “droppings,” or by consuming food contaminated with rat feces. Participants were particularly concerned about food contamination in their homes, and one participant who volunteered at a soup kitchen highlighted their concern for contamination of food served to DTES residents.

“It’s just a fact of like they carry diseases and, you just never know like, one bite ‘n god knows what can happen to you... it’s just health issues... cuz they get into everything, they chew up everything and even their droppings, like you just never know like and if you miss one or something.” – Aubrey (F)

Fear of being bitten was not just associated with disease risks, but also with pain due to the strength of a rat’s bite. Some participants recounted being bitten by rats, or stories of other residents being

bitten. Rat bites were often related to the tendency for rats to be aggressive, although one participant believed that these aggressive behaviours were “like any animal... even us”. In line with associations of aggression, two participants mentioned that when they thought of rats, they were reminded of the horror movies *Willard* and *Ben* from the early 1970s that involve rats attacking and killing people.

“A rat’s mouth – those teeth? They’re chewin’ through brick. So, you can imagine when they chomp on you? Wake up nothin’, you’ll be screamin’ in pain.” – Fred (M)

While rats were considered a public health concern, they were largely thought to be about as important as other pests (e.g., cockroaches and bedbugs). In fact, bedbugs were seen by some to be more concerning as they occupy the home and bite people. For example, one participant identified bedbugs as a concern when looking for housing, while none of the interviewed participants identified the presence of rats as a condition when renting an apartment. Rats may have been seen as comparable to other pests because most participants could not recount an instance where someone they knew became seriously ill from coming into contact with a rat. For example, several participants indicated that rats would gain more community-level significance if there was an outbreak of a rat-associated disease.

“I think [rats are] pretty important right now, but not more important than some of the other stuff. I think it’s important in terms of public health.” – Bruce (M)

Interestingly, several participants mentioned that rats were vilified or judged in a way that reflected how participants themselves felt judged by the Vancouver community.

“I feel like we’re being looked at like we’re overpopulated like the rats.” “It makes me feel sad. Because, the way people look down on us, they discriminate us, they judge us. It’s like, me talkin’ about rats right now, I feel like I’m [pause] judging them.” – Renee (F)

Because many DTES residents have rats as pets (either domesticated or wild caught) participants also associated rats with pets. Although pet rats were described as generally different from alley rats in appearance, only one participant expressed that it was “nice to see” pet rats. While one participant found pet rats to be “just another domesticated animal”, the majority of participants described uneasiness around them due to the potential that they “carry disease” and/or because of the supposed tendency of rats to defecate or urinate on their owners. In this way, it did not seem to matter to participants “what kind of rat it is”, with pet rats and wild rats embodying similar threats.

“Rats as, for a pet? I’m sorry. To me that is stupid. I [pause] to have a rat?... The people have them in their shirts ‘n their jackets. The rats pee and poo on ‘em. Who wants to have a pet that pees on ‘em? Poos on ‘em? I don’t. But these people here do. I don’t get it. I don’t get it and I don’t want to get it.” – Ernest (M)

Rats were viewed as “almost the same” as other urban exploiter species (e.g., pigeons), pests (e.g., mice and cockroaches) and people. For some, the filth associated with rats and other urban animals was considered to be a result of living in the DTES and not necessarily an independent characteristic of the animal. Although parallels were drawn between mice and rats in their ability to infest buildings and carry disease, the mice’s appearance and behaviours were considered “cute” and “playful”. Participants who highlighted the commonality of rats with other animals also tended to view rats as natural parts of the environment or as serving a purpose.

“Well rats are pretty dirty, eh? Uh, but I guess everything that lives down here is, ya’know? Even the birds ‘n, and the skunks and everything that’s runnin’ around... Doesn’t really bother me... I’m sure there’s lots of ‘em that – that live here, ya’know? Even after we’re gone, they’ll still be here... there’s not too much we can do about it, ya’know? You can’t really kill ‘em all, I’m sure they serve a purpose, ya’know.” – Phil (M)

In contrast, because rats are “not native” to North America, some felt that they either “don’t belong” in the DTES, or that they were responsible for the eradication of other native species.

“Instead of chipmunks, there’s rats. Or, instead of squirrels, there’s rats.” – Noreen  
(F)

Participants who held this viewpoint believed that rats should be “absolutely eliminated”.

Finally, participants emphasized commonalities between the behaviours of rats and people. For example, participants told stories of rats stealing residents' belongings (e.g., drugs), or acquiring addictions to drugs. These stories were recounted with humour and appeared to be commonly shared in the community.

“Actually, there was a picture of one... sucking on the end of the syringe... we made jokes about it all the time. Heroin rats ‘n stuff.” – Claudia (F)

“Have you heard other stories about heroin rats?” – Interviewer

“Yea. Like... they’ll come out and take peoples stuff [heroin]...” – Claudia

“Why do you think they take it?” – Interviewer

“Because they’ve already tried before, right? So [pause] they know what it is and they’re taking it just like people would do, right?” – Claudia

**EMOTIONAL AND PHYSICAL RESPONSES: “MAYBE PEOPLE WITH HOMES, THEY DON’T HAVE THIS KIND OF PROBLEM”**

Rats were considered more important for those living with them, either in their residence or when they were homeless, than for participants without rats in their home. This may be because for those without rats in their home, the distance from rats physically put them “out of sight out of mind”, whereas participants living with rats were continuously reminded of their presence. For example, one participant joked that when living with rats it was as though they were “in [the rat’s] space now, more than he’s in mine”. The invasive and pervasive nature of rats led one homeless participant to indicate that rats were the second most important factor in their life after possession theft.

“It’s exhausting. You – you never, you can never – they’re just – they’re so fuckin’ persistent they won’t leave you alone. You live on the Eastside and you live outside, bein’ homeless. I dunno, maybe people with homes, they don’t have this kind of problem. But I’m outside all the time and they’re always there. They’re always there.” – Ima (M, H)

On a physical level, participants living with rats described damage to their belongings, an inability to store food, and effects on their sleep. Participants revealed that the impact of rats at night “turns into somethin’ different”. Specifically, some participants altered where and when they slept to correspond with times that were relatively “rat free”. These changes ultimately affected the amount and quality of sleep they achieved.

“I remember gettin’ woken up and they were like, I don’t know what they were doing, they were nibbling on my hand or, ‘cuz I was sleepin’ and somethin’ woke me up, ya’know? Whether it ran by my hand or I don’t know, but, yea, they used to really bother me in there.” – Phil (M)

Impacts on sleep were attributed to the “skittering” sounds made by rats which were considered unsettling. Participants particularly affected by these sounds emphasized their volume, with one participant comparing the noises to “a six-foot male... moving furniture”. The rich description of the sounds made by rats indicated a keen awareness of their presence.

“The visual – somehow that’s expected, I don’t know. But the noises, you don’t know what it’s going to sound like, or, or the power that’s there in their little feet or something.” – Charlie (M)

Sounds made by rats were also disturbing during the day. One participant vividly recounted overhearing a mischief of rats:

“I was over by (building name) and I could hear them. Like, in the [pause] like, tons of them running across umm, the garage doors on top of the garage? Oh my god, it freaked me out, like it just freaked me out, it just ugh [pause] scared me. I thought they were gonna come falling out of the ceiling or something [pause] it was horrible.” – Claudia (F)

The participant later indicated that following this encounter she couldn’t sleep at night.

On a psychological level, the majority of participants were bothered by the presence of rats. Participants described encounters with rats as alarming, unsettling, angering, exhausting, worrisome or eliciting fear. These feelings were particularly pronounced for participants where rat encounters were “reoccurring”, and the continued alarm from confronting rats raised concerns of being bitten. In some instances, this constant exposure to rats resulted in increased sensitization to their presence such that any contact with rats elicited an immediate negative response. Indeed, the perceived consequences of living with rats went beyond direct interactions (i.e., rat bites) as

described by one participant who articulated a potential cascade of negative effects from a rat infestation.

“Just how to get, how to get rid of them. What I could do to get them out of the house. Yea um [pause] and worry about is, are the walls going to start to smell, is it, you know, is this place gonna be all disgusting? If my cat gets a hold of one and eats one, will I have a sick cat on my hand? Will I get sick from touching my cat if she eats a rat? Those kind of thoughts.” – Charlie (M)

Fear was the principal feeling associated with rats and was evidenced in the characteristics attributed to them (e.g., disease and biting) and in the stories told by participants.

“I think about horror movie type things like... you’ve injured yourself and can’t move, and then rats will start eating you... I’ve heard of things like that happening down here.” – Noreen (F)

Fear was particularly acute among women. All female participants described fear of rats, and men indicated that their female friends or partners were also afraid. One male participant specifically mentioned their female friends becoming “unsure, nervous, and uncomfortable” in alleys where they had encountered rats before. One female participant who was particularly afraid of rats emphasized her inability to be alone and required that her partner carry her to the tent where they were living for fear of being touched.

“Every night I had – my boyfriend would have to carry me up the hill, because of the rats, right? I – ‘cuz I didn’t want them to touch me or anything right? I was living in a tent... I was... never alone, right? I wouldn’t sit by the door. Yea, I don’t know. I don’t know why I’m so scared of them.” – Joanne (F, H)

Anger was the second most cited emotional response to the presence of rats due to the observed impact of rats on other community members and because of the perceived inaction of responsible bodies to control rats.

“It makes me mad only that I know the reason that the rat’s usually around is that somebody’s not doing the right thing” – Mike (M)

In response to these negative feelings, purposefully avoiding rats was common among participants, but considered difficult due to their ubiquity. For some, it seemed that the only way to avoid rats was to “get out of [the] neighbourhood”. When outdoors, participants described “keep[ing their] distance” from rats by avoiding heavily infested areas or choosing to sit in areas in alleys where they were less likely to be approached by rats. Some participants described more purposeful avoidance of rats. For example, one participant mentioned that rats prevented them from participating in social activities that they enjoyed, including volunteering at a community garden and walking in alleys in the evening.

“Even when we were umm, doin’ the garden, there was rats. And I used to love working in the garden like, volunteering, but now I won’t go because of the rats.”

– Renee (F)

Another participant vividly described the precautions they took to prevent contact with rats while sleeping. These precautions included hanging food, a “proximity alarm” to alert them of the presence of rats, and efforts to “cocoon” themselves inside of their blankets while sleeping, with only “a little vent hole for their mouths.”

