

The evolutionary and ecological factors that shape ectoparasite populations and
communities at multiple scales

by

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Examining Committee Membership

The following served on the examining committee for this thesis. The decision of the Examining Committee is by majority vote.

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Statement of Contributions

Alexandra Sauk was the sole author for Chapters 1 and 5, which were written under the supervision of Dr. Hugh Broders and not intended for publication.

This thesis consists of three (3) manuscripts which are being prepared for publication. As lead author of these manuscripts, I contributed to conceiving study designs, carrying out data analysis, and drafting manuscripts.

Throughout the manuscripts I use the pronoun “we” instead of I to reflect the collaborative nature of the work.

Abstract

Although parasites are one of the most prolific and diverse consumer groups on the planet, they are often excluded from biodiversity surveys as they are difficult to detect and identify. This deficit limits our understanding of host-parasite relationships and parasite diversity. The vast diversity of host-parasite relationships means that many ecological and evolutionary forces may be at play, shaping the evolution of host and parasite in different ways and varying between species pairs. Bats and their ectoparasites provide a unique system to study the factors influencing parasite populations and communities. The different ecological niches and social behaviours of bats provide variation in the ectoparasites they encounter, and the selective forces experienced by the ectoparasites. I hypothesised that certain attributes of ectoparasite infections (*e.g.*, ectoparasite diversity and infection level) are influenced by the life history traits of both host and ectoparasite and be the environmental restrictions of individual ectoparasite species. Using a collection of ectoparasites passively collected from bats throughout Atlantic Canada between 1999 and 2017, I quantified the ectoparasite communities of two bat species, *Myotis lucifugus* and *M. septentrionalis*, and used model-based inferences to assess the differences in infection of their two most common ectoparasites, the mite *Spinturnix americanus* and the flea *Myodopsylla insignis*. I found that both bat species had similar ectoparasite communities while *S. americanus* and *M. insignis* showed opposing trends in presence and abundance between the two bat species, in keeping with their different life history strategies. I also used a subset of this collection to compare how life history traits and host-parasite dynamics influence the genetic structure and biogeography of co-infecting ectoparasites. I found limited genetic structure with *M. insignis* exhibiting some isolation by distance between Labrador and Nova Scotia and *S. americanus* exhibiting regional differentiation between the island of Newfoundland and the mainland. I also provide a synthesis of the currently described bat ectoparasites in North America

and an analysis of how host characteristics and environmental factors influence ectoparasite richness and geographic distribution. I found that estimated ectoparasite richness varies widely between host species but is influenced by sampling effort. Bat ectoparasite diversity appears consistent with the predictions of the latitudinal diversity hypothesis with a 3.4% decrease in species richness for every degree increase in latitude. Overall, my findings add to the evidence that ectoparasite populations and communities are shaped by life history traits of the host and ectoparasite. I suggest multidisciplinary collaborations between bat biologists, parasitologists, and taxonomists are necessary to collect ectoparasites and catalogue bat-ectoparasite associations to better understand the ecological and evolutionary forces that shape these communities and to better be able to conserve them in the face of ongoing threats from climate change and landscape changes.

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Land Acknowledgement

In ecology we strive to understand how the creatures we share this planet with live and interact with each other and ourselves, in part to understand how to steward wild spaces and conserve species. I would be remiss to do so without acknowledging the original stewards of Turtle Island where the work for this thesis took place. I respectfully acknowledge that:

Kitchener Waterloo, where I live and work, is situated on the Haldimand Tract, the 6 miles of land on both sides of the Grand River that was granted to Haudenosaunee of the Six Nations of the Grand River, and within the territory of the Neutral, Anishinaabe, and Haudenosaunee peoples.

The ectoparasite collection that much of my work is based on comes from work that was carried out in Atlantic Canada on the traditional land of many Indigenous peoples. The island of Newfoundland (Ktaqmkuk) is the ancestral homelands of the Mi'kma'ki and Beothuk peoples. Labrador is the ancestral home of the Inuit Nunangat, Nunatsiavut, Nitassinan (Innu) and Nuntukavut peoples. Nova Scotia, New Brunswick, and Prince Edward Island are the ancestral territories of the Mi'kma'ki and Wabanki peoples. New Brunswick is also the ancestral home of the Wolastoqiyik peoples.

The literature used in the review of my fourth chapter is from work that was carried out across North America/Turtle Island and I acknowledge that this work was carried out on the ancestral homeland for many Indigenous, Metis, and Innu peoples.

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List of Abbreviations

AICc	Conditional Akaike's Information Criterion
AMOVA	analysis of molecular variance
ANCA	<i>Androlaelaps casalis</i>
BOLD	Barcode of Life Database
CCDB	Canadian Centre for DNA Barcoding
CIAD	<i>Cimex adjunctus</i>
COI	cytochrome oxidase I subunit c
DNA	deoxyribonucleic acid
<i>e.g.</i>	for example
GDM	generalized dissimilarity modelling
GLM	generalized linear model
GLMM	generalized linear mixed model
HVII	hypervariable region II
I	mean intensity of infection
<i>i.e.</i>	that is
IUCN	International Union for Conservation of Nature
LEMY	<i>Leptotrombidium myotis</i>
MACR	<i>Macronyssus crosbyi</i>
MRM	multiple regression on distance matrices
mtDNA	mitochondrial deoxyribonucleic acid
MYIN	<i>Myodopsylla insignis</i>
NCBI	National Center for Biotechnology Information
NFLD	Newfoundland and Labrador
no.	number of
NS	Nova Scotia
ORCA	<i>Orchopeas caedens</i>
P	prevalence of infection
PCR	polymerase chain reaction
SD	standard deviation
SE	standard error
<i>sp.</i>	pertaining to multiple species
SPAM	<i>Spinturnix americanus</i>
USA	United States of America
WNS	white nose syndrome

List of symbols

%	percent
*	significant
<	less than
>	greater than
±	plus or minus
≤	less than or equal to
≥	greater than or equal to
=	equal to
≈	approximately
°	degree (as in degrees Celsius or degrees latitude)
ΔAICc	differences in Conditional Akaike's Information Criterion Value
C	Celsius
<i>D</i>	Simpson's Diversity Index (Chapter 2)
<i>D</i>	test statistic of Tajima's <i>D</i> (test of neutrality, Chapter 3)
<i>D</i> *	test statistic of Fu and Li's <i>D</i> * (test of neutrality)
df	degrees of freedom
<i>F</i> *	test statistic of Fu and Li's <i>F</i> * (test of neutrality)
<i>F</i> _{ST}	fixation index (measure of population differentiation due to genetic structure)
<i>H</i> '	Shannon Diversity Index
<i>J</i>	Pielou's Evenness
<i>km</i>	kilometers
<i>p</i>	<i>p</i> value (probability of obtaining test result given a specific hypothesis)
<i>r</i>	test statistic for Mantel test
<i>R</i> ²	coefficient of determination (R squared)
<i>S</i>	species richness
<i>t</i>	test statistics for Student's <i>t</i> test
<i>w_i</i>	Akaike weight
<i>β</i>	beta
Φ _{CT}	phi statistic region-total, population differentiation statistics from AMOVA
Φ _{SC}	phi statistic samples-region, population differentiation statistics from AMOVA
Φ _{ST}	phi statistic samples-total, population differentiation statistics from AMOVA

Quote

“From Lankaster to Lorenz, scientists have gotten it wrong. Parasites are complex, highly adapted creatures that are at the heart of the story of life. If there hadn't been such high walls dividing scientists who study life - the zoologists, the immunologists, the mathematical biologists, the ecologists - parasites might have been recognized sooner as not disgusting, or at least not merely disgusting. If parasites were so feeble, so lazy, how was it that they could manage to live inside every free-living species and infect billions of people? How could they change with time so that medicines that could once treat them became useless? How could parasites defy vaccines, which could corral brutal killers like smallpox and polio?”

— **Carl Zimmer, *Parasite Rex: Inside the Bizarre World of Nature's Most Dangerous Creatures***

Chapter 1: General Introduction

1.1 Host-parasite relationships

Parasites are organisms that harm or live at the expense of another organism without outright killing the host (Roberts et al., 2012). Together the host and parasite form a symbiosis with parasites dependent on their hosts for survival, with needs ranging from nutrition and shelter (Prendergast and Jensen, 2011; Froeschke et al., 2013; Krasnov and Poulin, 2015) to initiating reproduction (Rothschild and Ford, 1973). The variation in life history strategies and lifestyles of parasites influences the duration of the symbiosis and its effects on the host. When hosts are otherwise in good health and have a low parasite burden, the effect of parasitic infection may be minimal (Johnson et al., 2008; Prendergast and Jensen, 2011; Carlson et al., 2017; Taggart et al., 2018). Infections with coevolved parasites can prime the host immune system, providing the host an advantage over conspecifics without parasites when they encounter new parasites or allergens (Van Oers et al., 2002; Stringer and Linklater, 2014; Maizels and McSorley, 2016; Spencer and Zuk, 2016). Conversely, if a host is malnourished or experiencing a high level of infection, the health consequences can be significant (Crompton and Nesheim, 1982; Pence and Ueckermann, 2002). Hosts often experience changes to energy budgets, mechanical injury, inflammatory or immune responses, or nutrient loss because of parasite infection (Giorgi et al., 2001; Iwanowicz, 2011; Roberts et al., 2012a; Froeschke et al., 2013; Knutie, 2020). The antagonistic nature of the relationship between parasites and hosts has led to an evolutionary arms race affecting the life history traits, behaviour, and physiology of both parties (Appelgren et al., 2018; Meyer et al., 2022).

1.2 Parasite Evolution

1.2.1 Evolutionary history of parasites

Untangling the evolutionary history of parasitic groups can be difficult and relies on many lines of evidence based on mostly extant species (Nava et al., 2009). Many parasites have sparse fossil records due to many factors, such as their small size, soft bodies, and the amount of time spent in a host or vector (Dittmar, 2009; De Baets and Littlewood, 2015). Niches that parasites occupy on hosts (e.g., fur, feathers, and gastrointestinal tracts) are often not well preserved and soft-bodied endoparasites in particular are unlikely to be conserved (Dittmar, 2009). The lack of fossil evidence limits our information on the morphology and lifestyle of intermediate stages between free-living ancestors and extant parasitic organisms (Dittmar, Morse, et al., 2015; Dittmar, Zhu, et al., 2015; Dowling, 2015). Some individuals from extinct lineages have been preserved in fossilized amber, including fleas (Beaucournu and Wunderlich, 2001; Perrichot et al., 2012; Dittmar, Zhu, et al., 2015) and bat flies (Poinar and Brown, 2012; Dittmar, Morse, et al., 2015), and can provide some insight into the evolution of these groups. Amber fossils can also provide insight into the ecology and host-parasite relationships of parasites past when they are preserved with their hosts, such as with nematodes and their host insect (Luo et al., 2023). The ever-increasing sophistication of molecular techniques and DNA sequencing in combination with fossilized parasites has allowed for the analysis of ancient DNA and the ability to calibrate molecular clocks more accurately (Dittmar, 2009; De Baets and Littlewood, 2015). The combination of old evidence and new techniques can provide insight into parasite evolution.

1.2.2 Convergent evolution

Contemporary parasites possess both morphological and life history traits that make them effective parasites, many of which are convergent between distant parasite lineages. The immense selection pressure experienced by parasites to reproduce and avoid detection by the host has resulted in the convergent evolution of the many eukaryotic parasitic lineages towards six general parasitic strategies (Table 1.1; reviewed in Poulin and Randhawa (2015)). This convergent evolution has led to similar modes of transmission between hosts, methods for invading the host, and defense mechanisms for survival (Poulin and Randhawa, 2015). Many parasitic lineages have simplified morphologically or undergone genomic reductions while also evolving new means of sensing, attaching to, and feeding from hosts (Haag et al., 2014; Poulin and Randhawa, 2015; Slyusarev et al., 2020; Guo et al., 2022). The convergent evolution of different parasitic lineages to similar present-day morphologies, lifestyles, and life histories, suggests that these shared traits represent the adaptive optima for parasitism.