“I had a bag of chips beside me, but I put it there intentionally because when they touch that... it makes a noise and it wakes me up and it’s like a proximity alarm right? I know they’re gettin’ close so I can, I get up and I’ll scare ‘em away... And I heard that noise. And I glanced over... And this huge cat-like creature jumped up because I scared the shit out of it, and it jumped straight up and landed on my face, then he jumped up again and he landed right back on my face then he ran down my chest, underneath the blankets, all along my thigh, and out the – out the foot of the blankets.” – Ima (M, H)

Whether bothered or not by the presence of rats, most participants believed that they had become “just the norm”.

“Well, you see them all the time, right? So basically they’re a main part of your life, right? Like, they’re everywhere. So you see them at least every hour, if not less than that, unless you leave this area. Which I don’t do a lot of... Yea they’re in my life all day long so [pause] and it’s not like you get used to it, ‘cuz you can’t get used to that, you kinda do but you don’t right? Like, it’s – nothing surprises you right?”

– Claudia (F)

Some viewed this acclimatization to rats as necessary to cope with them because thinking of rats would heighten their anxiety, while others believed this approach to dealing with rats to be unnatural.

“People are so used to it already ‘cuz it’s gone so long, they don’t even – you don’t even hear anybody yell anymore. Before you used to hear a squeal, fuck! Seven years ago you used to hear girls every once in a while in the alley “Eeee!” You don’t even hear that anymore ‘cuz they’re so used to ‘em running around which is – that’s pathetic!” – Fred (M)

**POWER, CONTROL, AND RESPONSIBILITY: “IT’S NOT THE RATS THAT’RE WRONG, IT’S THE LANDLORD THAT’S WRONG”**

Rat control was mostly thought to be the responsibility of the city, building managers, and residents, although one participant mentioned the importance of involving port officials due to the potential for rats to enter the DTES via ships.

“The city. Umm [pause] homeowners too if they have them in their back lane and they put their garbage out and they know they have rats. Anybody that’s got a rat problem should be responsible. Not just the city.” – Ernest (M)

The desire for city-initiated trapping and poisoning programs to eradicate rats was mentioned by most participants, although three participants preferred less “cruel” methods of control. Other necessary control actions were thought to be the establishment and training of a specialized “crew” of people to deal with rat infestations. Although one participant indicated that VANDU serves as a source of information on rats for community members (through their collaboration with the Vancouver Rat Project), participants underscored the importance of educating residents about rats, the diseases they carry, and how to control them.

“Like a pamphlet. I don’t see any kind of thing that say uhh ‘we have that problem down here and people need to be aware of it and this is how you deal with it.’” – Ian (M)

Improved cleanliness and the need for residents to tidy their own environments was stressed to reduce resource availability to rats. However, many did not believe that this approach would be adopted by everyone, particularly by those whose activities involved sorting through refuse for bottles or valuables. Additional methods of control mentioned were birth control and the introduction of predators.

Well I mean if people would clean up, like, clean up after themselves... I don't think you would see that many eh? Yea. Like in the last few years, I started seeing a bit more of them because people leave their garbage behind, right? – Hugh (M)

Few participants recognized visible control initiatives in the DTES, citing poison bait boxes and metal cage traps in the alleys. It is worth mentioning that these metal traps were not part of a control effort, but instead part of the Vancouver Rat Project's research. Indeed, four participants mentioned that they thought these traps were part of a study. Participants noted some ongoing efforts to clean the alleys and remove garbage that were thought to minimize the presence of rats. Regardless, participants felt that control efforts were insufficient.

“For one thing, they could clean up the alleys ‘n stuff more, but I know they try. See I’m making it sound like they’re not, and I know better. They try – I see it ‘n you hear the trucks all the time, but they just – they don’t have the manpower to keep up.” – Fred (M)

The majority of participants felt that there was little or no evidence of control efforts being enacted in the city. This perceived inaction was attributed to both the seemingly large population of rats and the absence of any observed control methods. Because of this, some participants revealed that they were unaware of who they could report rat infestations to.

“Who would you go to? Why wouldn’t you just deal with it yourself? [pause] I dunno, there’s not really anywhere to go is there? I dunno. I don’t think so... I assumed it was our own problem to deal with because nobody dealt with it before.”

– Claudia (F)

Moreover, some participants emphasized that even if reports of rats were made to building managers, that these reports were unlikely to receive any immediate action, underscoring the perceived futility of reporting rat infestations to building managers or landlords. This contributed to feelings that dealing with rats was the tenants’ own responsibility.

“I don’t know how quick they would act on it... like in these SROs? They don’t do nothin’. ‘Cuz I’ve lived in ‘em, I lived in (location) there in – they used to run from room to room at night, ya’know? Yea, big holes, ya’know? Just goin’ room to room.” – Phil (M)

In three instances, impacts from rat infestations culminated in participants moving out of their residence. However, many implied that avoiding rats by moving was impossible due to limited availability of housing.

“Well downtown here you don’t really ask you just gotta settle with what you can get as long as you got a bed, a roof over your head it’s [pause] you just gotta take it.” – Aubrey (F)

This connection between the availability of housing and the presence of rats revealed feelings of powerlessness, hopelessness, and anger among participants who felt “stuck” in the DTES.

“Your hands are tied ‘cuz where’re you gonna live for one thing? [pause] You’re stuck here anyways in this shit, right?” – Fred (M)

Overwhelmingly, participants indicated a lack of affordable housing as the chief issue facing the community. Indeed, a number of participants emphasized their disgust with city officials for what they perceived to be “zero” action around addressing homelessness in the DTES. Further, the housing available to residents was viewed as being of poor quality. In contrast to the importance of housing, prioritizing rat control was viewed as “silly”.

“There’s so much else to deal with, like c’mon. Let’s deal with homelessness before we deal with the rat situation, seriously. Honestly, like putting money into something like that is just silly over homelessness, right?” – Claudia (F)

The intersection between a lack of action in controlling rats, and the paucity of housing were attributed to a general disregard for the DTES and its residents by the city. Participants articulated feelings that their community was being neglected, and that DTES residents “don’t count” due to homelessness or drug use. Indeed, a few participants perceived this inaction to be purposeful, and that the government was “targeting” them in order to make the land available for wealthier residents. By comparison, participants believed that similar infestations elsewhere in Vancouver

would receive immediate action. When discussing this issue, many participants cited feelings of anger, while others listed hurt, sadness, depression, confusion and marginalization.

“I don’t think they think it’s that important... Well because it’s DTES right? So they really don’t care about the people down here. Because if they did they would have more housing for people, right?” – Hugh (M)

Although participants identified a need for control and were clear about who they believed to be responsible, many thought that the problem “couldn’t be fixed” due to rats’ prevalence, abundance, rapid reproductive rate, and their continuous potential to arrive to Vancouver on ships via the international shipping port. Moreover, the urgency to control rats was overshadowed by other important issues facing the DTES community such as the “fentanyl crisis,” and police harassment. When speaking of the fentanyl crisis, participants were concerned about the “safety surrounding people’s lives” and emphasized that “a lot of friends [were] gone” due to overdose deaths. One participant implied that these losses were changing the close-knit dynamics of the community. In terms of police harassment, one participant viewed police inquiry as excessive, such that residents would get “jacked up, pulled over, for standing around”, emphasizing that they felt the need to keep moving to avoid police attention. For these participants, these issues were ongoing and disruptive, whereas rats were viewed as more of a nuisance than a serious concern.

## **6.5 DISCUSSION**

Our research describes the experiences of disadvantaged residents living with rats and reveals that the impacts of rats extend beyond disease-related risks. We demonstrate that chronic rat exposure

may influence both the mental and physical health of residents. Notably, rats cause distress and uneasiness among those living with them, and negatively impact the sleep of residents, causing them to take precautionary measures to decrease their interactions with rats. Further, due to the symbolism surrounding rats, they contribute to views of a neighbourhood as disordered, promoting feelings of social neglect and disregard. The effects of rats arise not only due to their presence, but also from a perceived lack of action to control rats by the groups deemed responsible.

This study reveals that the public health threats posed by rats extend beyond those associated with the transmission of infectious diseases. Specifically, rats and rat-related issues may contribute to negative impacts on the mental health of residents. We document that exposure to rats was associated with feelings of anxiety, fear, and worry. In line with a quantitative study performed by German and Latkin (2016), we found that negative perceptions of rats were not restricted to those who see rats regularly. However, psychological impacts were amplified for those with daily rat exposure, especially among those who live in close contact with rats. For participants living with rats, we found that the effects were greatest at night, when rats, and the noises associated with them, disrupted participants' sleep. The relationship between sleep disturbance and poor mental health has been discussed previously (Ford and Kamerow 1989; Stansfeld *et al.* 1993; Tsuno *et al.* 2005) and studies suggest that stressors have a greater impact on individuals who have poorer sleep quality (Kishikawa *et al.* 2009; Sygna *et al.* 2014). Thus, the effects of rats on sleep quality could exacerbate their impacts on the psychological distress of individuals already vulnerable to rats, as well as sensitize them to other environmental hazards in their community.

Rats may serve as a chronic and uncontrollable stressor for residents with frequent exposure to them. In contrast to "acute" stressors, that occur over discrete time periods (e.g., an

argument with a family member), “chronic” stressors are frequent and ongoing (e.g., long-term problems with children) (Avison and Turner 1988; Thoits 1995; Avison *et al.* 2010). Participants in this study described everyday interactions with rats, whether while outdoors, visiting friends, or at home. Therefore, specific interactions with rats may serve as acute stressors, while continuous exposure to rats may represent a chronic stressor. This is concerning because chronic stressors may negatively affect mental health outcomes (e.g., psychological distress and depression) as much, if not more so, than acute stressors because they represent unresolved problems (Avison and Turner 1988; Miller and Townsend 2005). Such unavoidable issues can promote feelings of hopelessness (Landis *et al.* 2007), evidenced in the ways in which participants described their inability to avoid rats without leaving their neighbourhood. Indeed, rat presence was so ubiquitous that some participants recalled seeing hundreds of rats in a single day. The pervasiveness of rats in the environment underscores issues of environmental injustice, whereby residents of under-resourced settings are disproportionately affected by stressors such as rats in comparison to more affluent communities.

To mitigate the negative effects of rats, participants employed a number of coping mechanisms. Although several participants expressed a passive acceptance of rats as part of the environment, there was no clear evidence of desensitization (i.e., that repeated rat exposure decreased their negative psychological impact). Instead, participants described a heightened awareness of rats, wherein they actively employed avoidance techniques, such as sitting in places where they were less likely to be approached by rats, spending time in alleys known to have relatively fewer rats, or employing measures to prevent contact with rats while sleeping. In some instances, avoidance was more pronounced. For example, the presence of rats prevented participants from enjoying community activities (e.g., volunteering at a local garden). While

avoidance allows individuals to reduce their stress by removing the stressor from their daily experience (Pearlin and Schooler 1978), barriers to residents' abilities to engage in social activities can potentially strengthen the effect of rats on health. This is because engaging in community-level activities can provide opportunities for social support, that in turn buffers the negative effects of stressors on mental (Thoits 1995; Unger *et al.* 1998) and physical health outcomes (Uchino 2006).

Beyond the direct links between rats and the health of residents, rats may represent larger community-level issues. This may be due, in part, to the stigma around rats themselves. Almost universally, participants in this study described rats as filthy and diseased, likening them to characters from horror movies. Previous work has demonstrated that the symbolism embodied by certain neighbourhood elements can signify other, more complex community-level issues. For example, Derges *et al.* found that the disgust associated with the presence of dog feces hints at a greater dissatisfaction with a spectrum of issues including litter, drug use, crime, and feelings of marginalization (Derges *et al.* 2012). Indeed, some residents in our study likened their dislike of rats as being similar to their feelings of being stigmatized and marginalized by the greater Vancouver community. In this way, the symbolic presence of rats may contribute to and/or reflect feelings of social neglect. Similarly, rats may also denote issues of social injustice and contribute to the perception of a neighbourhood as inferior or decayed. In line with participants' descriptions of rats as dirty, they also described their neighbourhood as filthy and neglected. In fact, many residents implied that rats were more abundant in the DTES than elsewhere in the city because of poor neighbourhood sanitation. These negative perceptions of the neighbourhood environment can also contribute to poor mental health outcomes (Bond *et al.* 2012). For example, poor mental wellbeing, such as feelings of depression and hopelessness, has been linked to indices of

community disorder (e.g., litter, broken glass, building abandonment etc.) (Sheppard *et al.* 2012). As such, rats may have both a direct and indirect impact on the mental health of residents by intensifying other community-level stressors.

Mental health impacts may be compounded by the perceived inaction of responsible bodies to control them. We found that participants largely felt that rat control was the responsibility of landlords and the city, but that ultimately it fell to residents to perform their own control because they felt that neither the municipal government nor the landlords in the DTES prioritized rat infestations; this sentiment was consistent with a housing study performed in the same neighbourhood (Lazarus *et al.* 2011). Further, participants voiced concerns that they were unable to control rats themselves, which may be due in part to the limited resources available to disadvantaged residents (Mirowsky and Ross 1986). This view of rats as the landlord's responsibility, in combination with feeling incapable of addressing rat-associated issues personally, suggests that rats could affect mental health as an environmental hazard (Masuda *et al.* 2008). Indeed, perceived inaction by those seen as responsible was met with feelings of anger, frustration, helplessness, marginalization, and sadness. These findings support previous research that found that municipal government inaction to deal with rat infestations led to feelings of helplessness among low-income residents (German and Latkin 2016), while landlord inaction increased stress by creating landlord-tenant conflicts (Bachelder *et al.* 2016). Overall, our study revealed a strongly held belief that there was a lack of visible interest by those in positions of power to control rats due to a general disregard for the DTES and its residents. This perception appeared to contribute to adverse mental health outcomes for participants.

Rats are part of a spectrum of issues facing disadvantaged communities. Specifically, participants viewed housing availability/affordability and drug overdoses as the most significant

community concerns. In contrast to the urgent nature of the housing (Krieger and Higgins 2002) and drug overdose crises (Chu *et al.* 2018), rat infestations do not represent an immediate threat to residents. However, it is important to recognize that rats cannot easily be disentangled from the broader environmental health issues afflicting the community. For example, in a study interviewing female sex workers about the challenges of finding affordable housing in the DTES, individuals included rats as a contributor to deplorable and uninhabitable living conditions (Mirowsky and Ross 1986). Downplaying the importance of rat issues in light of other societal issues is problematic because it can lead to an ineffectual response to infestations and the consequences associated with them (Colvin and Jackson 1999).

#### **STRENGTHS AND LIMITATIONS**

This study has several limitations to be considered. First, our sampling of participants was restricted to members of a community-based organization, preventing us from making generalizations about the experiences of all residents in the DTES, or to residents of other low-income areas. Second, due to the sampling of our study, we are unable to offer rigorous comparisons about differences in experience arising in the data according to participant characteristics such as gender and housing status. For example, of the participants interviewed, five of 20 were women, while only two of 20 identified as living with rats while homeless. Given that women in our study emphasized feelings of fear and discomfort around rats, and that male participants also identified feelings of fear among their female partners and/or friends, further focus on how individuals experience rats in relation to gender is an important area for future research. Similarly, that participants identifying as homeless considered rats to be more important

to them than did those with homes suggests that future research in this area would benefit from explicit and purposive sampling of homeless persons.

Despite these limitations, this exploratory study is the first to our knowledge to qualitatively describe the experiences of residents with rats and strengthens the growing body of literature suggesting that interactions with rats can negatively impact the mental health of residents (Lam *et al.* 2018). Given this association, we suggest that future work build upon these findings to gather data which addresses the underlying pathways through which rats impact the health outcomes of residents, as well as how these interactions relate to other environmental hazards experienced in urban settings.

## **CONCLUSIONS**

This study supports the need to re-evaluate the ways in which we conceptualize the consequences of living with rats to incorporate diverse health outcomes. While the chronic nature of rat infestations in some low-income city settings may diminish the importance placed on their control, their potential role as an independent stressor and their contribution to other neighbourhood-level issues necessitates proactive approaches to rats. As such, integrated approaches engaging governments, landlords, and communities is necessary to monitor and mitigate the impacts of rats in the urban environment and promote effective control initiatives.

## CHAPTER 7: CONCLUSION

### 7.1 OVERVIEW

At the outset of my work, it was clear that despite amassing a great deal of disease data on rats in cities all around the world (Himsworth *et al.* 2013b), research has largely considered rats, people, and the environments in which they live as independent entities. This trend is not just true of rat-associated zoonoses, as evidenced by initiatives such as the Global Virome Project which conducts large-scale sampling of animals to test for novel viruses (Carroll *et al.* 2018). Such approaches are focused on identifying pathogens in the animals themselves, with secondary attention to the factors which might promote the spread of those pathogens from animals to people. And while identifying pathogen presence is a critical component of understanding human health systems – indeed accumulating a genetic database of viruses from wildlife has been instrumental in identifying a zoonotic origin of the SARS-CoV-2 virus (Zhou *et al.* 2020; Zhang *et al.* 2020) – these entities (i.e., animal, human, and environment) are not the sole drivers of health risks. Instead, my work points to the importance of understanding the interfaces where these entities interact. In this thesis, I take an interdisciplinary approach to explore how interactions between people, urban rats, and the environment could contribute to negative human health outcomes. My work illustrates that forward-thinking approaches to rats and our management of wildlife-associated health risks generally, must move away from focusing on entities alone and shift toward the interfaces.

### 7.2 WORKS REVISITED

The synthesis of published literature presented in **Chapter 2** reveals a number of important insights into how rats interact with and navigate the urban environment. First, given the difficulty

in tracking rats, this review demonstrates the utility of drawing on multiple methodologies to describe rat movement, including employing field studies and genetic analyses. Second, although there have been relatively few studies on urban rat movement – with much of it originating from only a few programs of research in the United States (i.e., Davis 1953a; Davis and Christian 1956; Calhoun 1963) – the collation of these studies indicates that rat movement is largely restricted to fine spatial scales. Barriers to movement including landscape features such as roads and waterways are likely contributors to these patterns (Combs *et al.* 2018a). Third, this review underscores the close relationship between rat movement ecology and resource availability. Specifically, that decreased access to resources, such as food, harbourage, and mates, can drive longer distance dispersal than is typical of these urban adapters (Creel 1915; Davis *et al.* 1948). This relationship between resources and movement is important because it demonstrates how disturbance to normal environmental features can have a ripple effect that extends to both rats and the pathogens they carry.

To build on previous studies, I investigated rat movement in Vancouver’s DTES, where prior research has documented a marked clustering of rat-associated pathogens at the level of the city block (Himsworth *et al.* 2013a; 2015a). However, based on the findings derived from Chapter 2, I determined that my approach would both need to incorporate multiple methodologies, as well as first consider whether trapping bias might confound movement estimates. In **Chapter 3** I address the issue of trappability and find that characteristics such as size influence the likelihood that rats will re-enter traps. As capture-mark-recapture (CMR) studies rely on the capture, tagging, and recapture of individuals, this suggests that movement estimates derived from CMR methods in this population would be biased toward collecting more data for younger individuals. If movement patterns of rats differ by age, then this sampling may over- or underestimate the true

distances travelled by rats. However, this work also establishes that trappability is greatest early-on in the trapping campaign, with the number of rats caught decreasing over time; this trend was particularly evident for larger, sexually mature rats. This increased trapping of larger individuals early in a campaign is particularly noteworthy for studies assessing zoonotic risks as pathogens such as *Leptospira interrogans* are more prevalent among larger, sexually mature rats (Himsworth *et al.* 2013a; Minter *et al.* 2017). Therefore, short trapping protocols aimed at assessing prevalence of pathogens such as *L. interrogans* may overestimate prevalence in the population.

Given that estimates from CMR studies are prone to biases toward capturing younger individuals, I attempted to use two approaches to study rat movement. In **Chapter 4** I tested the utility of using Global Positioning System (GPS) tags to track urban rats. These technologies have been difficult to deploy on small mammals until relatively recently due to issues of balancing tag size and battery life (LaPoint *et al.* 2015). Despite tag miniaturization and technological advances which allow for remote-download of data in the field, I demonstrate that the use of such technologies remains challenging for urban rats due to issues of tag removal and tag obstruction. With future advances in GPS technologies, these tools may become more promising for use in urban rats but until that time the costs appear to outweigh the benefits.