Table 1.1: Convergent parasitic lifestyles (summarized from Poulin and Randhawa (2015))

Phenotype	Description
Parasitoids	Early development stages occur within the host, with the parasite growing to relatively large sizes. The parasite almost inevitably kills the host when they emerge from the host. Parasitoids usually occur at low prevalence and low mean intensity, allowing for sustainable exploitation. Parasitoid wasps may be the most well-known of this group and new species continue to be discovered (Reséndiz-Flores et al., 2014; Alvarado, 2020; Fagan-Jeffries and Austin, 2021).
Parasitic castrators	In early stages of infection, parasites suppress host reproduction and use the hosts resources for its own reproduction. Like parasitoids, they have relatively large body sizes and persist at low prevalence and intensity in the host population. Parasitic castrators include barnacle and isopod parasites of crustaceans and fish (Fogelman et al., 2009; Lafferty and Kuris, 2009).
Directly transmitted parasites	Parasites require a single host individual per generation. Parasites in this category are diverse in terms of invasion method and pathology. These parasites often exhibit aggregated distributions within the host population, with a few hosts harbouring the majority. Taxa of directly transmitted parasites are diverse and include lice (Villa et al., 2019; Vanstreels et al., 2020), mites (Bruyndonckx, Dubey, et al., 2009), and monogeneans (MacKenzie and Abaunza, 2013).
Trophically transmitted parasites	Parasites require two or more host species to complete their life cycle, with maturation and reproduction occurring in the final, definitive host. Parasites are acquired by the definitive host when it consumes the intermediate host and the parasites it contains. Trophically transmitted parasites exhibit an aggregated distribution within the host population. Trophically transmitted parasites include cestode tapeworms (O'Neal et al., 2012; Kuchta et al., 2018) and trematodes (Greiman et al., 2016).
Vector transmitted parasites	Parasites require two hosts to complete their life cycle which includes an intermediate micropredator invertebrate host, such as a mosquito, that acts as a vector for transmission to the definitive, vertebrate host. Vectors may pass the parasite onto the definitive host at a bite site through their saliva or feces. Vector transmitted parasites are small and potentially highly virulent as they replicate within the definitive host. Vector transmitted parasites include many of global health concern, including <i>Plasmodium spp.</i> , <i>Trypanosoma cruzi</i> and <i>Leishmania spp.</i> that are responsible for Malaria, Chagas disease, and Leishmaniasis, respectively (Matthews, 2011).
Micropredators	Micropredators use an indeterminate number of hosts per generation, from a potentially wide host range. Each brief interaction with a host lasts from seconds to days, followed by time off host for moulting or laying eggs. Direct impact on the host from feeding is generally minimal but the transmission of virulent pathogens during feeding can have severe consequences for the host. Micropredators include mosquitoes (Yaro et al., 2012; Abella-Medrano et al., 2018), biting midges (Leavell et al., 2022), and ticks (Eisen and Eisen, 2018; Occi et al., 2022).

1.3 Parasite Diversity

1.3.1 Metazoan parasite diversity

Parasites are organisms that harm or live at the expense of another organism (the host) without outright killing the other, except in the case of parasitoids (Roberts et al., 2012b). Metazoan parasites are those that fall within the animal kingdom and are diverse in terms of their taxonomy, morphology, and ecology, spanning many phylogenetic lineages. The parasitic lifestyle has evolved independently at least 223 times in 15 animal phyla (Weinstein and Kuris, 2016). Parasites are estimated to account for at least half of animal species (Windsor, 1998; De Meeûs and Renaud, 2002; Weinstein and Kuris, 2016; Carlson et al., 2020). Weinstein and Kuris, (2016) found that 90% of parasitic animal species belong to the 10 largest parasitic clades, which themselves account for about 40% of animal species. Parasites are well represented within three of the four hyper diverse insect orders including Hymenoptera, Coleoptera, and Diptera, the latter of which has at least 60 independent transitions to parasitism (Weinstein and Kuris, 2016). Mites (Acari) also experienced at least 31 independent transitions to parasitism (Weinstein and Kuris, 2016). Beyond the arthropods, the Nematoda, Platyhelminthes, Mollusca, and Annelida also contain a diverse parasite fauna, each with at least 9 transitions to parasitism. Of course, some animal lineages have very few or no parasitic branches (Weinstein and Kuris, 2016), suggesting that the free-living ancestors were not predisposed to evolving parasitism or the lifestyle was not advantageous in those lineages.

1.3.2 Factors influencing parasite diversity

While parasites may have largely converged on six overarching phenotypes (Poulin and Randhawa, 2015), the factors influencing parasite species richness and diversity are varied and with sometimes opposite effects on different host-parasite systems. Mammals largely follow the

latitudinal diversity hypothesis with increasing diversity at lower latitudes (Kaufman and Willig, 1998; Mittelbach et al., 2007) which is mirrored in some taxa parasitizing mammals, such as protozoans infecting primates (Nunn et al., 2005), but not others, such as fleas of small mammals or helminths of primates (Krasnov et al., 2004; Nunn et al., 2005). The determinants of parasite species richness are rooted in both ecology and epidemiology. For example, mammals with large range sizes may experience more opportunities for encountering parasites, correlating with higher micro- and macroparasite species richness (ecology), but if the large range size is associated with lower host density, the transmission of parasites may be lower (epidemiology) (Bordes et al., 2009; Morand, 2015). Parasitism may support diversification of lineages through co-speciation of hosts and parasites (Krasnov and Poulin, 2015; Jezkova and Wiens, 2017) and niche partitioning on hosts which can lead to the evolution of parasites specialized to specific areas of the host (Feder and Forbes, 2010; Stefan et al., 2015; Jezkova and Wiens, 2017). For example, feather lice exhibit phenotypic matching with their hosts, having adapted to sizes that allow them to avoid detection or damage during preening (Bush and Clayton, 2006). The parasitic diversity seen in wildlife populations are likely a result of interactions between parasite and host life history traits (e.g., growth, survival, reproduction) that are mediated by evolutionary and ecological forces (Morand, 2015).

1.3.3 Factors affecting ectoparasites

Parasite communities are influenced by both abiotic and biotic factors (Wilson et al., 2001). The magnitude of the effect of abiotic factors on parasites varies between parasite lifestyles. The influence of abiotic factors may be greater for parasites that are exposed to the environment for periods of time, including temporary ectoparasites and parasites with free-living stages, than those that live permanently on their hosts (Moyer et al., 2002; Benoit and Denlinger,

2010; Froeschke et al., 2013; Brunner and Eizaguirre, 2016; Wu et al., 2019). Ectoparasites that are exposed to seasonal fluctuations in environmental conditions may experience corresponding fluctuations in abundance and burdens on their hosts. For example, development times for arthropod ectoparasites can be reduced during periods of higher temperatures but this may also be associated with a greater risk of desiccation and mortality if combined with low humidity (Marshall, 1982a; Benoit and Denlinger, 2010). As well, some micropredators, such as *Anopheles gambiae* mosquitoes, experience reproductive depression during dry seasons (Yaro et al., 2012).

The diversity and abundance of ectoparasites on a host are affected by host characteristics such as size, sex, and immunocompetence (Cox and John-Alder, 2007; Fagir et al., 2015; Webber, McGuire, et al., 2015). Larger hosts may experience a greater ectoparasite burden due to the greater supply of resources they provide which can result in sex biased parasitism in sexually dimorphic host species (Krasnov et al., 2005; Froeschke et al., 2013). The relationship between host sex, host size, and ectoparasite burden is complex and can vary across species (Presley and Willig, 2008; Kiffner et al., 2013; Kiffner et al., 2014). Sexes may experience differential exposure to parasites or have different levels of immunocompetence, resulting in sex biased rates of parasitism (Kowalski et al., 2015). For example, males of many rodent species have greater home ranges than females, facilitating the interaction with more parasites (Krasnov et al., 2011; Kowalski et al., 2015). Sex differences in parasite infection can also be mediated by hormonal and immunological mechanisms (Klein, 2004).

1.4 Parasite management and conservation

Historically, parasite research has largely focused on parasites of medical or veterinary importance, with little concern for parasite description and conservation (Gómez and Nichols,

2013; Bordes and Morand, 2015; Dougherty et al., 2016; Carlson et al., 2020). When combating severe disease-causing parasites in humans and livestock, eradication has understandably been the goal as several neglected tropical diseases are caused by parasitic worms or microparasites transmitted by insect vectors (Lustigman et al., 2012; Pérez-Molina and Molina, 2018; Hodson, 2023). Recovery programs to save imperiled wildlife species may intentionally or unintentionally eradicate host-specific parasites when efforts are focused on the host alone (Gompper and Williams, 1998). In the absence of disease threats, management and conservation of parasites may provide more benefits in the long run than eradication.

As parasite research has expanded beyond the immediate threats to human health, we have become more aware of ecosystem services provided by parasites and their contributions to global biodiversity (Hudson et al., 2006; Gómez and Nichols, 2013). Parasites play an important role in ecosystems and food webs whereby their consumption and infection of host species, particularly if they modify host behaviour, facilitates the transfer of energy between trophic levels (Dougherty et al., 2016). For example, Sato et al. (2011) found that nematomorph (*Gordionus* spp.) infected grasshoppers and crickets are 20 times more likely to jump into streams, where their biomass can contribute a remarkable 60% of the energy intake of endangered fish populations. Similarly, the tapeworm *Echinococcus granulosus* alters the behaviour of ungulate hosts, making them more susceptible to predation by wolves, potentially aiding efforts to establish reintroduced wolf packs (Lafferty and Kuris, 2014).

The large-scale changes that affect host species, such as climate change, habitat fragmentation and destruction, can also affect parasites (Cizauskas et al., 2017; Bitters et al., 2022; Wood et al., 2023; Trájer and Grmasha, 2024). Co-extinctions are predicted to be the most severe in mutualistic and parasitic interactions (Dunn et al., 2009). Carlson et al. (2017)

estimated that 5-10% of parasite species are committed to extinction by 2077 from climate change related habitat loss alone, with extinctions rates increasing when host extinction is factored in. Ectoparasites are expected to fair disproportionately worse than endoparasites (Carlson et al., 2017). Loss of many parasite species and dramatic range shifts in others resulting in parasite species turnover could have long term effects on host-parasite interactions and co-evolutionary dynamics as well as disease epidemiology (Carlson et al., 2017).

1.5 Bats as a study system

Bats (Chiroptera) are the second most speciose mammal order and inhabit a variety of environments across six continents, making them an exceptional system to study the evolution of host-parasite interactions and the factors that influence them. Bats are diverse in size (Barclay and Brigham, 1991; Taylor et al., 2012; Schmieder et al., 2015; Ulian and Rossi, 2017) and diet choice, having exploited niches from nectarivore and frugivore to insectivore and carnivore (Barclay and Brigham, 1991; Moosman et al., 2012; Clare et al., 2014; Santana and Cheung, 2016; Oelbaum et al., 2019; Gual-Suárez and Medellín, 2021; Oelbaum et al., 2022). Three species have even specialized to feed on the blood of other vertebrates (Arellano-Sota, 1988; Aguiar and Antonini, 2011; Bohmann et al., 2018). Bats exhibit a variety of roosting behaviours, including cave dwelling (Niu et al., 2007; Deleva and Chaverri, 2018), tent-making (Kunz et al., 1994; Herrera-Victoria et al., 2018), and living in anthropogenic structures (Pearce and O'Shea, 2007; Postawa et al., 2014). These different roosting preferences may impose different environmental pressures on ectoparasite communities (Poissant et al., 2010; Postawa et al., 2014). The social behaviour of bats ranges from solitary bats to species that form roost groups of upwards of a million bats (Kerth, 2008; Hristov et al., 2010; Klug and Barclay, 2013). These roost group sizes and their social organization may vary seasonally with reproduction, migration,

and hibernation (Cheng and Lee, 2004; Kerth, 2008; Hristov et al., 2010) and may influence the rate of ectoparasite transmission between individuals and between sexes (Presley, 2012; Webber, McGuire, et al., 2015; Zamora-Mejías, Morales-Malacara, et al., 2020). This variation in form and behaviour of bats provides a suite of factors that can be investigated for their influence on ectoparasite communities.

1.6 Bat ectoparasites

Bats are host to a variety of arthropod ectoparasites (Table 1.2), parasitic organisms that live on the outside of the host, feeding on blood, tissues, or secretions. Many of these bat ectoparasites are poorly understood in terms of their biology and their relationship to their host. Like other host species, bats may experience negative consequences of parasitism (Marshall, 1982a; Giorgi et al., 2001; Godinho et al., 2013). Ectoparasites elicit an energetic cost to their hosts as the bats attempt to remove the ectoparasites through grooming (Giorgi et al., 2001; Godinho et al., 2013) or bats may switch roosts when ectoparasite densities become too high (Ter Hofstede and Fenton, 2005; Bartonička, 2008). Many bat ectoparasites also act as pathogen vectors that can contribute to bats acting as reservoirs for zoonotic diseases (Luis et al., 2013; Brook et al., 2015; Reeves et al., 2016; Szentiványi et al., 2019). Bat flies have even been found to vector the white nose syndrome causing fungus, *Pseudogymnoascus destructans* (Lučan et al., 2016).

Table 1.2: Groups of Insecta and Acari that are ectoparasitic on bats.

Taxa		General information
Insecta	Fleas (Order Siphonaptera, family Ischnopsyllidae)	Adult fleas parasitize bats in the tropics (Seneviratne et al., 2009; R. Frank et al., 2014) through to temperate areas (Czenze and Broders, 2011a; Burazerović et al., 2018) where they inhabit bat roosts.
	Bat bugs (Order Hemiptera, families Cimicidae and Polytidenidae)	Cimicidae are temporary ectoparasites of bats worldwide (Kock et al., 1998; Reeves et al., 2016; Talbot et al., 2016; Burazerović et al., 2018) whereas the Polytidenidae are restricted to the tropics and subtropics (Kock et al., 1998; Esbérard et al., 2005).
	Bat flies (Order Diptera, families Streblidae and Nycteribiidae)*	Bat flies are highly specialized, morphologically diverse ectoparasites that live in the fur or on wing membranes of bats worldwide (Bendjeddou et al., 2017; Szentiványi et al., 2019).
Acari	Mites (Orders Mesostigmata and Trombidiformes, various families)	Mites commonly parasitize bats, including wing membrane parasites in Spinturnicidae (McCoy, 2009; Czenze and Broders, 2011) and the parasitic larvae of mites of Trombiculidae (Seneviratne et al., 2009; Zajkowska et al., 2018).
	Ticks (Order Ixodida, families Argasidae and Ixodidae)	Species of both hard and soft ticks parasitize bats and ticks that feed on bats can be found both tropic and temperate regions (Seneviratne et al., 2009; Sándor et al., 2019).