While CMR and GPS-based approaches face considerable logistical and technical limitations, the literature review undertaken in Chapter 2 identified genomics-based approaches as another promising alternative to infer rat movement. In **Chapter 5**, I use tissue samples collected as part of the first phase of the Vancouver Rat Project to identify related rats and the distances between relatives. I find that highly related rats (i.e., parent-offspring and full-sibling pairs) are trapped in close proximity to each other with the vast majority (99% of pairs) caught within the same block. This genetic data supports the growing body of evidence that urban Norway rats

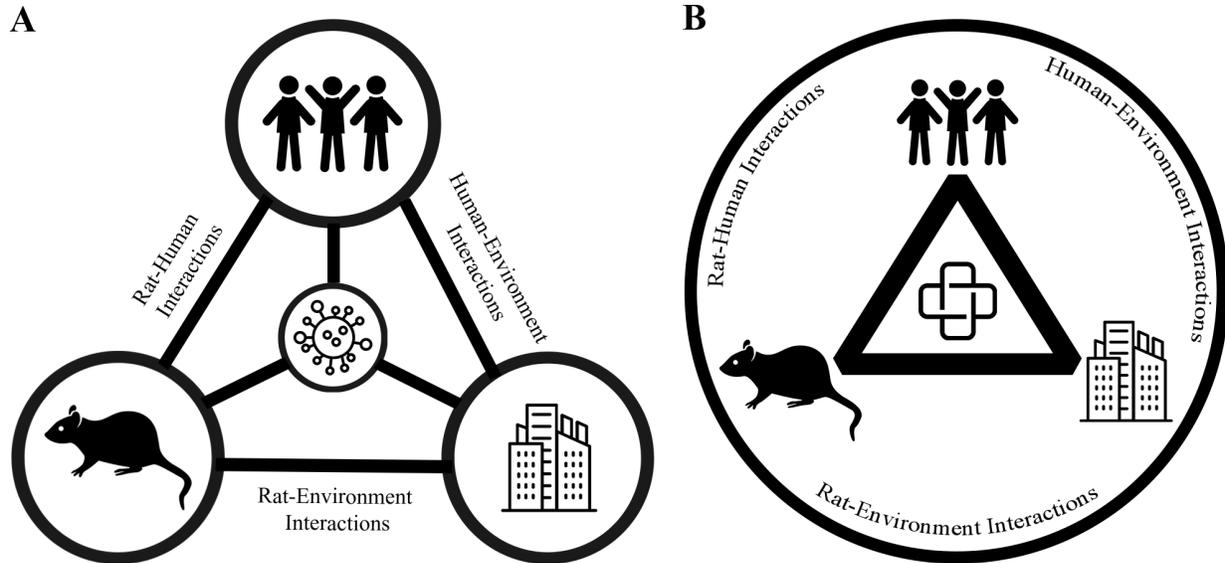
remain close to home, with few cases of inter-block movement (Byers *et al.* 2019b). I then compare these spatial data to the distributions of rat-associated pathogens described in the first phase of the Vancouver Rat Project, and find that minimal movement events align with the clustering of the rat-associated pathogens *L. interrogans* and *Bartonella tribocorum*. However, incorporating family relationships into previous models evaluating pathogen status in rats did not improve model estimates, suggesting that the importance of family-relationships in shared pathogen status may be masked by clustering at the level of the block.

Finally, in **Chapter 6** I extend beyond rat ecology to better understand how rats and people in the DTES interact. Through interviews with DTES residents I learn that interactions with rats occur daily, most often in alleys but also occasionally in the home. Residents described these interactions as disturbing, recounting feelings of fear and anxiety in relation to rats due to the perception of rats as carrying disease. The impacts of living with rats were most severe for those persons with frequent encounters with them, primarily due to homelessness which reveals how rats can disproportionately affect those who are already living in disadvantaged areas. This work also revealed that residents felt unequipped to address rats themselves, due to a lack of resources made available to them. Importantly, a perceived inaction by the city and landlords to address rats served as an indicator of community neglect, adding to feelings of hopelessness among community members. Yet, although residents were adamant that they felt that rats should be controlled, in comparison to other pressing issues such as housing, rats were perceived as a less urgent matter. Therefore, I reason that rats themselves can serve as an independent stressor, as well as contribute to other community-level stressors that impact the mental health of residents, urging a reconsideration of rat-associated health risks to include mental health outcomes.

## **7.3 AN INTERFACE-MANAGEMENT W5: THE ONE HEALTH FRAMEWORK**

### **REVISITED AND REVISED**

At the outset of this thesis, I introduced the One Health framework as a lens through which to assess and address zoonotic disease risks (Figure 7-1A). In philosophy, One Health seeks to mitigate health threats by understanding the systems in which people, animals, and the environment intersect (Daszak *et al.* 2000; Cunningham *et al.* 2017), and yet the interactions among entities at the core of these systems are often under-appreciated. Using rats as a model for wildlife-health related issues, I propose that we revisit and revise this framework to both place more focus on the interfaces wherein entities interact, as well as broaden our consideration of health risks to include non-physical outcomes such as mental health (Figure 7-1B). By considering how wildlife, people, and the environment intersect, we reveal opportunities for management of One Health issues which I am terming an “Interface Management W5” approach. Below, I discuss some ways in which tenets of the One Health framework could be applied to urban rat-associated health issues using this approach.



**Figure 7-1: Revisiting and revising a One-Health framework for assessing rat-associated health risks.** In the previously proposed framework A) humans, rats, pathogens, and the environment are presented as interconnected but separate entities. By contrast, the revised framework B) places a greater emphasis on understanding the interfaces where these entities interact to influence both physical and mental health outcomes.

#### WHEN TO ENACT MANAGEMENT?

**Striking before the iron is hot.** Current approaches to wildlife management are often reactive, addressing issues only after they arise. For rats, this reactive approach is particularly apparent (Colvin and Jackson 1999; Meyer 2003; National Association of Country and City Health Officials 2015), where managers act on complaints made by the public to address rat infestations that are already established. This reactive nature of rat management is problematic because it: 1) fails to address the underlying issues that promote rat infestations (such as access to food and spaces to burrow (Singleton *et al.* 1999; Lambert *et al.* 2008; Corrigan 2011; Feng and Himsforth 2014)); and 2) it assumes that all persons are equally likely to contact the municipality to report a complaint. In the first instance, without the successful removal of all rats in an area, populations are likely to rebound in numbers following the cessation of the control campaign (Barnett and Bathard 1953; Hacker *et al.* 2016). In the second instance, relying on rat complaints can

disproportionately place additional burdens on already disadvantaged communities who may be less likely to report rat sightings. Indeed, in Chapter 6, residents of Vancouver's DTES indicated that they would be unlikely to report rat issues due to the feeling that there would be a lack of action by those deemed responsible for their control. Given that residents in this neighbourhood reported frequent and close interaction with rats, this is a neighbourhood in particular need of rat mitigation efforts and also one that may be less likely to receive them. Extending beyond rats, this work demonstrates that management of wildlife-associated issues requires proactive approaches that minimize negative interactions between wildlife and people before they occur.

**Beyond a single signal for action.** The emphasis on controlling rats once they have become a “problem” begs the question of how we define a “problem”. Most reference to rat-associated issues in cities pertain to their propensity to transmit pathogens to people, the infrastructural damages they cause and their contamination of food stores (e.g., Pimentel *et al.* 2005; Meerburg *et al.* 2009; Himsforth *et al.* 2013b). In this thesis, I demonstrate that, even in the absence of these issues, interactions with rats can be overwhelmingly negative for those coming into continued contact with them. Therefore, I propose that the decision to “act” on mitigation should consider both the psychological and physical consequences of these interactions.

#### **WHERE TO TARGET AND SCALE EFFORTS?**

**There is no one scale to rule them all.** An interface-based approach requires that the scale of management efforts reflect the scale of the interface. For example, issues that concern a neighbourhood will require different approaches and resources than those that span a municipality. Indeed, rat-associated health risks can vary even within a single neighbourhood (Himsforth *et al.*

2013a; 2014a; 2014d; 2015a). While management may first prioritize those areas where people are more vulnerable to rats (i.e., areas of greater rat abundance and higher pathogen prevalence), an interface approach considers addressing the underlying factors that promote the interactions that determine these risks (i.e., human behaviours and the environmental features that support rat abundance). Beyond this, the interface will also vary based on the ecology of the wildlife species involved. For example, this thesis suggests that management of rat-associated health risks may be more effective if it encompasses an entire city block in order to reflect the extent to which rats move (i.e., termed an “eradication unit” (Abdelkrim *et al.* 2007)), although the size of this unit will vary by city (Combs *et al.* 2018a). For this reason, the appropriate approach will adapt to the scale of the interface, varying by system and across space and time.

**Ecosystems over entities.** As discussed in this thesis, health systems are complex and dynamic, encompassing people, animals, social systems and environments (Stephen 2014). Given rapid urbanization and environmental change (United Nations 2018; Hobbie and Grimm 2020), static approaches that focus on singular one-animal, one-risk tactics will quickly be outpaced. Proactive and adaptive solutions must then broaden their scope to the systems in which wildlife and people interface. In so doing, these approaches have the opportunity to address multiple issues simultaneously (Stephen 2018). One way to do this is by addressing the vulnerabilities of people and wildlife to health threats (Stephen 2014). For example, in this thesis I discuss how persons without homes are particularly vulnerable to the negative impacts of rats. Therefore, addressing issues of housing quality and affordability to minimize homelessness (identified by residents in this study as their most pressing concern), would in turn decrease human encounters with rats. More broadly, a systems-based approach to mitigating wildlife-health threats might focus on

improving the health of urban wildlife generally. This is because healthier wildlife are better able to cope with the challenges posed by environmental change (Nordenfelt 2011) and withstand disease themselves (Hawley *et al.* 2009; Serieys *et al.* 2018).

### **WHO SHOULD MAKE THE DECISIONS?**

**A transdisciplinary approach requires a multidisciplinary team.** The One Health framework is, at its core, an interdisciplinary and transdisciplinary approach. As evidenced in this thesis, addressing rat-associated health issues benefits from the proficiency of bioinformaticians, ecologists, epidemiologists, geneticists, veterinarians and pest-control professionals. As such, One Health approaches to urban wildlife should aim to bring together diverse teams of experts with their own unique perspectives in order to derive innovative solutions to address these dynamic interfaces.

**Deployment of this approach requires leadership.** Bridging the gaps between disciplines can be challenging, and this requires significant investment, planning, and coordination. While many entities could fill this role, for rat-associated issues municipalities are well-placed to take on leadership as they are able to facilitate these connections among stakeholders, as well as derive actionable guidelines based on their recommendations. For example, addressing rat-associated issues might be one part of a larger effort to manage human-wildlife interactions in cities. This process could bring together wildlife managers, urban planners, human health specialists, and pest control professionals to determine how best to collect data on these interactions and target mitigation efforts. Governments also have the ability to enforce policies and bylaws that may be

necessary for the success of these programs (i.e., enforcing proper waste disposal), which allows for the necessary movement from knowledge to action.