*Taxonomic and phylogenetic placement of bat flies needs systematic review as Diptera taxonomists have placed them within the family Hippoboscidae while bat researchers continue to use Streblidae and Nycteribiidae (GBIF Taxonomy Backbone)

1.7 Scope of research and research objectives

Parasites are intimately associated with their hosts and host-parasite dynamics often include coevolution that reshapes these host-parasite interactions over time and space, acting as a driver of biodiversity (Okamura et al., 2018). Parasites are often excluded or missed from ecological surveys for the very reasons that make them effective at what they do: they are small, hidden in or on a host, and have patchy distributions (Galloway and Danks, 1991; Okamura et al., 2018). As a result, our understanding of parasite diversity is limited and quite often biased towards larger metazoan parasites, particularly ones of medical, veterinary, and agricultural importance (Bordes and Morand, 2015; Okamura et al., 2018). Understanding what factors influence parasite population and community dynamics is essential for understanding the

evolution of parasites and their relationships with their hosts. Additionally, understanding how environmental factors shape their interactions and distributions is important for predicting how they may change in the face of climate change as many ectoparasites are at risk of extirpation or extinction due to the changing climate (Carlson et al., 2017).

My research aims to expand our understanding of the evolutionary and ecological factors that influence host-parasite interactions and parasite distributions using bats and their ectoparasites as a study system. The objective of my research in Chapter 2 is two-fold. Firstly, I aim to characterize the ectoparasite faunas of two insectivorous bats of the Vespertilionidae family, the little brown myotis (*Myotis lucifugus*) and the northern myotis (*M. septentrionalis*) in Atlantic Canada using a historical collection of ectoparasites found on these bats between 1999 and 2017. Secondly, I use a generalized linear mixed model analysis to determine the host factors influencing infections by the two most common ectoparasites, a wing mite (*Spinturnix americanus*) and a bat flea (*Myodopsylla insignis*). I hypothesize that the two species of bat will share similar ectoparasite faunas due to their shared evolutionary history and geographic overlap whereas the differences in social dynamics and roosting behaviour of the two bat species will influence infection prevalence and intensity of *S. americanus* and *M. insignis* through variation in ectoparasite transmission and maintenance of infections.

In Chapter 3, I analyze the genetic diversity and population structure of *S. americanus* and *M. insignis* in comparison to their host *M. lucifugus*. The objective of this research is to determine how parasite life history traits (permanent vs temporary ectoparasitism) and reproductive strategies (viviparous vs oviparous), in combination with host landscape ecology, influence the genetic structure and biogeography of co-infecting ectoparasites across a regional scale. I predict that *M. insignis* will exhibit greater genetic restructure regionally than *S.*

americanus as the development of immature life stages in the roost limits dispersal to adult fleas. I predict that the genetic structure of *S. americanus* will be reflective of the movement patterns and structure of *M. lucifugus* given the permanent nature of their association. Additionally, I predict that both ectoparasites will exhibit genetic signatures indicating historical population growth, similar to the population expansion seen with *M. lucifugus* following the deglaciation in the region (Burns et al., 2014). This work provides insight into how host-parasite dynamics differ between co-infecting parasites and provides further evidence of movement patterns of *M. lucifugus* in the region.

In Chapter 4, I take a much broader look at bat ectoparasites to examine their associations in Canada, the United States of America, and Mexico. The objective of this review is to determine the current state of knowledge about bat ectoparasites in North America and assess the host and environmental factors that influence ectoparasite richness and distribution. I predict that ectoparasite richness will be consistent with the latitudinal diversity hypothesis (Rohde and Heap, 1998; Poulin, 2004) and ectoparasite richness will be greater at lower latitudes. I also predict that the distributions and range limits of ectoparasite taxa will be limited by their environmental constraints, such as humidity and temperature, as they each have environmental requirements for development (Marshall, 1982b). Without understanding the current state of North American bat ectoparasite research, we cannot take steps to further our discovery of ectoparasites and predict how climate change and habitat loss will affect these species. Additionally, broadening our scope of ectoparasite research will allow for more hypothesis testing of host-parasite dynamics and the evolutionary and ecological forces that shape them.

1.8 Study sites, bat species, and historical collection of ectoparasites

The ectoparasites used in Chapters 2 and 3 of this research were collected as part of long-term monitoring and other research projects of little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) in Atlantic Canada. These two bat species are small, insectivorous members of the Vespertilionidae family (Fenton and Barclay, 1980; Caceres and Barclay, 2000). Bat captures were carried out at both maternity sites, where female bats congregate to have and raise their young during the spring and summer months, and swarming sites where bats from multiple maternity sites and male bats congregate prior to hibernation (Davis and Hitchcock, 1959; Fenton and Barclay, 1980; Anthony et al., 1981; Foster and Kurta, 1999; Broders and Forbes, 2004; Lacki et al., 2009). Locations include anthropogenic structures, such as houses, bat boxes, and mine shafts, and natural caves, flyways within forests and near waterways. Bats were caught in mist nets (Avinet, Dryden, New York, USA) and/or harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and examined visually to determine their species, sex, and age. Ectoparasites were passively sampled from the wings, body, and ears of the bats with some systematic sampling for specific projects (Poissant and Broders, 2008; Czenze and Broders, 2011) and then stored in 70% ethanol and frozen for long term storage. Ectoparasites in this study were collected between 1999 and 2017 from 56 sites across Nova Scotia, New Brunswick, Prince Edward Island, Newfoundland and Labrador.

Chapter 2: Ectoparasite diversity on two sympatric Atlantic Canadian bat species, *Myotis lucifugus* and *M. septentrionalis* (Chiroptera: Vespertilionidae)

2.1 Abstract

Parasites are an abundant and diverse group of organisms that are often excluded from biodiversity surveys, limiting our understanding of host-parasite relationships and parasite diversity. Parasites are dependent on their hosts for survival and parasite populations are at risk if their hosts decline due to disease or habitat loss. The aim of our study was to quantify and compare the ectoparasite communities of two sympatric Atlantic Canadian bat species, *Myotis lucifugus* and *M. septentrionalis*. Ectoparasites were passively collected from bats captured for bat studies throughout Atlantic Canada between 1999 and 2017. The prevalence and mean intensity of infection was calculated for each identified ectoparasite species and generalized linear mixed models were used to assess host differences in infection by the two most abundant ectoparasites. Both bat species were host to five species of ectoparasite with communities dominated by the mite *Spinturnix americanus* and the flea *Myodopsylla insignis*. Despite being the most common ectoparasites of both species, our results suggest that infections of these ectoparasites vary greatly between them with nearly opposite trends in prevalence and abundance. The survival of these ectoparasites following the declines of their hosts due to the spread of the white-nose syndrome causing fungus, *Pseudogymnoascus destructans*, is not yet known. This highlights the importance of monitoring parasites concurrently with focal species for biodiversity conservation and to understand the concurrent ecological consequences to host-parasite dynamics when hosts undergo drastic demographic changes.

2.2 Introduction

Parasites are an evolutionarily successful and diverse group of organisms estimated to account for more than half of extant animals (Bordes and Morand, 2015; Krasnov and Poulin, 2015). Despite this diversity, parasites are often excluded or missed from ecological surveys for the very reasons that make them effective parasites: they are small, hidden in or on a host, and have patchy distributions (Galloway and Danks, 1991; Gómez and Nichols, 2013; Okamura et al., 2018). This paucity of data on parasites means that biodiversity estimates from some ecological surveys may be under representations of actual biodiversity (Galloway and Danks, 1991; Gómez and Nichols, 2013; Bennett et al., 2021). This under representation further limits our understanding of parasite communities and host-parasite relationships, leading to bias towards larger metazoan parasites, particularly ones of medical, veterinary, and agricultural importance (Bordes and Morand, 2015; Okamura et al., 2018). Additionally, understanding what factors influence parasite diversity and communities is essential for understanding the evolution of parasites and the dynamics of host-parasite relationships.

Parasites are dependent on their hosts for nutrition and shelter (Prendergast and Jensen, 2011; Froeschke et al., 2013; Krasnov and Poulin, 2015; Bellay et al., 2020; Zhou et al., 2022) and for some host-parasite relationships, to initiate reproduction (Rothschild and Ford, 1973). Host characteristics such as size, sex, and immunocompetence can influence the diversity and abundance of parasites infecting a host (Poulin and Valtonen, 2001; Cox and John-Alder, 2007; Duneau and Ebert, 2012; Waterman et al., 2014; Fagir et al., 2015; Webber, Czenze, et al., 2015). Behavioural differences between hosts may affect the encounter or transmission rate of parasites. For example, males of many rodent species have greater home ranges than females and travel over larger distances, facilitating interaction with more parasites (Krasnov et al., 2011; Kowalski et al., 2015). Differences in sociality between sexes (Waterman et al., 2014) or

differences in foraging locations (Reimchen and Nosil, 2001) may also explain variation in parasite community composition. Variation in host behaviour in conjunction with environmental factors may also affect ectoparasites as host individuals can choose different nesting and foraging locations with varying microclimates or ecological characteristics (Gómez-Díaz et al., 2008; Mize et al., 2011; Castaño-Vázquez et al., 2022). Temperature and humidity affect when ectoparasite reproduction and development occurs, leading to seasonal or regional variation in ectoparasite abundance and burden on hosts (Marshall, 1982a; Benoit and Denlinger, 2010; Yaro et al., 2012). The influence of abiotic factors may be greater for parasites that are exposed to the environment for extended periods of time than those that live permanently on their hosts, including ectoparasites that feed intermittently or both endo- and ectoparasites with free-living stages (Moyer et al., 2002; Benoit and Denlinger, 2010; Froeschke et al., 2013; Brunner and Eizaguirre, 2016; Wu et al., 2019). The variation among hosts and environments shapes ectoparasite communities and contributes to the aggregated distributions characteristic of parasitic species (Shaw and Dobson, 1995; Poulin, 2007).

One host group with great species diversity and variation in host characteristics and behaviours within and between species is bats (Order: Chiroptera). Ectoparasite assemblages of bats often consist of both insect and acarine ectoparasites and can vary between bat species and location. For example, big brown bats (*Eptesicus fuscus*) in Colorado and little brown myotis (*Myotis lucifugus*) in Manitoba have similar group-living behaviours but were host to different numbers of ectoparasites species (11 species and two species, respectively; (Pearce and O'Shea, 2007; Webber, McGuire, et al., 2015). The different roosting behaviours of bats, including cave-dwelling (Niu et al., 2007; Deleva and Chaverri, 2018), tree-roosting (Vonhof and Barclay, 1996; Boyles and Aubrey, 2006; Kühnert et al., 2016), and living in anthropogenic structures (Pearce

and O'Shea, 2007; Postawa et al., 2014; Kühnert et al., 2016), may impose different environmental selection pressures on ectoparasite communities (Poissant et al., 2010; Postawa et al., 2014). Additionally, social organization differs between bat species and may influence the rate of ectoparasite transmission between individuals and sexes (Czenze and Broders, 2011a; Presley, 2012; Webber, McGuire, et al., 2015).

The little brown myotis (*Myotis lucifugus*) and northern myotis (*Myotis septentrionalis*) are sympatric species of the Vespertilionidae family with large geographic ranges in North America (Fenton and Barclay, 1980; Caceres and Barclay, 2000). Both species are insectivorous and of similar sizes (Fenton and Barclay, 1980; Caceres and Barclay, 2000). Females of both species form maternity colonies during the summer months with males roosting individually or in small groups (Davis and Hitchcock, 1959; Fenton and Barclay, 1980; Anthony et al., 1981; Foster and Kurta, 1999; Broders and Forbes, 2004; Lacki et al., 2009). The roosting behaviours vary between the two species with *M. lucifugus* congregating in larger roost groups with high roost fidelity for a select number of preferred roosts and the smaller groups of *M. septentrionalis* switching to new roosts more frequently (Lewis, 1995; Menzel et al., 2002; Broders and Forbes, 2004; Johnson et al., 2009). Both species of bats roost in trees, however, *M. lucifugus* appears to have a much greater affinity to anthropogenic structures, including houses and bat boxes (Davis and Hitchcock, 1959; Fenton and Barclay, 1980; Foster and Kurta, 1999; Broders and Forbes, 2004; Lacki et al., 2009; Randall et al., 2014).

This study aims to quantify and compare the diversity of ectoparasites infecting *M. lucifugus* and *M. septentrionalis* across Atlantic Canada and assess patterns of infection across hosts and ectoparasite species. This study builds on the previous work by Czenze and Broders (2011) that characterized bat ectoparasite assemblages of *M. lucifugus* and *M. septentrionalis* at

fall swarming sites in Nova Scotia and New Brunswick and expands it across Atlantic Canada for both summer maternity and fall swarming sites. Both *Myotis lucifugus* and *M. septentrionalis* were found with infections of *Spinturnix americanus* (Order: Mesostigmata), *Macronyssus crosbyi* (Order: Mesostigmata), and *Myodopsylla insignis* (Order: Siphonaptera) in Nova Scotia and New Brunswick, with *M. septentrionalis* hosting an additional three ectoparasite species (Czenze and Broders, 2011). Both bat species were also found infected with *Leptotrombidium myotis* (Order: Trombidiformes) at Hayes Cave in Nova Scotia in prior work (Poissant and Broders, 2008).