**Public engagement is essential.** Ultimately, efforts toward mitigating negative health outcomes associated with wildlife are for the good of the public, and the public, in turn, has a role to play. In order for the policies put in place by municipalities to be effective, these programs require public involvement. For example, many cities rely on citizens to report rat sightings to inform where to target control efforts (Margulis 1977; Murray *et al.* 2018). While complaints may not adequately reflect rat activity in all areas, in Chicago, USA areas with heightened rat complaints were found to have higher relative rat abundance (Murray *et al.* 2018) suggesting that efforts to improve reporting among citizens (i.e., through educational campaigns) could make this a valuable tool for inferring rat abundance across neighbourhoods. Further, gaps in reporting due to differential engagement of community members could be filled by building lines of communication with community organizations and front-line responders (i.e., police officers) who work with the public and frequent a breadth of community areas. Ultimately, by improving public buy-in, such programs will improve their ability to detect and respond to wildlife-health related issues.

#### **WHAT IMPORTANT ISSUES REMAIN?**

As detailed above, the research undertaken as a part of this thesis has made considerable strides in facilitating a better understanding of how rats and people interact in the urban environment. And while the strength of this collective work lies in its interdisciplinary nature – bridging ecology, epidemiology, genetics, and the social sciences – it represents only some of the foundational

information we still require on the nuances of how rats, and wildlife generally, interface with humans in urban environments.

**The social context.** First, we require a better understanding of the factors that promote pathogen acquisition in rats. Although many rat-associated pathogens are thought to be spread among rats through close contact and social interactions (Bitam *et al.* 2010; Himsforth *et al.* 2013b; Lee *et al.* 2018), much of wild rat social biology remains unknown (Schweinfurth 2020). Uncovering how rats interact with each other and how these contacts facilitate pathogen spread is important because it can resolve how actions that disrupt colonies can affect pathogen prevalence. Indeed, previous research has found that the culling of only some rats in a city block resulted in an increase in the number of rats carrying *L. interrogans*, thought to be due to the impacts of culling on rat social structures (Lee *et al.* 2018). Similar impacts of culling on animal behaviours and pathogen spread have been documented in badgers (*Meles meles*) (Donnelly *et al.* 2006) and Egyptian fruit bats (*Rousettus aegyptiacus*) (Amman *et al.* 2014), exemplifying how anthropogenic actions can have unintended consequences that actually increase human health risk.

**The consequences of disturbance.** The need to clarify how anthropogenic disruptions impact wildlife and the pathogens they carry is particularly evident at the time of writing. Regarding rats, with the closure of restaurants due to the COVID-19 pandemic, pest control professionals are marking increased rat activity (Marris 2020; Neustaeter 2020). Given that the distances travelled by rats are influenced by resource availability (Davis *et al.* 1948; Low *et al.* 2013; Oyedele *et al.* 2015), changes in access to food could lead to changes in movement. In turn, any deviation from normal movement patterns may affect pathogen spread as rats move to new areas and interact with

neighbouring colonies. Therefore, our ability to adapt to wildlife-associated issues also requires a nuanced understanding of how wildlife respond to environmental change.

**Disentangling mental health stressors.** While this thesis made a number of important discoveries regarding how rats impact the mental health of residents, it has revealed the need to investigate this relationship in greater depth. Beyond qualitative description, mental health impacts may be elucidated by incorporating standard metrics for assessing mental health such as by using the Centre for Epidemiological Studies Depression Scale (Eaton *et al.* 2004). Further, given that rats exist among a suite of neighbourhood stressors affecting residents, future studies are needed to quantify these impacts in relation to other stressors. This might be achieved through pairing qualitative interviews with cohort studies which compare health outcomes for those who are exposed vs unexposed to rats (Song and Chung 2010), while accounting for the presence and abundance of other neighbourhood-level stressors (e.g., housing availability, sanitation, etc.). Together, these approaches may be better able to quantify and articulate the role of rats in mental health outcomes.

**Broadening to a socio-ecological scope.** Finally, while this thesis has focused largely on how rats impact people, humans have a considerable impact on rats. The use of rodenticides to control rats has become an issue of increasing concern due to the accidental poisoning of non-target wildlife (Serieys *et al.* 2015; Koivisto *et al.* 2018; Hong *et al.* 2019). Despite growing evidence that such one-and-done approaches to rat control efforts are largely ineffective, and that proactive control requires environmental measures which reduce access to resources (Singleton *et al.* 1999; Colvin and Jackson 1999; Corrigan 2011), these methods continue to be routinely employed. Therefore,

one other area of interesting future research is to evaluate how and why people take the actions that they do in addressing rat infestations, and evaluate whether these actions have consequences for other wild and domestic animals in these areas. Such research will build a better understanding of these socio-ecological systems and how they contribute to the health of wildlife in cities.

### **WHY SHOULD WE EXTEND OUR EFFORTS BEYOND PREDICTING THE NEXT PANDEMIC?**

In light of the current COVID-19 pandemic, it is clear that we must do a better job of protecting ourselves and our societies. Although cities in North America may be relatively free of rat-associated disease in people now, opportunities for the introduction and emergence of known or novel pathogens will fluctuate with land use change and the global movement of people and wildlife. Indeed, with thousands of potential pathogens yet to be discovered (Carroll *et al.* 2018), and with tremendous variability in spillover potential and probability (Plowright *et al.* 2017) predicting spillover events from wildlife to people is incredibly challenging due to the complexity of the systems in which these transmission events occur. Therefore, to address these problems we need equally complex and multifaceted solutions. And while we may not be successful in predicting the next pandemic, there are proactive steps that can be taken now to manage the interactions between wildlife and people in cities to reduce public health risks.

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## APPENDICES

### APPENDIX A: SUPPLEMENTARY MATERIALS FOR CHAPTER 2

**Table A-1:** Details of the literature search procedure

Concept	Keyword
Urban	urban* OR residential OR city OR cities OR suburban OR metropol*
AND	
Rats	“ <i>Rattus norvegicus</i> ” OR “Norway rat*” OR “brown rat*” OR “ <i>Rattus rattus</i> ” OR “roof rat*” OR “black rat*”
AND	
Movement	dispersal OR emigration OR expansion OR immigration OR migration OR movement OR boundar* OR distribution OR domain OR “home area*” OR “home range*” OR “site fidelity” OR zone

**Table A-2:** Number of unique published studies (N = 37) by continent

Continent	Number of Studies
Africa	3 <sup>1</sup>
Asia	4 <sup>1</sup>
Europe	8
North America	19 <sup>2</sup>
Oceania	0
South America	5 <sup>2</sup>
Antarctica	0

<sup>1</sup> Study site is transcontinental Egypt (Petrie 1923)

<sup>2</sup> Multi-city comparison including samples from both North and South America (Combs *et al.* 2018a)

**Table A-3:** Relevant details of studies included in a review of urban rat movement (N = 39)

Study	Location	Species	Sample Size	Method	Relevant Results
Andrews and Belknap, 1983	Ralston, NE, USA	Norway	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• Within six months of control efforts, rats emigrated from, and immigrated to, the site of control efforts</li> </ul>
Angley <i>et al.</i> , 2018	New York, NY, USA	Norway	100	Genetics (SNPs)	<ul style="list-style-type: none"> <li>• Rats in ecologically similar areas were more genetically similar than were rats in different habitat types, suggesting that rats moved among similar habitats (e.g., residential parks vs. mixed-used infrastructure)</li> <li>• Ectoparasite communities (transmitted among hosts via close contact) were more similar among rats near each other than rats further apart, which may be due, in part, to short-distance movements and interactions among colonies</li> </ul>
Barnett and Bathard, 1953	London, England	Norway	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• Following reductions of rats in two sewers by poisoning (to 10% the size of the population), the population rebounded within six months of post-control</li> <li>• The authors posited that the increase in rat numbers following control was partly due to the invasion of rats from the surface into the sewer</li> </ul>
Bentley <i>et al.</i> , 1958	London, England	Norway	Unknown	Proxy (bait uptake, dyed feces)	<ul style="list-style-type: none"> <li>• Rats moved up to 255ft in one section of the sewer</li> </ul>
Bentley <i>et al.</i> , 1959	England	Norway	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• Following poisoning, population increases of &gt;3% per week were hypothesized to be due, in part, to the migration of rats from the surface and from adjacent sewers</li> </ul>

Berthier <i>et al.</i> , 2016	Niger	Black	230	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Individuals within the city were more closely related to each other than they were to rats outside of the city</li> <li>• No evidence for isolation by distance**</li> <li>• Sites connected by roads were more genetically similar than sites that were not, suggesting potential human-mediated dispersal via roadways and rivers</li> <li>• Nineteen rats were potential migrants (genetically assigned to an area other than the one of their capture)</li> </ul>
Byers <i>et al.</i> , 2017	Vancouver, BC, Canada	Norway	14 (tagged) 3 (recaptured)	Continuous (GPS)	<ul style="list-style-type: none"> <li>• Geographical Positioning System tags were unsuccessful in obtaining rat movement data, which may be due to tag removal by rats and line-of-site obstruction</li> </ul>
Calhoun, 1948	Baltimore, MD, USA	Norway	273	Capture-Mark-Recapture	<ul style="list-style-type: none"> <li>• Rats were recaptured within 110ft of their initial capture site</li> <li>• Rats introduced to an unfamiliar block would occasionally emigrate. If the block was near to their home block, an equal number of rats would stay in the new block as would return home (N = 6). When rats were released into a block further from their home block, fewer rats were recaptured in the block of release, suggesting emigration or mortality</li> </ul>
Colvin <i>et al.</i> , 1998	Boston, MD, USA	Norway	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• Rodenticide presence in sewer rats was possibly an indication of movement among the surface and sewers as poisoning was conducted on the surface but not in sewers</li> <li>• The activity of surface rat populations did not necessarily correspond with sewer rat activity, suggesting that rats did not regularly move between the surface and sewer</li> </ul>
Combs <i>et al.</i> , 2018a	New York, NY, USA;	Norway	1220	Genetics (SNPs)	<ul style="list-style-type: none"> <li>• Evidence for isolation by distance** suggested similar patterns of dispersal across cities</li> <li>• Rats within 500m of one another were generally closely related</li> </ul>