Hosts with shared evolutionary history are more likely to have parasite species in common from a shared ancestor or possess similar traits that make them susceptible to the same parasites (Poulin, 2007), as such we expect *Myotis lucifugus* and *M. septentrionalis* will have a similar diversity of ectoparasites. *Myotis lucifugus* and *M. septentrionalis* are sympatric species within the monophyletic Nearctic New World *Myotis* clade and are estimated to have shared a common ancestor 6 to 8.5 million years ago (Stadelmann et al., 2007). In contrast, we hypothesize that the differences in roosting dynamics and the level of social aggregation between the two species will affect transmission of ectoparasites and maintenance of infections. We predict that *M. lucifugus* will have higher infection prevalence (percent of examined bats that are infected) and intensity (number of ectoparasite individuals per examined bat) than *M. septentrionalis* due to their greater aggregations and more consistent use of roost sites. Prevalence and mean intensity of infection for both host species will be assessed across their range in Atlantic Canada and related to the biology of the hosts and ectoparasites.

2.3 Methods

2.3.1 Ectoparasite collection and identification

Ectoparasites were collected opportunistically from bats captured in Nova Scotia, New Brunswick, Newfoundland and Labrador, and Prince Edward Island between 1999 and 2017 as part of bat studies in the region. Bats were caught in mist nets (Avinet, Dryden, New York, USA) and/or harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and examined visually to determine their species, sex, and age. Ectoparasites were passively sampled from the wings, body, and ears of the bats. (Poissant and Broders 2008, Czenze and Broders 2011) Visible parasites were collected from the bats when time and resources permitted with priority given to minimizing handling time and stress for the bats. Some systematic ectoparasite sampling was completed for specific projects (Poissant and Broders 2008, Czenze and Broders 2011) but ectoparasite collections were not comprehensive for all bats. Ectoparasites were removed using forceps and stored in 70% ethanol and frozen at -20 C or -80 C for long term storage. Dates during which ectoparasites were collected at each site are included in Supplemental Table 2.1 in Appendix A. Ectoparasites collected and/or identified during work Czenze and Broders (2011), Talbot et al. (2016), and Banerjee et al. (2020) included as part of the larger collection.

In the lab, ectoparasites were examined using microscopy and identified to the lowest taxonomic rank possible using morphological characteristics. *Spinturnix americanus* are one of several mites found on bats in Atlantic Canada (Poissant and Broders, 2008; Czenze and Broders, 2011). *Spinturnix americanus* can be distinguished by the four pairs of legs that are large in relation to their body size and organized radially around the idiosoma (Whitaker, 1982). In comparison, chiggers (Trombiculidae) are only parasitic during their larval stages, possessing only three pairs of legs which are much smaller in relation to their bodies and positioned

anteriorly (Ebeling, 1975; Whitaker, 1982). *Spinturnix americanus* is similar in appearance to *Spinturnix bakeri*, another North American *Spinturnix* mite parasitizing bats, but can be distinguished by the number and placement of setae. *Spinturnix bakeri* possess long posteroventral and anteroventral setae on the leg II and leg III, respectively, the pair of proximal dorsal setae on femora I and II consist of one long and long short setae, and the proximal posterodorsal setae of femora III and IV are long (Rudnik, 1960; Whitaker, 1982). In comparison, *S. americanus* possess tiny ventral setae and proximal dorsal setae of femora I and II, generally giving *S. americanus* a less hairy appearance than *S. bakeri* (Rudnik, 1960; Whitaker, 1982). The flea *Myodopsylla insignis* is a member of the Ischnopsyllidae family which exclusively parasitizes bats (Marshall, 1982; Czenze and Broders, 2011). *Myodopsylla insignis* are identified based on the presence of two genal spines on the front portion of the head instead of the back, a truncate maxilla, the presence of a pronotal comb, and the plate of the anterior portion of the head is wide and smooth – almost appearing translucent under some microscope lighting (Whitaker, 1982). The eastern bat bug *Cimex adjunctus* are the largest ectoparasites collected from bats in Atlantic Canada and are similar in appearance to other *Cimex* species, including the bed bug *C. lectularius*. *Cimex adjunctus* is distinguished from other *Cimex* species in North America by the presence of long, thin bristles at the side of the pronotum that are only slightly serrated at the ends where other species have noticeably serrate bristles (Usinger, 1966). The pronotal bristles of *C. adjunctus* are as long as or longer than the width of the eyes (Whitaker, 1982).

2.3.2 Diversity metrics

Ectoparasite species richness (Spellerberg and Fedor, 2003), Shannon diversity index (H) (Spellerberg and Fedor, 2003), Simpson's diversity index (D) (Simpson, 1949) and Pielou's

evenness (J) (Pielou, 1966) were calculated per host species across Atlantic Canada and within regions. Regions include the provinces of Nova Scotia, Prince Edward Island, and New Brunswick, with Newfoundland and Labrador treated as separate regions as the island of Newfoundland is separated from the mainland of Labrador by the Strait of Belle Isle (minimum width 15 km). All sites and collection dates were grouped within regions for the calculations. Shannon's index and Simpson's index are both measures of diversity; however, the former emphasizes rare species whereas the latter emphasizes common species, providing insight into different interpretations of community composition. Shannon's index typically ranges between 1.5 and 3.5 and rarely exceeding 4.5 for macro-ecological studies (Ortiz-Burgos, 2016) whereas Simpson's diversity ranges between 0 (low diversity) and 1 (high diversity) (Simpson, 1949). Shannon and Simpson's diversity indices were calculated using the "diversity" function in the R package *vegan* (Oksanen et al., 2018) and Pielou's evenness was calculated from the Shannon index divided by the natural logarithm of the number of species. A species accumulation curve was produced to validate species richness estimates for Atlantic Canada using the "specaccum" function in *vegan* (Oksanen et al., 2018). The 'random' accumulation method was used to produce the mean species accumulation curve of the ectoparasite data as per Gotelli and Colwell (Gotelli and Colwell, 2001) and the 'coleman' accumulation method was used to estimate the expected species accumulation curve as per Coleman *et al.*, (Coleman et al., 1982).

2.3.3 Host-parasite associations

A matrix representing ectoparasite species abundance on both *Myotis lucifugus* and *M. septentrionalis* was generated for Atlantic Canada collectively and for each region. The associations between host and ectoparasites were visualized using the R package *circlize* (Gu et al., 2014).

2.3.4 Modelling variation in ectoparasite load

After identifying the ectoparasites infecting *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada, we used generalized linear mixed models (GLMMs) to quantify the extent to which intra- and interspecific variation in ectoparasite load can be explained by differences between hosts. We focussed on the two most common ectoparasites of these bats: the wing mite *Spinturnix americanus* and the bat flea *Myodopsylla insignis*. We separately investigated the factors affecting their prevalence and abundance on *Myotis lucifugus* and *M. septentrionalis* as these two ectoparasites exhibit different relationships with their host. Collection data for *S. americanus* and *M. insignis* were converted to presence/absence data to test for factors affecting presence of infection while counts of fleas or mites per host bat were used to examine factors affecting ectoparasite abundance.

We used GLMMs to assess whether the fixed effects of bat species, sex, and age class influenced mite and flea infections. GLMMs are parametric models suitable for ecological studies where response variables are counts and random effects are needed to account for variation within the data, such as the different collection sites and years included in this study (Bolker et al., 2009; O'Hara and Kotze, 2010). To test for effects on ectoparasite presence, logistic regression models with a binomial distribution were used with presence as a binary response variable (1=infected and 0=uninfected) and the cloglog link function (Horn, 2015; Zamora-Mejías, Morales-Malacara, et al., 2020). To test for effects on ectoparasite abundance, logistic regression models with a Poisson distribution were used with abundance as the response variable and the log-link function (O'Hara and Kotze, 2010; Wood et al., 2020; Zamora-Mejías, Morales-Malacara, et al., 2020).

All bats for which ectoparasite presence/absence, host species, age class, and sex data were available were used to test for effects on presence. A subset of the data, consisting of all

bats with the above criteria that were caught and examined in 2010, were used to test for effects on abundance as more systematic sampling was conducted during this year (Czenze and Broders, 2011b) and abundance data from this year was considered exceptional based on Cook's distance results when diagnostics were done on the global models with the full data set. Highly sampled sites (Rawdon Mine, NS and Salmonier Nature Park, NFLD) were influential (Cook's distance > 1); however, this is due to greater numbers of bats being examined in these locations as part of other studies and this data was not removed. Ectoparasite collections were greatest in 2010 with 877 total ectoparasites collected, with 373 *Myodopsylla insignis* and 451 *Spinturnix americanus* collected

The global model for presence included host species (*M. lucifugus* or *M. septentrionalis*), host sex (female or male), and host age class (adult or juvenile) as fixed effects and site and year as random effects:

$$Presence \approx \beta_1(species) + \beta_2(sex) + \beta_3(age\ class) + (1|site) + (1|year)$$

The global model for abundance included host species, host sex, and host age class as fixed effects and site as a random effect:

$$Abundance \approx \beta_1(species) + \beta_2(sex) + \beta_3(age\ class) + (1|site)$$

Candidate models investigated the effects of host species, sex, and age class separately to test for host effects (Table 2.4 and 2.5). Host species is included to evaluate for differences in infection between *Myotis lucifugus* and *M. septentrionalis* that may be a result of roosting or social differences at the species level (Lewis, 1995; Menzel et al., 2002; Broders and Forbes, 2004; Johnson et al., 2009). Previous work has found variation in infection between adult female, adult male, and young-of-the-year for both species (Czenze and Broders, 2011), as such age class and sex are included to account for this variation and test whether these patterns persist more widely for these host species in Atlantic Canada. To account for spatial variation in bat and ectoparasite

distributions, site is included as a random effect. Year is included as a random effect to account for sampling variation across years for prevalence but not for abundance as only data from 2010 was included in the models for abundance. Twelve *M. lucifugus* individuals had records in two years and both records were included in the dataset. A further seven *M. lucifugus* individuals had two ectoparasite collections within the same year of either *M. insignis*, *S. americanus*, or both, from which one record was chosen randomly to be included in the dataset. Individual was not included as a random effect in either the presence or abundance models to avoid singularities and overfitting (Barr et al., 2013).

GLMMs were fit using the ‘glmer’ function in the package *lme4* (Bates et al., 2015) in R (R Core Team, 2023). Global and candidate models were assessed using AIC_c to account for small sample sizes (Burnham and Anderson, 2002). Model ranking was done using the function ‘model.sel’ from the *MuMIn* package (Bartoń, 2023). Models in the 95% confidence set were averaged using ‘model.avg’ from the package *MuMIn* (Burnham and Anderson, 2002; Bartoń, 2023) and the 95% confidence intervals of the β values were calculated using ‘confint’ (R Core Team, 2023) on the model average, which reports values based on the conditional average.

2.3.5 Infection parameters

Infection parameters of prevalence and mean intensity were calculated for each ectoparasite species as per (Busht et al., 1997). Prevalence is the percentage of hosts infected with a given parasite species divided by the number of hosts examined and mean intensity is the sum of the number of parasites of a given species divided by the number of hosts infected (Busht et al., 1997). Prevalence and mean intensity were calculated for each host species as a whole and for age and sex demographics across regions in Atlantic Canada. Prevalence of each ectoparasite was compared to the number of hosts examined per region as an estimate of sampling effort to

check for correlation (Bell and Burt 1991, Jovani and Tella 2006). Infection parameters and correlation between prevalence and number of hosts were calculated using the “cor.test” function with the Pearson correlation coefficient in the R (R Core Team, 2023) . Relative abundance of each ectoparasite order was calculated as the percentage of total specimens for each order and was calculated for region and host species. Relative abundances were visualized using *ggplot* (Wickham, 2011; R Core Team, 2023).

2.3.6 Ethics approval

All bats were captured and released according to animal care protocols approved by the animal care committees of Saint Mary’s University, Halifax, Nova Scotia and the University of Waterloo, Waterloo Ontario. Wildlife scientific research permits were obtained from the government agencies of the provinces of Nova Scotia, New Brunswick, Prince Edward Island, and Newfoundland and Labrador.

2.4 Results

We collected 2271 ectoparasites from 858 *Myotis lucifugus* and 224 ectoparasites from 111 *Myotis septentrionalis* individuals from 56 sites across Atlantic Canada between 1999 and 2017 (Fig. 2.1). In addition, 582, 28, and 60 specimens were previously identified by Czenze and Broders (2011), Talbot et al. (2016), and Banerjee et al. (2020), respectfully. Most specimens were collected from Newfoundland (1457) and Nova Scotia (1270) as part of long-term studies in these regions while fewer ectoparasites were collected from Labrador (376), New Brunswick (140), and Prince Edward Island (27). Eight species were identified from the collection and 29 specimens too small or damaged for species level identification were identified to order. Mesostigmata and Siphonaptera were the two most collected orders across the two bat species and across Atlantic Canada (Fig. 2.2 A and B). Both the mean species accumulation and

expected species accumulation curves asymptote at eight species (Supplemental Figure 2.1), suggesting that our opportunistic sampling was sufficient to sample the diversity of ectoparasites infecting *M. lucifugus* and *M. septentrionalis*. Previous systemic sampling of the bats in the system produced similar ectoparasite assemblages to the passive sampling at the sites included here and missed ectoparasites are suspected to be rare (Poissant and Broders, 2008; Czenze and Broders, 2011b).