	New Orleans, LA, USA;				<ul style="list-style-type: none"> <li>• Gene flow indicated movement of rats among city blocks, with infrequent long-distance movements of up to 1.5km in NYC, 1.5km in New Orleans, and 3km in Salvador</li> <li>• Areas which appeared to disrupt gene flow were a “resource desert” in NYC, major waterways in New Orleans, and roads in Salvador and Vancouver; these areas were hypothesized to serve as barriers to movement.</li> </ul>
	Vancouver, BC, Canada;				
	Salvador, Brazil				
Combs <i>et al.</i> , 2018b	Manhattan, New York City, NY, USA	Norway	262	Genetics (SNPs)	<ul style="list-style-type: none"> <li>• Gene flow among adjacent rat colonies supported isolation by distance**</li> <li>• First order relatives (e.g., siblings and/or parent-offspring) were found 45.3m apart on average</li> <li>• Restricted movement across the “midtown” area of the city was hypothesized to be due to landscape features or greater pest control efforts in the area</li> <li>• One rat was suspected of travelling 7.5km, although whether this was anthropogenically-mediated was unknown</li> <li>• There was no evidence of male-biased dispersal</li> </ul>
Costa <i>et al.</i> , 2016	Salvador, Brazil	Norway	446	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Rats with a high probability of siring offspring (&gt;99%) were found within the same valley as the pregnant female</li> <li>• The distance between females and males with a high probability of siring offspring ranged from 0 – 149.6m, with a mean inter-parent distance of 70m ± 58m</li> </ul>
Creel, 1915	New Orleans, LA, USA	Norway	292 (tagged) 163 (recaught)	Capture-Mark- Recapture	<ul style="list-style-type: none"> <li>• Rats released in an unfamiliar, resource-poor environment (warehouse district) travelled twice as far as did rats released into a residential area with greater resources (4 vs 2 miles)</li> </ul>
Davis <i>et al.</i> , 1948; Emlen <i>et al.</i> , 1949*	Baltimore, MD, USA	Norway	362 (tagged) 119 (recaught)	Capture-Mark- Recapture;	<ul style="list-style-type: none"> <li>• The diameter of the home range rarely exceeded 100 – 150m and rarely encompassed roads</li> <li>• &gt;70% of rats were recaught within 40ft of their original capture site, and 87% of dyed feces were found within 50ft of the bait station</li> </ul>

			Unknown	Proxy (dyed feces, tracks in snow)	<ul style="list-style-type: none"> <li>• The home range consisted of a narrow area connecting food and harbourage sites; the extent of movement was determined by the proximity of food and harbourage</li> <li>• Rats did not utilize the whole area of their home range</li> <li>• Rats changed home range in response to environmental change</li> <li>• The greatest distance moved by a rat (360ft) was by an adult female</li> <li>• Males tended to move further distances than females</li> <li>• Roads posed a barrier to movement (i.e., of 66 surveys of rat tracks in snow, there was only one instance of crossing)</li> <li>• Rats cross roads more often when resources were limited (i.e., in eight surveys of rat racks in snow, there were ten cases of rats crossing roads)</li> <li>• Alleys limited movement, with the majority of bait-dyed feces found on the same side of the alley as the bait station</li> <li>• Rats did not appear to invade city blocks where trapping occurred, suggesting that trapping did not prompt rat ingress into these blocks</li> </ul>
Davis and Christian, 1956	Baltimore, MD, USA	Norway	156 (tagged)	Capture-Mark-Recapture	<ul style="list-style-type: none"> <li>• Rats were introduced into a new city block to simulate immigration. In blocks with “stationary” populations (e.g., the population was not growing), when the number of resident rats were replaced with a similar number of alien rats, the population remained stationary. When resident rats were replaced with four times as many alien rats, the population decreased by 25%</li> <li>• In an “increasing” population of rats, replacement of resident rats with a similar number of alien rats resulted in the cessation of population growth. Lactation rate also decreased suggesting that the decrease in growth rate was due, in part, to a reduced reproductive rate</li> </ul>
Desvars-Larrive <i>et al.</i> , 2017	Gennevilliers, France	Norway	86	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Evidence for isolation by distance**</li> <li>• Evidence for gene flow between rats in an urban park and outside colonies</li> </ul>

Gardner-Santana <i>et al.</i> , 2009	Baltimore, MD, USA	Norway	277	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Evidence for sex-biased dispersal – females near to each other were more closely related to each other than were males. Further, four first generation migrants which originated from outside of the park were all males</li> <li>• Movement among the park and surrounding areas was hypothesized because rodenticides were found in park rats, where rodenticides were banned</li> </ul>
Glass <i>et al.</i> , 1989	Baltimore, MD, USA	Norway	372 (tagged) 107 (recaptured)	Capture-Mark-Recapture;  Direct Observation;  Proxy (Tracks in snow)	<ul style="list-style-type: none"> <li>• Evidence for strong site fidelity as 95% of rats were genetically assigned to their area of capture</li> <li>• Evidence for isolation by distance**</li> <li>• Most rat movement was generally restricted to a city block (~62m) with individual movements ranging from 30 – 150m</li> <li>• Relatives were found within 1.7km of each other (~11 city blocks)</li> <li>• Some rats were genetically assigned from 2–11.5km away from their capture site, indicating infrequent long-distance movement</li> <li>• The majority of migrants identified were sexually mature adults</li> <li>• There was no evidence of sex-biased dispersal</li> <li>• Genetic differentiation between east and west populations coincided with a fast-moving waterway</li> </ul>
			Unknown		<ul style="list-style-type: none"> <li>• Of the 107 rats recaptured, those in residential areas were recaptured 27.3% of the time at the same location while parkland rats were recaptured 7.8% of the time at the same location (the number of recaptured rats at each location was not specified)</li> <li>• Distances travelled in residential areas were generally less than 15m, and restricted to a single alley system</li> <li>• Rats moved further in parkland (24.7m; N = 64 movements) than in residential areas (13.5m; N = 77)</li> <li>• Movements derived from tracks in snow in residential areas were longer than determined by capture data (21.6m, N = 39 tracks)</li> <li>• Rats rarely moved longer distances, with two rats moving &gt;85m and one individual moving 165m in 15 mins (which involved crossing an alley and major roadway)</li> </ul>

					<ul style="list-style-type: none"> <li>• Movement was generally between harborage and food sources and was along fences and other cover</li> <li>• During a 21hr period, rats crossed alleys 80 times more often than they crossed roads (41.5 rats/hr crossed alleys, 0.5 rats/hour crossed roads) – these levels varied depending on levels of rat and human activity</li> </ul>
Glass <i>et al.</i> , 2016	Baltimore, MD, USA	Norway	722	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Evidence of strong site fidelity as 97% of rats were genetically assigned to their block of capture</li> <li>• Four of the 16 unassigned rats could not be assigned to the region of capture</li> <li>• By genotyping pregnant females, their offspring, and males, they found that females mostly mated with males that did not reside in their city block</li> <li>• For half of the pregnant females, offspring were fathered by more than one male; these males resided in the same alley as each other, which was different from that of the female, suggesting that either the female or a group of males traveled to mate</li> <li>• The average distance between females and their mates was 114.3m (range: 8 – 352.5m)</li> </ul>
Gras <i>et al.</i> , 2012	Bologna, Italy	Norway and/or black	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• Surface rat infestations were strongly correlated with surface but not sewer bait uptake, suggesting that surface infestation is not necessarily a reflection of sewer infestation</li> </ul>
Greaves <i>et al.</i> , 1968	Portsmouth, England	Norway	Unknown	Proxy (bait uptake)	<ul style="list-style-type: none"> <li>• The mean rate of increase of the population following control efforts was 20% per week</li> <li>• Re-infestation of sewer sites following control efforts began at the outer edges of the controlled area, which was hypothesized to be due, in part, to rats invading from more heavily populated surrounding areas</li> </ul>
Hacker <i>et al.</i> , 2016	Salvador, Brazil	Norway	Unknown	Proxy (track plates)	<ul style="list-style-type: none"> <li>• Rat mark intensity on track plates (an indicator of rat abundance and activity) rebounded within four weeks of an intensive control program</li> </ul>

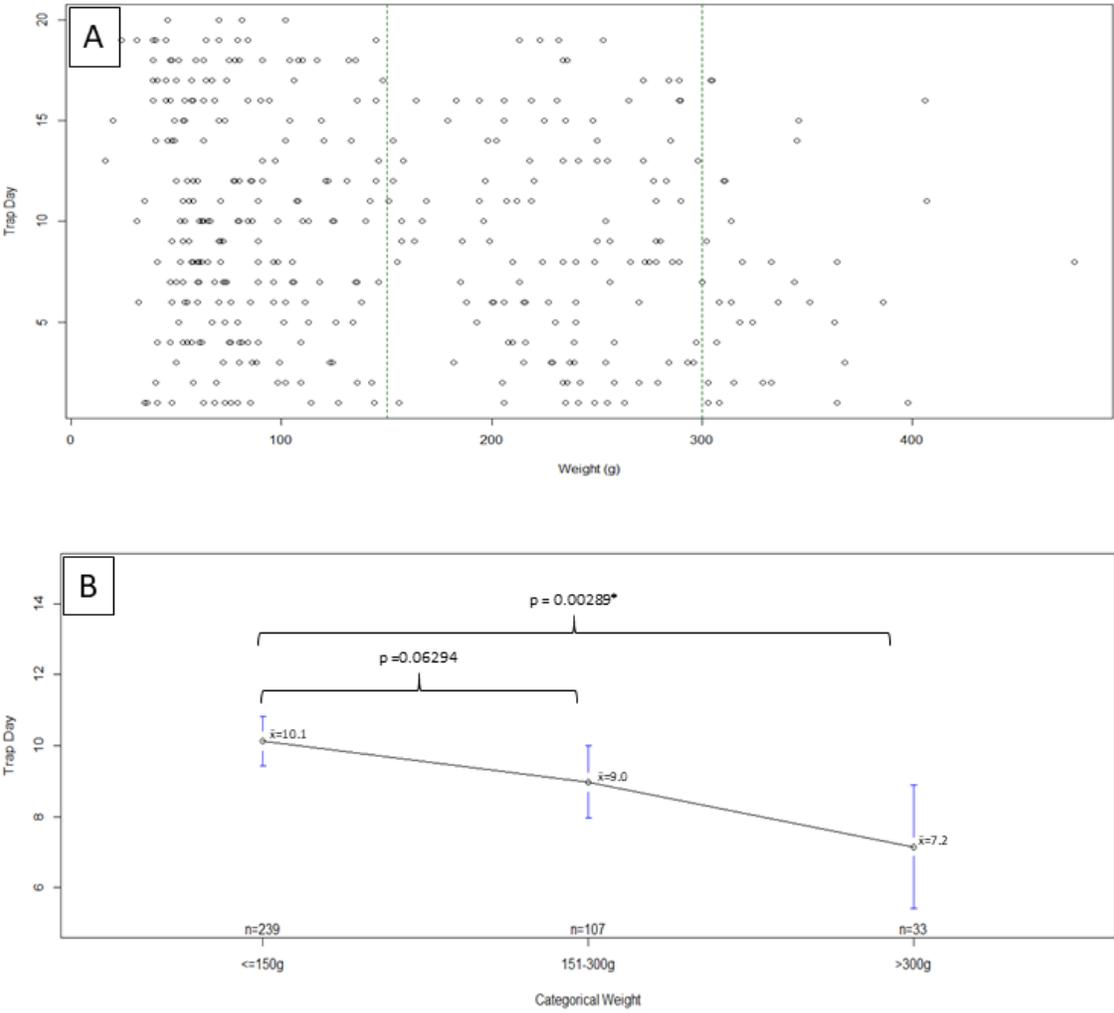
					<ul style="list-style-type: none"> <li>• Trapping of rats in homes also resulted in fewer rats in surrounding houses, suggesting that rats moved among households</li> </ul>
Heiberg <i>et al.</i> , 2012	Copenhagen, Denmark	Norway	332 (tagged) 213 (recaught)	Capture-Mark-Recapture (PIT tags)	<ul style="list-style-type: none"> <li>• Rats appeared to be confined to the sewers in which they were born, with home ranges within the extent of the sewer</li> <li>• Average maximum day-to-day movement was 200m</li> <li>• There was no difference between males and females in distances travelled and males and females moved together in the same areas</li> <li>• Areas with high to moderate water flow were found to have higher rat activity, potentially signifying foraging sites</li> <li>• No evidence of movement between two adjacent but separate sewer systems</li> <li>• One third of rats were caught once, and many of these individuals were caught in manholes linked to smaller sewer lines suggesting that sewer rats may wander long distances or rats from the surface may visit sewers</li> <li>• No sewer rats were found on the surface</li> </ul>
Kajdacs <i>et al.</i> , 2013	Salvador, Brazil	Norway	146	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• There was no evidence for isolation by distance**</li> <li>• Evidence for sex-biased dispersal</li> <li>• The majority of migrants (9/10) were mature males</li> <li>• There were possible dispersal/migration routes within and across valleys and neighbourhoods</li> <li>• In the second year of sampling (i.e., following trapping and removal of rats in the previous year), some rats were genetically similar to the rats sampled in the previous year, and others were not, suggesting both population replacement and re-colonization of sites by invading rats</li> </ul>
King, 1950	Lawrence, KS, USA	Norway	20 (tagged) 8 (recaught)	Capture-Mark-Recapture	<ul style="list-style-type: none"> <li>• Evidence for strong site fidelity with 63% of rats recaught in the same trap (5/8)</li> <li>• Rats moved among adjacent buildings, with 25% of rats recaught near to or in a building other than the one of their first capture (2/8)</li> </ul>