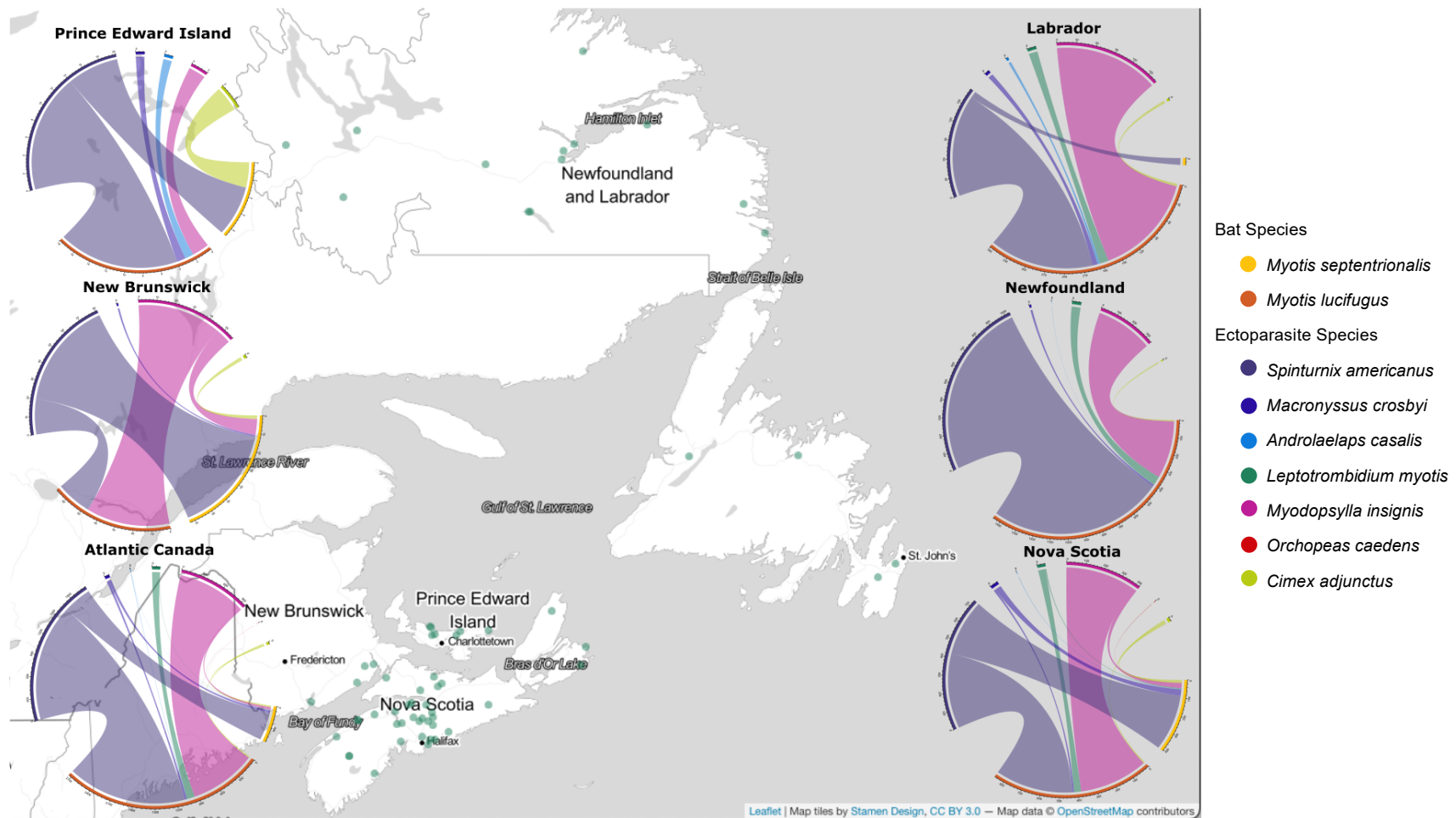


Figure 2.1. Host-parasite associations between *Myotis lucifugus* and *M. septentrionalis* and their ectoparasites in Atlantic Canada. The ectoparasite-bat interactions within each region and Atlantic Canada as a whole are represented by a chord diagram. The perimeter of each chord diagram represents the number of observations of each ectoparasite or bat species (from ectoparasite-bat interactions) with the curved bars illustrating the interactions between species. Green circles on the map indicate collection locations. Map visualized using the package *leaflet* in R with map tiles by Stamen Design (CC BY 3.0) and map data from OpenStreetMap (openstreetmap.org/copyright)

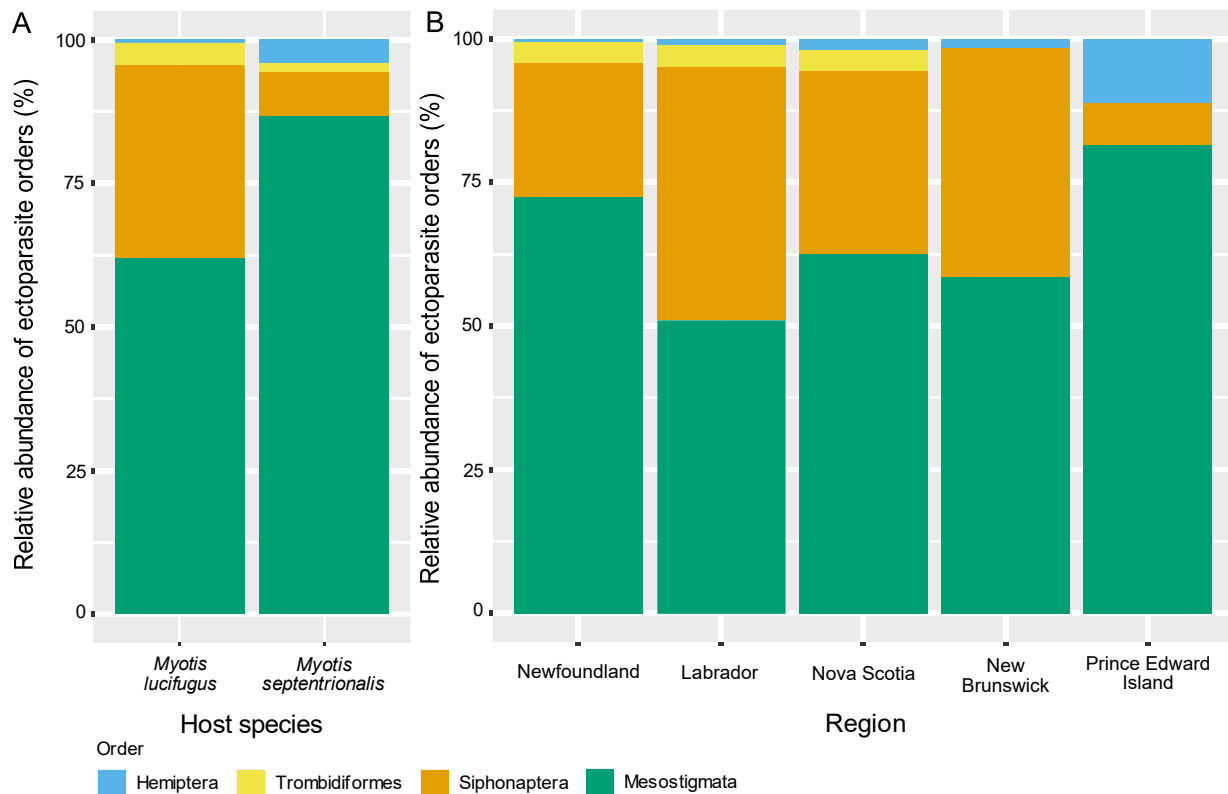


Figure 2.2. Relative abundance (%) of ectoparasite orders collected (A) from hosts *Myotis lucifugus* and *M. septentrionalis* and (B) in the five regions of Atlantic Canada: Newfoundland, Labrador, Nova Scotia, New Brunswick, and Prince Edward Island. Newfoundland and Labrador are treated as separate regions due to their geographic separation and different sampling regimes carried out in the regions. Identified arthropod orders are: Siphonaptera (orange), Hemiptera (blue), Mesostigmata (green), and Trombidiformes (yellow).

2.4.1 Infection parameters

For *Myotis lucifugus*, the wing mite *Spinturnix americanus* and the flea *Myodopsylla insignis* exhibited consistently high prevalence of infection (41.2-79.6% and 16.7-73.9% for *S. americanus* and *M. insignis*, respectively) across regions while prevalence of infection was below 10% for other ectoparasites (Table 2.1). *Spinturnix americanus* and *M. insignis* also showed average infection intensity greater than 1.0 parasite per infected host as did *Leptotrombidium myotis*. For *M. septentrionalis*, *S. americanus* exhibited the highest prevalence and average infection intensity with other ectoparasites either not being present or present at low

numbers (Table 2.2). *Spinturnix americanus* and *M. insignis* were present on males and females of both adult and juvenile *M. lucifugus* and *M. septentrionalis* at varying levels of intensity (Supplemental Tables 2.2-2.5). The prevalence of the ectoparasites is not significantly correlated with the number of hosts sampled for *M. lucifugus* (Supplemental Table 2.6). Three *M. septentrionalis* ectoparasites (*S. americanus*, *C. adjunctus*, and *M. insignis*) show no significant correlation between prevalence and the number of hosts sampled whereas the rarer *A. casalis*, *L. myotis*, *M. crosbyi*, and *O. caedans* show significant positive correlations (≥ 0.98 , $p \leq 0.02$) between the prevalence of these ectoparasites and the number of hosts examined. The correlation between prevalence of the rare ectoparasites and the number of bats examined is expected as rarer species require more effort to detect such that rare ectoparasites may evade detection when it is not possible to examine all bats.

Table 2.1. Prevalence and mean intensity of ectoparasite infections on *Myotis lucifugus* for each region. Number of bats sampled per region is included in brackets beside the region name. The number of infected individuals is included in brackets beside the prevalence values. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*. P = prevalence of infection (%); I = mean intensity of infection (+/- SE).

Ectoparasite	Labrador (113)		Newfoundland (514)		Nova Scotia (403)		New Brunswick (46)		Prince Edward Island (12)	
	P	I	P	I	P	I	P	I	P	I
ANCA	3.5 (4)	1.0 +/- 0.0	0.2 (1)	1.0 +/- 0.0	0	0	0	0	8.3 (1)	1.0 +/- 0.0
CIAD	3.5 (4)	1.0 +/- 0.0	1.0 (5)	1.4 +/- 0.4	1.7 (7)	1.0 +/- 0.0	0	0	0	0
LEMY	6.2 (7)	2.0 +/- 1.0	1.9 (10)	5.3 +/- 2.5	4.5 (18)	2.2 +/- 0.8	0	0	0	0
MACR	6.2 (7)	1.1 +/- 0.1	1.9 (10)	1.2 +/- 0.1	2.0 (8)	1.3 +/- 1.3	0	0	8.3 (1)	1.0 +/- 0.0
MYIN	34.5 (39)	4.3 +/- 1.0	27.6 (142)	2.4 +/- 0.3	42.9 (173)	2.2 +/- 0.2	73.9 (34)	1.4 +/- 0.1	16.7 (2)	1.0 +/- 0.0
SPAM	70.8 (80)	2.1 +/- 0.2	79.6 (409)	2.5 +/- 0.1	60.8 (245)	1.7 +/- 0.1	41.2 (14)	1.4 +/- 0.2	75 (9)	0.6 +/- 0.2

Table 2.2. Prevalence and mean intensity of ectoparasite infections on *Myotis septentrionalis* for each region. Number of bats sampled per region is included in brackets beside the region name. The number of infected individuals is included in brackets beside the prevalence values. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*. P = prevalence of infection (%); I = mean intensity of infection (+/- SE).

Ectoparasite	Labrador (3)		Nova Scotia (208)		New Brunswick (42)		Prince Edward Island (9)	
	P	I	P	I	P	I	P	I
ANCA	0	0	0.5 (1)	2.0 +/- 0.0	0	0	0	0
CIAD	0	0	6.7 (14)	1.1 +/- 0.1	4.8 (2)	1.0 +/- 0.0	33.3 (3)	1.0 +/- 0.0
LEMY	0	0	1.0 (2)	2.5 +/- 1.5	0	0	0	0
MACR	0	0	8.2 (17)	2.1 +/- 0.7	2.4 (1)	1.0 +/- 0.0	0	0
MYIN	0	0	13.0 (27)	1.0 +/- 0.0	21.4 (9)	1.0 +/- 0.0	0	0
ORCA	0	0	1.0 (2)	1.0 +/- 0.0	0	0	0	0
SPAM	100 (3)	3.7 +/- 1.7	80.8 (168)	1.9 +/- 0.1	85.7 (36)	1.7 +/- 0.2	66.7 (6)	1.0 +/- 0.0

2.4.2 Host-parasite associations

The ectoparasite assemblages of *Myotis lucifugus* and *M. septentrionalis* shared six ectoparasite species: *Spinturnix americanus*, *Myodopsylla insignis*, *Macronyssus crosbyi*, *Cimex adjunctus*, *Leptotrombidium myotis*, and *Androlaelaps casalis*, a predatory mite (Fig. 2.1).