					<ul style="list-style-type: none"> <li>• Rarely, rats moved longer distances, with two rats moving up to 113ft and 404ft</li> <li>• Alleys seemed to limit the movement of rats, as only one individual was caught on both sides of the alleyway</li> </ul>
Low <i>et al.</i> , 2013	Christmas Island, Australia	Black (assumed)	10 (collared) 6 (tracked)	Continuous (VHF)	<ul style="list-style-type: none"> <li>• Males (N = 2) had larger home ranges than females (N = 4) which was hypothesized to be due to differences in mate-searching behaviours</li> <li>• Male average home range size was 1.06ha (KDE) and female average home range size 0.27ha (KDE) for an average home range size of 0.53ha</li> <li>• Male average core home range size was 0.32ha (KDE) and female average core home range size was 0.09ha (KDE) for an average home range size of 0.17ha</li> <li>• Male home ranges overlapped with other males and females while female home ranges excluded other females</li> </ul>
Mangombi <i>et al.</i> , 2016	Franceville, Gabon	Black	480	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Evidence for isolation by distance**</li> <li>• The mean dispersal distance between parents and offspring was 496m</li> <li>• Low levels of genetic structuring suggested relatively high levels of dispersal</li> <li>• The Mpassa river which ran through the centre of the city (width = 80m) did not appear to impede gene flow</li> </ul>
Oyedele <i>et al.</i> , 2015	George Town, Malaysia	Norway	12	Continuous (VHF)	<ul style="list-style-type: none"> <li>• Home range size differed between rats caught in two sites, this was hypothesized to be due to differences in resource availability</li> <li>• Males had larger total home ranges (N = 6; 241m<sup>2</sup> (95% HM)) and core home ranges (N = 6; 23m<sup>2</sup> (50% HM)) than females (N = 6; total = 19m<sup>2</sup> (95% HM), core = 4.6m<sup>2</sup> (50% HM))</li> <li>• Rats moved along the same pathways day-to-day</li> <li>• Males emerged from their burrows one to two hours before females and returned to the nest at the same time or one hour after females; this pattern differed between the two sites</li> </ul>

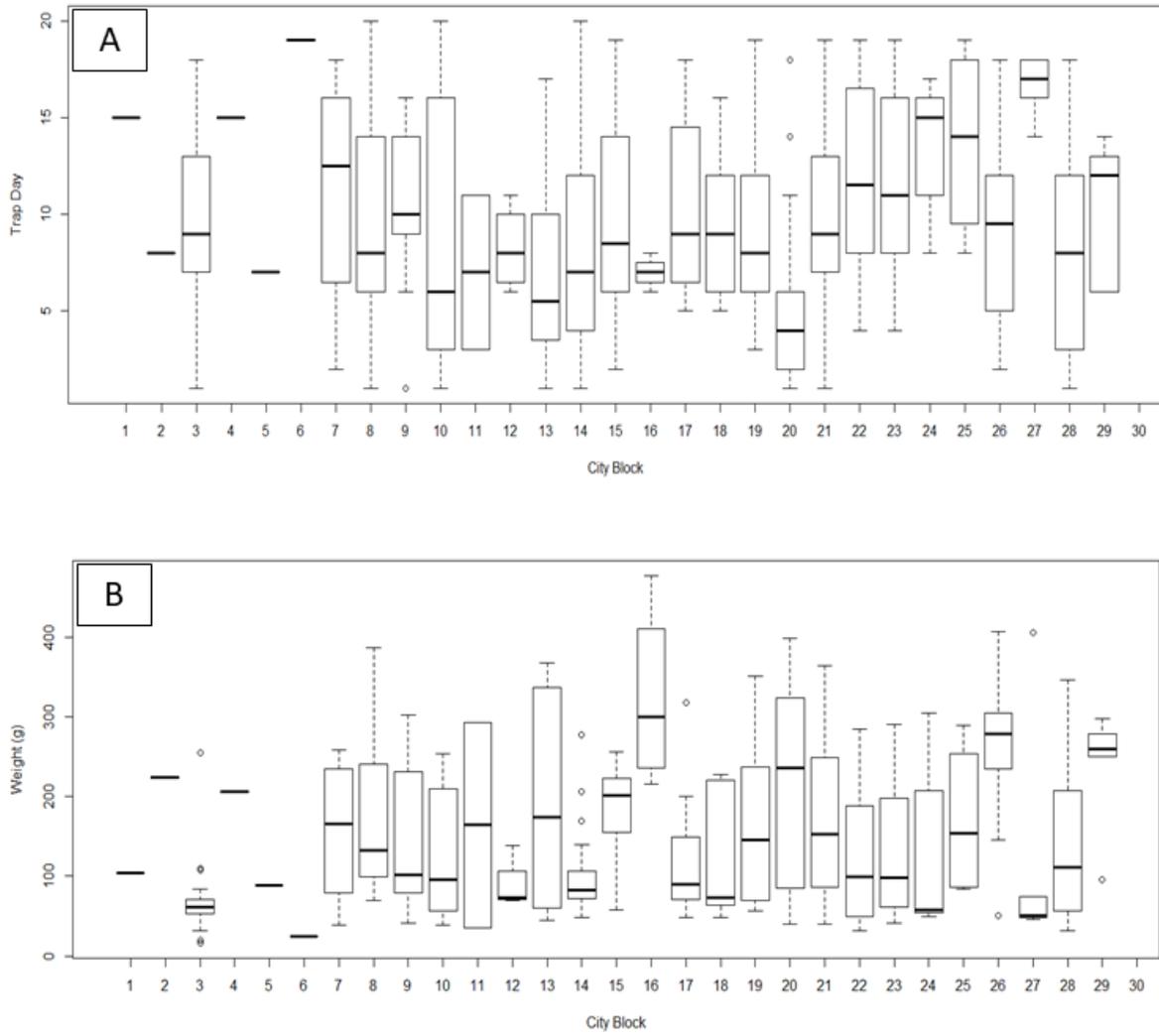
Parsons <i>et al.</i> , 2015	New York City, NY, USA	Norway	13 (tagged) 7 (recaught)	Capture-Mark-Recapture (PIT)	<ul style="list-style-type: none"> <li>• Only rats released within 10m of a scanning station returned to the scanning area, rats released further away (e.g., 20m) did not return</li> <li>• Females were active between 6am to 7pm, while males were active throughout the day; both sexes were less active between 9am and 1pm</li> </ul>
Petrie and Todd 1923; Petrie <i>et al.</i> , 1924*	El Motiâ, Egypt	Black	341 (trapped) 146 (recaught)	Capture-Mark-Recapture	<ul style="list-style-type: none"> <li>• Of the 146 recaptured rats, 53 were caught in more than one house</li> <li>• Most movements (N = 68) were between contiguous houses</li> <li>• Broader streets appeared to act as a barrier to rat movement, with only one rat travelling to a nearby community square</li> <li>• The furthest distance travelled by a rat was 250m</li> </ul>
Recht, 1982	Carson, CA, United States	Norway	4	Continuous (VHF)	<ul style="list-style-type: none"> <li>• Home ranges were irregularly shaped, and were determined by the presence of vegetation</li> <li>• Rats used specific pathways around the home range</li> <li>• Home range use did not decrease towards the edges</li> <li>• Home range use varied by individual</li> <li>• Alternate burrows were used, but rats returned to the home burrow regularly</li> <li>• Rats altered movement patterns and activity with food availability, human activity, and weather</li> <li>• Two rats were active during the night and two were active during the day</li> </ul>
Recht <i>et al.</i> , 1983	City of Orange, CA, United States	Black	5	Continuous (VHF)	<ul style="list-style-type: none"> <li>• Rats were nocturnally phased</li> <li>• Home ranges were irregularly shaped and did not exceed 30.5m in diameter</li> <li>• Home range use did not decrease towards the edges</li> <li>• Rats used specific pathways around the home range</li> <li>• Alternate burrows were used in response to environmental change (e.g., flooding, construction)</li> </ul>