Myotis septentrionalis was host to *Orchopeas caedens*, a squirrel flea, for which there was no evidence of its occurrence on *M. lucifugus*. The highest number of host-parasite interactions for both *M. lucifugus* and *M. septentrionalis* occur with *S. americanus* while interactions with *M. insignis* are also common. Interactions with other ectoparasites and *Androlaelaps casalis* and *Orchopeas caedens* are rare. *Orchopeas caedens* was only collected from *M. septentrionalis* at swarming sites while all other ectoparasites were collected at both summer and swarming sites.

2.4.3 Diversity metrics

The ectoparasite assemblages of *M. lucifugus* and *M. septentrionalis* had a species richness of 6 and 7, respectively, across Atlantic Canada, with species richness ranging from 2-6 and 1-6 across regions for *M. lucifugus* and *M. septentrionalis*, respectively (Table 2.3). The Shannon diversity index was low (<1 , except for *M. lucifugus* in Labrador, $H' = 1.025$) for all regions and host species, indicating a low overall diversity of species. The Simpson's diversity index was low to mid range $0.2 < D < 0.6$ for all host species and regions, similarly, indicating low diversity of ectoparasites with slightly greater diversity in Nova Scotia and Labrador on *M. lucifugus*. The Shannon diversity index may help to highlight the rarer and more aggregated ectoparasites whereas the Simpson's diversity index may be more reflective of host-parasite associations at a population level as it emphasizes more common species and the evenness of species (Morris et al., 2014). The ectoparasite assemblages exhibited mid-range values for Pielou's evenness, ranging between $0.408 < J < 0.585$ for all regions and host species except for

New Brunswick for *M. lucifugus* and Prince Edward Island for *M. septentrionalis* which may be an artifact of low ectoparasite species richness ($S=2$) and sample sizes.

Table 2.3. Diversity metrics for ectoparasite communities of *Myotis lucifugus* and *Myotis septentrionalis*. S = species richness; H' = Shannon-Weiner diversity index; J = Pielou's evenness; and D = Simpson's diversity index.

Region	<i>Myotis lucifugus</i>				<i>Myotis septentrionalis</i>			
	S	H'	J	D	S	H'	J	D
Atlantic Canada	6	0.895	0.499	0.521	7	0.792	0.407	0.359
Newfoundland	6	0.773	0.431	0.433	NA	NA	NA	NA
Labrador	6	1.025	0.572	0.577	1	0	NA	0
New Brunswick	2	0.609	0.879	0.419	4	0.565	0.408	0.286
Nova Scotia	5	0.942	0.585	0.559	6	0.796	0.444	0.367
Prince Edward Island	4	0.761	0.549	0.377	2	0.637	0.918	0.444

2.4.4 Modelling variation in ectoparasite load

The modelling dataset included 980 *Myotis lucifugus*, of which 12 individuals had two records, and 195 *M. septentrionalis*. Two records of *M. lucifugus* were included for individuals where recaptures occurred in different years. Through model selection using AICc it was determined that the global model best explained mite presence and abundance ($w = 0.77$ and $w = 0.82$, respectively, Table 2.4). For the fleas, the global model best explained presence ($w = 0.53$) whereas the model that included host species and age class (model 1) best explained flea abundance ($w = 0.54$, Table 2.5). Model-averaged parameter estimates were calculated for the models in the 95% confidence set and suggested that host species and host age class explained the most variation in mite and flea infection as the 95% CIs did not cross 0 (Tables 2.4 and 2.5). Variation from the random effects of site and year on bat infestation by mites and fleas was <1 for all top models except for year for flea presence (mean = 1.67 ± 1.29 SD) suggesting limited variability between individuals is accounted for by the random effects.

Table 2.4: Models explaining the presence and abundance of *Spinturnix americanus* infections on *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada between 1999 and 2017. Models in the 95% confidence set are highlighted. K = number of parameters; AICc = Akaike Information Criterion for small sample sizes; ω_i = Akaike weight; $\Sigma\omega_i$ = sum of Akaike weights.

Model		K	AICc	Δ AIC	ω_i	$\Sigma\omega_i$
<i>Presence</i>						
Global Model	age class + species + sex + (1 site) + (1 year)	7	1235.6	0	0.77	0.77
Model 1	age class + species + (1 site) + (1 year)	6	1238.1	2.48	0.22	1.00
Model 2	species + (1 site) + (1 year)	5	1247.0	11.31	0	
Model 3	age class + (1 site) + (1 year)	5	1256.4	20.77	0	
Null	1 + (1 site) + (1 year)	5	1267.4	31.76	0	
Model 4	sex + (1 site) + (1 year)	5	12.69.3	33.64		
<i>Abundance</i>						
Global Model	age class + species + sex + (1 site)	5	749.9	0	0.82	0.82
Model 1	age class + species + (1 site)	4	753.3	3.43	0.15	0.96
Model 2	species + (1 site)	3	756.1	6.23	0.04	1.00
Model 3	age class + (1 site)	3	774.0	24.16	0	
Model 4	sex + (1 site)	3	778.9	29.01	0	
Null	1 + (1 site)	2	779.2	29.34	0	

Table 2.5. Models explaining the presence and abundance of *Myodopsylla insignis* infections on *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada between 1999 and 2017. Models in the 95% confidence set are highlighted. K = number of parameters; AICc = Akaike Information Criterion for small sample sizes; ω_i = Akaike weight; $\Sigma\omega_i$ = sum of Akaike weights.

Model		K	AICc	Δ AIC	w_i	$\Sigma\omega_i$
<i>Presence</i>						
Global Model	age class + species + sex + (1 site) + (1 year)	7	1186.1	0	0.53	0.52
Model 1	age class + species + (1 site) + (1 year)	6	1186.3	0.20	0.47	1.00
Model 2	species + (1 site) + (1 year)	5	1196.5	10.43	0	
Model 3	age class + (1 site) + (1 year)	5	1237.5	51.47	0	
Null	1 + (1 site) + (1 year)	5	1252.0	65.96	0	
Model 4	sex + (1 site) + (1 year)	5	1253.8	67.78	0	
<i>Abundance</i>						
Model 1	age class + species + (1 site)	4	647.4	0	0.54	0.54
Global Model	age class + species + sex + (1 site)	5	648.7	1.29	0.28	0.82
Model 2	species + (1 site)	3	649.2	2.20	0.18	1.00
Model 3	age class + (1 site)	3	723.7	76.30	0	
Null	1 + (1 site)	2	730.8	83.36	0	
Model 4	sex + (1 site)	3	730.9	83.49	0	

The effects of host characteristics were opposite for the two ectoparasites when interpreting the beta coefficients. *Spinturnix americanus* were 90% more likely to be infecting *M. septentrionalis* relative to *M. lucifugus*, with 89% more abundant infections on *M. septentrionalis* ($\beta = 0.640 \pm 0.140$ SE and $\beta = 0.638 \pm 0.131$ SE, respectively, Table 2.6). In contrast, *M. insignis* was 79% less likely to be present on *M. septentrionalis* relative to *M. lucifugus*, with 82% lower abundance ($\beta = -1.570 \pm 0.240$ SE and $\beta = -1.734 \pm 0.230$ SE, respectively, Table 2.7). For age demographics, *S. americanus* were 46% more likely to be present on juveniles relative to adults, with a 38% greater abundance, whereas *M. insignis* were 41% less likely to be present on juveniles, with 30% lower abundance. Sex was a significant determinant of infection for *S. americanus*, with males exhibiting a weak negative relationship relative to females, with males being 20% less likely to be infected than females, with 26% lower abundance. Sex was not a significant parameter for *M. insignis* as the 95% CI crossed 0 for flea prevalence and infection. These results suggest that *M. septentrionalis* individuals less likely to be infected with fleas and exhibit less abundant flea infections than *M. lucifugus* but more likely to be infected with mites.

Table 2.6. Model averaged parameter estimates, standard errors, and the 95% confidence interval for variables affecting presence and abundance of *Spinturnix americanus* infections on *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada between 1999 and 2017. Adult, female *M. lucifugus* were the reference category.

Metric	Parameter	Estimate	Standard Error	Lower CI	Upper CI
<i>Presence</i>	juvenile	0.375	0.105	0.168	0.582
	male	-0.226	0.107	-0.435	-0.016
	septentrionalis	0.640	0.140	0.365	0.915
	intercept	-0.308	0.294	-0.884	0.268
<i>Abundance</i>	juvenile	0.324	0.129	0.070	0.577
	male	-0.295	0.127	-0.544	-0.046
	septentrionalis	0.638	0.131	0.381	0.896
	intercept	-0.311	0.138	-0.582	-0.039

Table 2.7. Model averaged parameter estimates, standard errors, and the 95% confidence interval for variables affecting presence and abundance of *Myodopsylla insignis* infections on *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada between 1999 and 2017. Adult, female *M. lucifugus* were the reference category.

Metric	Parameter	Estimate	Standard Error	Lower CI	Upper CI
<i>Presence</i>	juvenile	-0.528	0.155	-0.833	-0.223
	male	0.229	0.153	-0.071	0.529
	septentrionalis	-1.570	0.240	-2.040	-1.099
	intercept	-1.370	0.416	-2.187	-0.554
<i>Abundance</i>	juvenile	-0.363	0.231	-0.719	-0.008
	male	-0.129	0.145	-0.414	0.157
	septentrionalis	-1.734	0.230	-2.187	-1.282
	intercept	0.057	0.231	-0.398	0.511

2.5 Discussion

The bat ectoparasite assemblages in Atlantic Canada consisted of six species for the little brown myotis and seven species for the northern myotis. Assemblages for both were dominated by mites (Mesostigmata) and fleas (Siphonaptera), particularly the wing mite *Spinturnix americanus* and the bat flea *Myodopsylla insignis*. Parasites often exhibit aggregated distributions (Poulin, 2007), and this is especially evident in the rare ectoparasites of *M. lucifugus* and *M. septentrionalis*, particularly for the chigger mite *Leptotrombidium myotis* which was abundant on a select number of bats. The ectoparasite assemblages found across Atlantic Canada are consistent with those previously found at swarming sites (Poissant and Broders, 2008; Czenze and Broders, 2011). These assemblages are more species rich than assemblages on *M. lucifugus* in Manitoba for which there was only evidence of infection with *S. americanus* and *M. insignis* (Webber, McGuire, et al., 2015) but lower than that seen for other bat species in the central U.S.A. (Pearce and O'Shea, 2007; Schumann, 2019). The family level ectoparasite assemblage composition in Atlantic Canada is similar to temperate bats in Europe, however,

European bats can also be infected with ticks (Argasidae and Ixodidae) and bat flies (Nycteribiidae) (Zahn and Rupp, 2004; McKee et al., 2016; Sándor et al., 2019).

The presence and abundance patterns of the two most common ectoparasites, *Myodopsylla insignis* and *Spinturnix americanus*, arise from a combination of ectoparasite and bat life history traits. *Myodopsylla insignis* was found on both bat species at summer and swarming sites suggesting multiple generations are occurring on both species throughout the year, however, it was found at higher prevalence and intensity on *M. lucifugus* than *M. septentrionalis*. Our model analysis found that the northern myotis was 79% less likely to be infected by fleas than the little brown myotis and supports previous reports of *M. lucifugus* as the more compatible host (Smith and Clay, 1988), likely due to the differences in roosting behaviour between the two bat species. Early life stages of *M. insignis* develop within the roost litter and require bats to continue to use the roost for newly emerged adult fleas to find new hosts (Smith and Clay, 1988). This flea life history strategy may be more compatible with the little brown myotis as they congregate in larger groups at maternity colonies and switch roosts less frequently than the northern myotis (Lewis, 1995; Menzel et al., 2002; Broders and Forbes, 2004; Johnson et al., 2009). The differences in social behaviour may mean that *M. lucifugus* is a more stable and reliable food source for *M. insignis*, allowing for the maintenance of larger populations of fleas whereas the more frequent roost switching of the *M. septentrionalis* results in a lower probability of being able to continue their life cycle.

In comparison, *S. americanus* mites are permanent ectoparasites that complete their life cycle attached to the membranes of their host and require direct contact with potential new hosts for transmission (Rudnik, 1960; Christie et al., 2000; Ter Hofstede and Fenton, 2005). *Spinturnix americanus* was found at greater than 60% prevalence for both host species in all regions, except

New Brunswick for *M. lucifugus*, and the modelling results suggest that these mites are 90% more likely to be infecting *M. septentrionalis* than *M. lucifugus*. The life cycle and direct transmission of *S. americanus* may enable the mites to persist regardless of host roosting behaviour, unlike *M. insignis*. The higher density of bats at *M. lucifugus* roosts may allow mites to aggregate on the most susceptible bats, such as juveniles, rather than spreading to the majority of bats in the smaller roost groups of *M. septentrionalis*. *Spinturnix* mites are considered host specific ectoparasites that feed on one or a few closely related host species (Bruyndonckx, Henry, et al., 2009) and *Spinturnix americanus* has been found parasitizing several North American *Myotis* bats (Whitaker and Wilson, 1974), suggesting that they may not have a particular preference for *M. lucifugus* or *M. septentrionalis*, but for *Myotis* bats generally. The presence of *S. americanus* on both *M. lucifugus* and *M. septentrionalis* across Atlantic Canada is consistent with previous investigations in Nova Scotia and New Brunswick (Poissant and Broders, 2008; Czenze and Broders, 2011) and confirms that *S. americanus* is a widespread ectoparasite of *Myotis* bats in Atlantic Canada.

The rare ectoparasite fauna of *M. lucifugus* and *M. septentrionalis* consists of *Cimex adjunctus*, *Leptotrombidium myotis*, and *Macronyssus crosbyi*. Each of these ectoparasites were previously identified from *M. lucifugus* and *M. septentrionalis* by Czenze and Broders (2011) in Nova Scotia and New Brunswick and *C. adjunctus* was identified from Prince Edward Island and Newfoundland and Labrador by Talbot *et al.*, (Talbot et al., 2016). *Cimex adjunctus* and *L. myotis* are both temporary ectoparasites of bats. While *C. adjunctus* is widespread in North America east of the Rocky Mountains (Usinger, 1966; Czenze and Broders, 2011a; Talbot et al., 2016), it is only present on the bats to feed and spends much of its time within the roost. Bats were checked for ectoparasites during netting events at maternity colonies or in flyways and this

may have reduced the likelihood of collecting bat bugs who only occasionally disperse with their hosts (Usinger, 1966). *Leptotrombidium myotis* is parasitic in its larval stage and free-living as adults (Whitaker, 1982). Trombiculid larvae may be able to feed on mammal species other than their primary host but are often restricted to the available hosts in the habitat of adult Trombiculids (Whitaker, 1982; Schumann, 2019). *Leptotrombidium myotis* was collected from the ears of *M. lucifugus* and *M. septentrionalis*, as is typical for this species (Pearce and O'Shea, 2007; Czenze and Broders, 2011). *Macronyssus crosbyi* has previously been identified from *E. fuscus* and several *Myotis* bats throughout North America (Whitaker and Wilson, 1974). Protonymphs of macronyssid mites are often found crawling on the wings of their bat hosts which is consistent with our collection of *M. crosbyi* individuals from the wings *M. lucifugus* and *M. septentrionalis* (Whitaker, 1982).

Our collection also included two species that are unlikely to be direct ectoparasites of these bat species: the predatory mite *Androlaelaps casalis* and the squirrel flea *Orchopeas caedens*. *Androlaelaps casalis* is a predatory mite that feeds on eggs and larval stages of other mites, such as those parasitizing bats and bird nests as well as pests of cereal crops (Barker, 1968; Whitaker and Wilson, 1974). *Androlaelaps casalis* is likely incidental on little brown and northern myotis bats but is a potential predator of *L. myotis* and *M. crosbyi* when present. Similarly, *O. caedens* is likely incidental on *M. septentrionalis* as these bats commonly roost in trees and transmission could occur from the primary squirrel host. *Orchopeas caedans* was previously recorded from squirrels in New Brunswick and in Maine, U.S.A., from the northern flying squirrel (*Glaucomys sabrinus*) (Brown, 1955; Eckerlin and Gardner, 2021).

This historical collection of ectoparasites provides us with a look into past relationships between *M. lucifugus* and *M. septentrionalis* and their arthropod ectoparasites prior to the arrival

the white-nose syndrome (WNS) causing fungus *Pseudogymnoascus destructans* in Atlantic Canada. The fungus was first detected in the United States in 2006 and Canada in 2010 and since then most of the known hibernacula in the northeastern United States and eastern Canada have experienced massive declines (Environment Canada, 2018). Three bat species in Atlantic Canada have been declared endangered as a result of WNS and other factors: the little brown myotis (*M. lucifugus*), the northern myotis (*M. septentrionalis*), and the tri-colored bat (*Perimyotis subflavus*) (Environment Canada, 2018). The declines of these host species can have repercussions for the survival of their ectoparasites as they can experience secondary extirpations when their hosts are removed from the ecosystem (Lafferty, 2012; Wood et al., 2020). Given the host specificity of some of these ectoparasites, it is likely that they also experienced population declines alongside their hosts. Which ectoparasite species may still be persisting in remanent host populations is currently unknown.

2.6 Conclusions

Ectoparasite communities of *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada consist of eight ectoparasites species and are dominated by the mite *Spinturnix americanus* and the flea *Myodopsylla insignis*. Life history traits and behaviours of both the ectoparasites and the hosts influence the host-parasite interactions. The effect of life history traits on host-parasite relationships is apparent with *M. septentrionalis* exhibiting lower infections of *M. insignis*, potentially due to the temporary nature of the flea parasitism and the increased roost switching of *M. septentrionalis*. The permanent nature of the life history of *S. americanus* made it an almost ubiquitous parasite of examined hosts. Both bat species were also host to the predatory mite *Androlaelaps casalis* while *M. septentrionalis* was an incidental host of the squirrel flea *Orchopeas caedens*. Distributions across individual bats appear to be highly aggregated for the

rare species. The secondary effects of the spread of *Pseudogymnoascus destructans* on the bat ectoparasites is currently unknown and highlights the importance of studying the parasites of focal species to understand the complexity of their interactions and create a more complete picture of an area's biodiversity. Future work on remaining or recovering bat populations should include investigations of the ectoparasites to determine if the communities have changed or persisted post-WNS. Habitat management plans should take into consideration the need for bats to switch roosts to avoid high ectoparasite loads. For *M. lucifugus* this could include the provision of alternate roosts, such as bat boxes or rocket boxes, in locations with few maternity roost options whereas for *M. septentrionalis* the protection of mature trees, including standing dead or dying trees, throughout forested areas could provide potential suitable alternate roosts.

Chapter 3: Host-parasite association dynamics influence genetic diversity of co-infecting ectoparasites of the little brown myotis (*Myotis lucifugus*)

3.1 Abstract

Host-parasite dynamics vary between species pairs and these dynamics can affect dispersal and transmission of parasites. *Myodopsylla insignis* (Rothchild, 1903), a bat flea, and *Spinturnix americanus* (Banks, 1902), a bat wing mite, are two common ectoparasites of the little brown myotis (*Myotis lucifugus*, Le Conte 1831) that differ in life cycles and time spent on the host. The goal of this study was to compare how life history traits and host-parasite dynamics influence the genetic structure and biogeography of co-infecting ectoparasites using *Spinturnix americanus* mites and *Myodopsylla insignis* fleas that feed on *Myotis lucifugus* bats. Ectoparasites were collected from bats captured at maternity roosts between 2010 and 2017 in Atlantic Canada and sequenced for cytochrome oxidase c subunit 1. We barcoded 223 *S. americanus* and 87 *M. insignis* specimens, and examined their genetic diversity, genetic structure, and biogeography. We found limited genetic structure with *M. insignis* exhibiting some isolation by distance between Labrador and Nova Scotia and *S. americanus* exhibiting regional differentiation between the island of Newfoundland and the mainland, similar to *M. lucifugus*. There is also evidence to support that *M. insignis* underwent historical population expansion and some evidence that *S. americanus* underwent historical population expansion or selection. Our study highlights how host-parasite relationships are influenced at multiple scales by both host and parasite biology and why an understanding of both host and parasite is necessary for predicting how these dynamics will be affected by disturbances such as climate change, disease and species introductions, and land use changes.

3.2 Introduction

Each species in a host-parasite relationship has unique traits that shape the relationship dynamics and the degree of congruence of their genetic variation (Mazé-Guilmo et al., 2016). Parasite population genetic structure is generally considered to be dependent on host dispersal (Mazé-Guilmo et al., 2016), but several other factors can influence the patterns of genetic variation between host and parasite. Parasite traits that affect their genetic structure include population size, dispersal ability, life cycle complexity (e.g., number of intermediate or reservoir hosts), reproductive mode (e.g., self-fertilizing or sexually reproducing), and their susceptibility to stochastic events (Nadler, 1995; Engelbrecht et al., 2016; Cole and Viney, 2019). The abundance, distribution, vagility, and movement behaviour of the host may also affect the genetic structure of parasites through influences on dispersal and population connectivity (Nadler, 1995; McCoy et al., 2003; Criscione et al., 2005).

Host-parasite comparative phylogeographic approaches are a useful application of population genetics for understanding biogeographic histories of both host and parasite (Nieberding and Olivieri, 2007; Galbreath and Hoberg, 2012). Parasites that are strongly associated with their hosts, such as chewing lice of pocket gophers in North America (Demastes et al., 2012) or Spinturnid mites of bats in Europe (Bruyndonckx, Dubey, et al., 2009), are expected to have congruent phylogenies with their hosts, such that historical speciation or isolation events are reflected in both (Nieberding and Olivieri, 2007). Parasites that are highly host specific or vertically transmitted between generations of host retain the genealogical history of their host better than those with free-living stages or intermediate hosts as parasite dispersal is limited to host movements in highly dependent parasites (Hafner et al., 2003; Whiteman and Parker, 2005; Wirth et al., 2005; Nieberding and Olivieri, 2007; Bruyndonckx, Dubey, et al.,

2009; Jones and Britten, 2010; Speer et al., 2019). Host-parasite phylogeographic approaches can help elucidate historical origins of host species, determine locations of ice age refugia, and assess barriers to dispersal (Nieberding et al., 2004; Galbreath and Hoberg, 2012; Speer et al., 2019).

The ectoparasites of little brown myotis (*Myotis lucifugus*) provide an opportunity to investigate how differences in parasite life history and host dependence affect parasite biogeographic patterns and genetic structure. Little brown myotis are small, insectivorous bats with a wide geographic range in North America (Davis and Hitchcock, 1959; Fenton and Barclay, 1980). Female bats form maternity groups during the summer months with males roosting individually or in small groups (Fenton and Barclay, 1980; Anthony et al., 1981; Broders and Forbes, 2004). Males and females of the species congregate during autumn at swarming sites which is followed by overwinter hibernation (Fenton and Barclay, 1980; Burns and Broders, 2015a; Burns and Broders, 2015b). Previous studies of the population genetic structure of *M. lucifugus* have shown low to moderate levels of population differentiation because of the nature of their aggregations (Burns et al., 2014; Johnson et al., 2015; McLeod et al., 2015; Vonhof et al., 2015).

In terms of the biogeography of *M. lucifugus* in eastern Canada, they are hypothesized to have tracked the recolonizations of forests following the Pleistocene deglaciation, leading to a population expansion in the area (Burns et al., 2014). During the last glacial maximum of the Pleistocene, refugia extended along the eastern coast from just south of Nova Scotia that could have provided suitable forest habitat for bats (Shaw et al., 2006; Burns et al., 2014). The high vagility of bats would have allowed them to follow the recolonization of forests after the ice sheet receded (Burns et al., 2014). A subset of early migrants to the region would likely have been infected with parasites, creating founding populations and the potential for coinciding

parasite population expansions. Within Atlantic Canada, little brown myotis inhabit both mainland and island locations during the summer, making use of both natural and anthropogenic structures for roosts. Previous work by McLeod et al. (2015) identified that the oceanic straits between the mainland and islands of the Gulf of the St. Lawrence did not create an impenetrable barrier to gene flow for *M. lucifugus* but the bats on the island of Newfoundland did show less genetic diversity and less population genetic connectivity to bats from elsewhere. Regional genetic differentiation between mainland and island groups may be more evident in bat parasites due to their shorter generation time and more limited dispersal.

Spinturnix americanus is a common ectoparasite found on the wings of bats in North America (Ubelaker, 1966; Whitaker, 1973; Dick et al., 2003; Villegas-Guzman et al., 2005; Czenze and Broders, 2011a; Schumann, 2019). *Spinturnix americanus* has been recorded from *Antrozous pallidus* (Whitaker and Easterla, 1975), *Corynorhinus mexicanus* (Villegas-Guzman et al., 2005), and several *Myotis* species (Ubelaker, 1966; Whitaker, 1973; Czenze and Broders, 2011) among others. It has been found infecting *M. lucifugus* from central to eastern Canada (Poissant and Broders, 2008; Czenze and Broders, 2011; Webber, Czenze, et al., 2015), with increased infection on adult female bats and juveniles of both sexes (Czenze and Broders, 2011). Spinturnicidae wing mites are permanent ectoparasites completing their life cycle attached to the membranes of their host (Rudnik, 1960; Dowling, 2015), often with high host specificity at the species or genus level (Christe et al., 2000; Ter Hofstede and Fenton, 2005; Bruyndonckx, Dubey, et al., 2009). The wing mites are transmitted between bat hosts vertically from mother to offspring or horizontally during physical contact between bats, such as during roosting aggregations or copulation (Christe et al., 2000; Ter Hofstede and Fenton, 2005). Most population genetic studies have focused on European species of spinturnids, with the exception

of the work by Zamora-Mejías et al. (2022) on *Periglischrus paracaligus* in Mexico and Brown (2016) on *Spinturnix americanus* in Atlantic Canada. Genetic population structure of Spinturnids appears to be dependent on the movement and social behaviour of their host species (Bruyndonckx, Dubey, et al., 2009; Van Schaik et al., 2014; Van Schaik et al., 2015; Zamora-Mejías, Trejo-Salazar, et al., 2022). Brown (2016) found greater genetic diversity from and more gene flow between mites collected from *M. lucifugus* than *M. septentrionalis* at Hayes Cave, Nova Scotia, positing that the behaviours and life history of *M. lucifugus* facilitate more interbreeding of mites. Additionally, the reduced contact between roost groups of *Myotis bechsteini* (Bechstein's bat) corresponds to higher genetic structuring in *Spinturnix bechsteini* (Bruyndonckx, Henry, et al., 2009) whereas the movement of migratory females of *Leptonycteris yerbabuenae* (lesser long-nosed bat) allows for gene flow in *Periglischrus paracaligus* (Zamora-Mejías, Trejo-Salazar, et al., 2022). Due to the dependence of *Spinturnix americanus* on their host, we would expect their genetic structure to resemble the low genetic structure of *M. lucifugus* in Atlantic Canada.