Richardson <i>et al.</i> , 2017	Salvador, Brazil	Norway	706	Genetics (microsatellites)	<ul style="list-style-type: none"> <li>• Evaluated relatedness among rats across three valleys</li> <li>• There was limited movement among study sites, with 79% of movement occurring within the valley of capture</li> <li>• Migration of rats into valleys ranged from 10 – 29% of individuals</li> <li>• There was a sharp genetic break between two valleys separated by 50m; there was a high-traffic roadway running between the valleys which was thought to serve as a barrier to movement</li> </ul>
Takahashi and Lore, 1980	NJ, USA	Norway	235 sightings	Continuous (Direct Observation)	<ul style="list-style-type: none"> <li>• Activity was greatest two to three hours following sunset and prior to sunrise</li> <li>• Foraging activity did not appear to be affected by traffic or the presence of a trash compactor</li> </ul>
Tanaka and Kawashima, 1951	Kochi City, Japan	Norway	57 (tagged) 15 (recaught)	Capture-Mark- Recapture	<ul style="list-style-type: none"> <li>• There was evidence for strong site fidelity; many rats (7/15) did not move between recapture periods (5/9 females, 2/6 males)</li> <li>• Movement distances did not exceed 40m, and rats moved on average 20m (approximately the space of three to four adjacent houses)</li> <li>• The time between captures did not influence distances moved</li> <li>• Males generally moved further distances than females</li> </ul>
Traweger and Slotta- Bachmayr, 2005	Salzburg, Austria	Norway	166	Capture-Mark- Recapture	<ul style="list-style-type: none"> <li>• Resource-rich areas separated from other rat habitats by roadways had few rats, suggesting that roadways acted as a barrier to movement</li> </ul>
Worth, 1950	Tampa, FL, USA	Black	Unknown	Capture-Mark- Recapture	<ul style="list-style-type: none"> <li>• Home ranges did not overlap with Norway rats</li> <li>• Rats remained mostly within the block in which they were originally captured and were recaught within the same building or an adjacent building</li> <li>• Rats rarely moved across city streets</li> <li>• Rats inhabited elevated areas (e.g., attics) and they climbed shrubbery, pipes, and wires</li> </ul>

**APPENDIX B: SUPPLEMENTARY MATERIALS FOR CHAPTER 3**

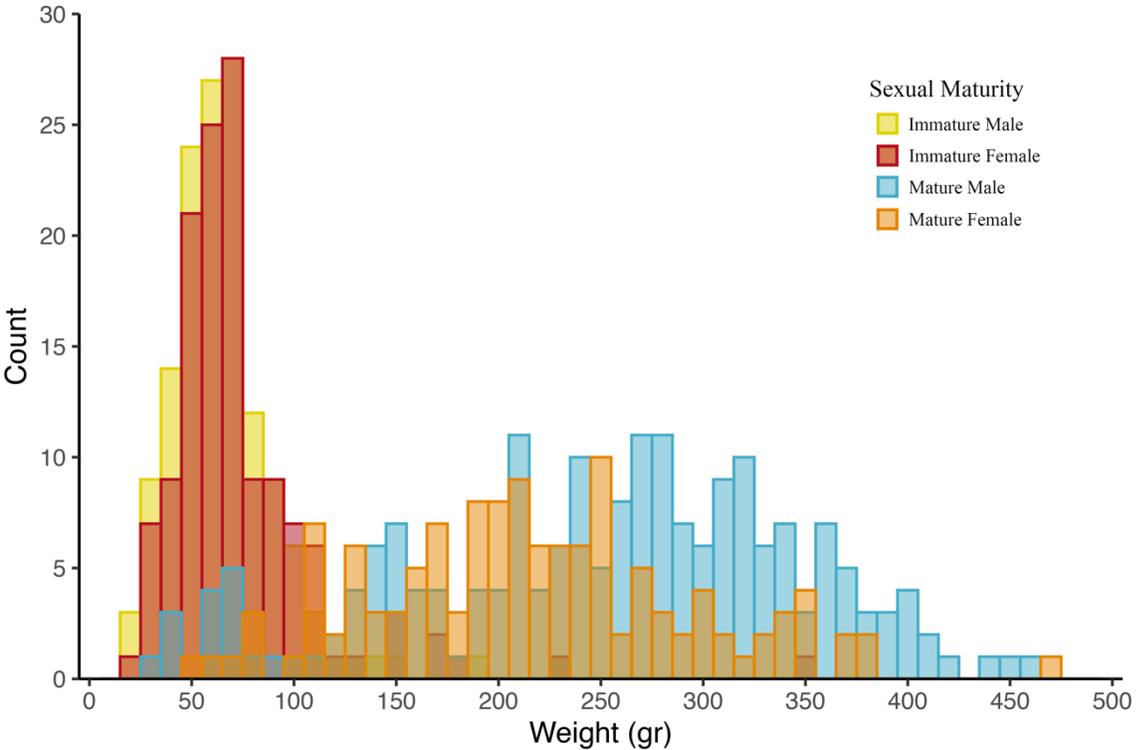


**Figure B-1: Distribution of rats (N = 379) by weight and trap day.** A) Individual rats plotted by continuous weight in relation to their day of capture (trap day). Vertical dashed lines distinguish among rats in three weight ‘classes’ ( $\leq 150g$ ,  $151-300g$ ,  $>300g$ ), created through visual inspection of breaks in the distribution. B) Mean trap day with associated error bars (95%CI) for rats caught within each weight category.



**Figure B-2: Distribution of rats (N = 379) by A) trap day and B) weight within each city block of capture (N = 31 blocks).**

**APPENDIX C: SUPPLEMENTARY MATERIALS FOR CHAPTER 5**



**Figure C-1: Distribution of weights for Norway rats (*Rattus norvegicus*) by sex and sexual maturity.** Weight in grams is displayed for rats identified as immature males (N = 139), immature females (N = 132), mature males (N = 192), and mature females (N = 129). Weights for pregnant females were adjusted by the average difference between pregnant and non-pregnant, sexually mature females.

## **APPENDIX D: SUPPLEMENTARY MATERIALS FOR CHAPTER 6**

### **Interview Guide**

How long have you lived in the Downtown Eastside (DTES)?

How often do you see rats? (e.g., every day, several times a week, once a week, once a month or never?)

Can you describe a typical encounter you might have with rats?  
(Prompts: Where, when)

Can you describe a memorable encounter with rats you had, or heard of?  
(Prompt: Are there any stories about rats that are told often in the community?)

When you see rats like this, how does that make you feel? Why?

Do you change your habits around rats?

What impacts do rats have on the community? What do they mean for the community?

Aside from the feelings you just said, do rats have any other meanings for you?

Are there any other issues associated with rats from your point of view?

Who do you think should be responsible for dealing with rats in the DTES?

Do you think rats are a bigger problem in the DTES than other parts of Vancouver?

Have rats affected where you live or how you feel about where you live?

Of all the things that you deal with in your day, how important are rats? Why do you think that?  
(Prompt: Are they the least important? Most important? The same as other things?)

I have asked you a lot of questions today. Is there anything else you would like to share with me about your experiences with rats in the DTES?

## APPENDIX E: PUBLICATIONS IN TANDEM WITH THE THESIS

In addition to the included thesis chapters, during the course of my PhD I have co-authored 12 published papers, with four additional papers in review. The published papers are listed below with mentees identified by \*:

Murray MH, Fidino M, Fyffe R, **Byers K**, Pettengill JB, Magle S, Rios MJ, Ortinou N,

Santymire R (In press) City sanitation and socioeconomics predict rat zoonotic infection across diverse neighbourhoods. *Zoonoses and Public Health*.

Lee MJ\*, **Byers KA**, Donovan CM\*, Patrick DM, Himsworth CG (In press) *Leptospira* spp. and urban rats: Is carriage a function of the urban environment? *Journal of Wildlife Diseases*.

Murray MH, Sánchez CA, Becker DJ, **Byers KA**, Worsley-Tonks KEL, Craft ME (2019) City sicker? A meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment*, **17**, 575-583.

Combs M, **Byers KA**, Himsworth CG, Munshi-South J (2019) Harnessing population genetics for pest management: Theory and application for urban rats. *Human-Wildlife Interactions*, **13**, 250-263.

Minter A, Himsworth CG, **Byers KA**, Childs JE, Ko A, Costa F (2019) Tails of two cities: Age and wounding are associated with carriage of *Leptospira interrogans* in Norway rats (*Rattus norvegicus*) in ecologically distinct urban environments. *Frontiers in Ecology and Evolution*, **7**, 14.

Lee MJ\*, **Byers KA**, Donovan C\*, Zabek E, Stephen C. Patrick DM, Himsworth CG (2018) Methicillin-resistant *Staphylococcus aureus* in urban Norway rat (*Rattus norvegicus*)

- populations: Epidemiology and the impacts of kill-trapping. *Zoonoses and Public Health*, **66**, 343-348.
- Murray MH, Fyffe R, Fidino M, **Byers KA**, Rios MJ, Mulligan MP, Magle SB (2018) Public complaints reflect rat relative abundance across diverse urban neighbourhoods. *Frontiers in Ecology and Evolution*, **6**, 189.
- Lam R\*, **Byers KA**, Himsworth C (2018) Beyond zoonosis: The mental health impacts of rat exposure on inner-city residents. *Journal of Environmental Health*, **84**, 8-12.
- Combs M, **Byers KA**, Ghersi BM, Blum MJ, Caccone A, Costa F, Himsworth CG, Richardson JL, Munshi-South J (2018) Urban rat races: Spatial population genomics of brown rats (*Rattus norvegicus*) compared across multiple cities. *Proceedings of The Royal Society B*, **285**, 20180245.
- Donovan CM\*, Lee MJ\*, **Byers KA**, Bidulka J, Patrick DM, Himsworth CG (2018) *Leptospira interrogans* shedding in urban rat (*Rattus* spp.) populations -- implications for rat-rat and rat-human transmission. *Journal of Wildlife Diseases*, **54**, 635-637.
- Lee MJ\*, **Byers KA**, Donovan CM\*, Bidulka J, Stephen C, Patrick D, Himsworth CG (2018) Culling increases the odds that urban Norway rats (*Rattus norvegicus*) carry *Leptospira interrogans*. *Emerging Infectious Diseases*, **24**, 356-360.
- Steiner L, **Byers K**, Sharp K, Luba M. 2016. Stepping stones in play: Benefits of risk and nature in childhood development. *Cutting Edge*, **2**, 33-41.