Myodopsylla insignis are found infecting bats in North America, including *M. lucifugus* (Dick et al., 2003; Poissant and Broders, 2008; Eckerlin and Gardner, 2021), *M. septentrionalis* (Chilton et al., 2000; Czenze and Broders, 2011a; Gikas et al., 2011), and *Eptesicus fuscus* (Phillips, 1966; Dick et al., 2003). These fleas are parasitic as adults with early development of larvae and pupae occurring in the roost substrate (Smith and Clay, 1988b). Once development is complete and adult *M. insignis* emerge from their pupal state, they must locate a bat host (Smith and Clay, 1988). Adult *M. insignis* are commonly found on *M. lucifugus* after the bats have left the roost for foraging or swarming (Poissant and Broders, 2008; Czenze and Broders, 2011a; Webber, McGuire, et al., 2015). This may allow for dispersal between roosts, however, bats are

also known to switch roosts to avoid heavy infestations of ectoparasites and their associated energetic costs (Wilkinson, 1985; Lewis, 1995; Bartonička, 2008). If fleas are prevented from dispersing with their hosts coupled with the flea development occurring off host, their susceptibility to stochastic events and genetic drift may increase, affecting their genetic structure (Nadler, 1995; Mazé-Guilmo et al., 2016). While *M. insignis* is associated with multiple bat species in North America (Phillips, 1966; Smith and Clay, 1988; Chilton et al., 2000; Poissant and Broders, 2008; Czenze and Broders, 2011), no studies have yet determined the genetic structure for this flea species, limiting insight into if and how dispersal and gene flow occurs between roosts.

The goal of this study was to compare how life history traits and host-parasite dynamics influence the genetic structure and biogeography of co-infecting ectoparasites. Our aim was to characterize the genetic structure present in *S. americanus* and *M. insignis* in relation to the genetic structure of the host, *M. lucifugus*, and assess their regional biogeographic patterns. Given the permanent nature of the host-parasite relationship between *S. americanus* and *M. lucifugus*, we predict that *S. americanus* will have similarly low levels of genetic differentiation to *M. lucifugus*. Conversely, we predict *M. insignis* will show at least somewhat higher levels of genetic structure as portions of their life cycle is spent in the roost, which limits transmission to adult fleas. *Myotis lucifugus* experienced a population expansion approximately 12,500 to 1,250 years before present after moving into the region after the last deglaciation and we hypothesize that there will be evidence that *M. insignis* and *S. americanus* had experienced similar population expansion. We predict that there will be genetic signatures of this expansion indicated by deviations from neutral theory and characteristic starburst haplotype distributions where high frequency haplotypes are central to several low frequency haplotypes. Understanding the host-

parasite dynamics of these species will provide insight into the factors affecting parasite genetics at different geographic scales and provide important conservation context for the movement patterns of an elusive and endangered host.

3.3 Methods

3.3.1 Specimen collection

Spinturnix americanus and *Myodopsylla insignis* specimens were collected from *Myotis lucifugus* bats in Atlantic Canada between 2010 and 2017 from maternity roosts as part of ongoing bat population research projects. Bats were caught in either mist nets (Avinet, Dryden, New York, USA) or harp traps (Austbat Research Equipment, Lower Plenty, VIC, Australia) positioned close to maternity roosts. Ectoparasites were opportunistically sampled from the wings, ears, and body fur of the bats. Collected ectoparasites were stored in 70% ethanol in the field and stored at -80°C for long term storage. Identification of specimens were confirmed using microscopy and diagnostic characteristics (Whitaker, 1982). *Spinturnix americanus* can be distinguished from other mites found on bats in Atlantic Canada by the four pairs of legs that are large in relation to their body size and organized radially around the idiosoma and presence tiny ventral setae and proximal dorsal setae of femora I and II (Rudnik, 1960; Whitaker, 1982). *Myodopsylla insignis* are identified based on the presence of two genal spines on the front portion of the head instead of the back, a truncate maxilla, the presence of a pronotal comb (Whitaker, 1982).

3.3.2 Specimen sampling

Specimens for this study were restricted to those collected from maternity roosts where female adult *M. lucifugus* give birth and raise their young (Davis and Hitchcock, 1959; Fenton and Barclay, 1980). *Spinturnix americanus* specimens were included from nine sites in Nova Scotia, one site in Prince Edward Island, 10 sites in Labrador and four sites from the island of Newfoundland. *Myodopsylla insignis* specimens were included from five sites in Nova Scotia, five sites in Labrador, and three sites from the island of Newfoundland.

Spinturnix americanus specimens were selected from different hosts (*i.e.*, individual *M. lucifugus*) where possible to sample a greater range of specimens however some locations had fewer than 5 hosts sampled so multiple mites were sequenced from some hosts (Bruyndonckx, Henry, et al., 2009; van Schaik et al., 2011). All *M. insignis* were collected from hosts and multiple fleas were sequenced from some hosts however early flea development occurs in the roost, so this is not anticipated to affect sample diversity (Marshall, 1982a; Smith and Clay, 1988). A maximum of four mites or five fleas were sequenced from any individual bat with 57.9% of mite specimens and 50.5% of flea specimens being the sole mite or flea sequenced from the host. For 15 of 195 host bats, both mites and fleas were sequenced. Only locations with four or more specimens of either *S. americanus* or *M. insignis* were included as minimum samples sizes of three are needed to calculate Tajima's D and test for deviations from neutrality (Tajima, 1989). The number of specimens successfully sequenced from each site are included in Supplemental Tables 3.1 and 3.2 (Appendix B).

3.3.3 Cytochrome c oxidase subunit I gene sequencing

Spinturnix americanus and *M. insignis* specimens selected for sequencing were prepared as per Canadian Centre for DNA Barcoding (CCDB) guidelines and submitted to the CCDB for COI DNA barcoding. DNA extraction, polymerase chain reaction (PCR) amplification, and Sanger DNA sequencing were completed by the CCDB. DNA extractions were carried out using the protocol outlined in Ivanova *et al.*, (Ivanova and Hebert, 2006) with adjustments for extraction of arthropod DNA (Ivanova et al., 2006; Ivanova and Hebert, 2006). PCR amplification was conducted using the protocol by Ivanova and Grainger (Ivanova and Grainger, 2007). Forward and reverse COI mtDNA gene primers used for both *M. insignis* and *S. americanus* were C_LepFolF 5'-ATTCAACCAATCATAAAGATATTGG-3' and 5'-

TAAACTTCTGGATGTCCAAAAAATCA-3' (Hernández-Triana et al., 2014). Specimen metadata was deposited into the Barcode of Life Database (BOLD) (Ratnasingham and Hebert, 2007). COI sequences are publicly available from datasets DS-SPIN and DS-MYOIN on BOLD for *S. americanus* and *M. insignis*, respectively. Sequences greater than 600bp were aligned using the default settings for MUSCLE (Edgar, 2004) in MEGA 11 (Kumar et al., 2018a).

3.3.4 *Myotis lucifugus* sequences

Sequences of the hypervariable region II (HVII) of the mtDNA control region from previous work by McLeod et al. (2015) were used to compare the population genetic structure of the mites and fleas to their host, *Myotis lucifugus*. Tissue samples from *M. lucifugus* were collected between 2008 and 2012 from 21 sites in the provinces of Quebec, Nova Scotia, Prince Edward Island, and Newfoundland and Labrador (McLeod et al., 2015). Collection of bat samples and ectoparasites overlapped in some years but ectoparasites were not selected based on whether they were collected from bats with sequences from McLeod et al. (2015). Haplotype sequences were downloaded from NCBI GenBank and a dataset was created based on the number of haplotypes present at each site (McLeod et al., 2015). Sequences were aligned using default settings for MUSCLE (Edgar, 2004) in MEGA X (Kumar et al., 2018b) with gaps removed from sites 16 and 22.

3.3.5 Genetic diversity

Genetic diversity statistics were calculated for the ectoparasites and *M. lucifugus*. Mean and maximum pairwise difference between sequences for *Spinturnix americanus*, *Myodopsylla insignis*, and *Myotis lucifugus* were calculated using MEGA 11 (Kumar et al., 2018a) and the Tamura-Nei distance (Tamura and Nei, 1993). Nucleotide diversity, the average number of nucleotide differences per site between two sequences (Nei and Li, 1979), and haplotype

diversity, the probability that two randomly sampled alleles will be different (de Jong et al., 2011), were calculated using DnaSP v. 6.12.03 (Librado and Rozas, 2009).

3.3.6 Genetic structure

To evaluate whether spatial processes contribute to genetic structure for *M. insignis* and *S. americanus*, the correlation between geographic distance and sequence divergence was calculated using the geo-distance correlation tool on BOLD using the Kimura 2 Parameter distance model (Kimura, 1980). The geo-distance tool aligns sequences using the BOLD aligner which is an amino acid based HMM. The geo-distance correlation tool conducts a Mantel Test (Mantel, 1967) between the geographic distance matrix (in kilometers, from collection site latitude and longitude) and the genetic divergence matrix and a comparison of spread using the minimum spanning tree of collection sites and the maximum intraspecific divergence (Blagoev et al., 2016).

DnaSP v. 6.12.03 was used to format haplotype data for analysis in Arlequin. Maternity sites were used to assign sequences to populations and regions were used for the group level structure. Three regions were included for *M. insignis* (Nova Scotia, Newfoundland, and Labrador) and four regions for *S. americanus* (Nova Scotia, Newfoundland, Labrador, and Prince Edward Island). Five regions were included for *M. lucifugus* based on capture locations in McLeod et al. (2015): Quebec, Nova Scotia, Newfoundland, Labrador, and Prince Edward Island.

To test for genetic differentiation between mainland regions and islands, Arlequin v. 3.5.2.2 was used to calculate analysis of molecular variance (AMOVA) (Excoffier and Lischer, 2010). AMOVA calculates the proportion of variance among groups (ϕ_{CT}), among populations within groups (ϕ_{SC}), and within populations (ϕ_{ST}) and evaluates the significance by randomly

permutating the sequences among populations (Tzeng et al., 2004). At low numbers of populations per group, it can be difficult to detect between group structure with analysis of molecular variance due to statistical limitations with the possible number of permutations of sampled populations (Fitzpatrick, 2009). For this study, all mites or fleas collected at a maternity roost were considered a population (referred to as a roost or roost site) and the regions were considered groups. A power analysis was conducted as per Fitzpatrick (2009) to ensure that the number of maternity roosts within regions would provide a sufficient number of permutations to result in p-values of < 0.05 if higher level population structure is present. Arlequin v. 3.5.2.2 was also used to calculate pairwise F_{ST} values for *M. insignis* and *S. americanus* as a measure of genetic differentiation between roosts.

3.3.7 Demographic history

To determine whether there is evidence that ectoparasites underwent a historical population expansion, we inferred haplotype networks from the mtDNA sequences and conducted tests of neutrality. Maximum parsimony haplotype networks were constructed using the ‘haploNet’ function from the R package *pegas* using the haplotype frequencies to visualize collection regions of the different haplotypes (Paradis, 2010). The ‘rmst’ function in the R package *pegas* was used to infer randomized minimum spanning trees (RMST) of the haplotypes and these trees were examined for star burst patterns that would indicate past range expansions (Paradis, 2010; Paradis, 2018; R Core Team, 2023). The RMST method is an alternative to the minimum spanning network method for inferring haplotype networks that involves fewer alternative links and resamples the distance matrix with randomized reordering to remove ambiguity or bias that could be introduced by the order of the data (Paradis, 2018). Haplotype networks were examined for starburst patterns, where a common central haplotype that differs

from many haplotypes branching off of it by one or two nucleotides, as these patterns are suggestive of demographic expansion (Yuan et al., 2010; Pulgarín-R and Burg, 2012). Three tests of neutrality were conducted: Tajima's D, Fu's F_S , Fu and Li's D^* and F^* (Tajima, 1989; Fu and Li, 1993; Fu, 1997). Tajima's D was calculated in Arlequin v. 3.5.2.2 for each population with four or more sequenced specimens. Tajima's D, Fu's F_S , and Fu and L's D^* and F^* were calculated for all specimens sequenced from Atlantic Canada using DnaSP v. 6.12.03.

3.4 Results

3.4.1 Genetic diversity

COI mtDNA gene alignment sequences of 653 and 611 nucleotides were generated for 87 *Myodopsylla insignis* and 223 *Spinturnix americanus*, respectively, across all roosts. The COI sequences for *M. insignis* included 7.8% variable sites (51) whereas the sequences for *S. americanus* included 4.1% variable sites (25). There were 45 and 27 haplotypes identified for *M. insignis* and *S. americanus*, respectively. The nucleotide diversity or average pairwise difference between sequences for *M. insignis* was 0.006, with a maximum of 0.022 (Table 3.1). For *S. americanus*, the average pairwise difference between sequences was 0.004, with a maximum of 0.012. In comparison, the HVII sequences for *M. lucifugus* produced an alignment of 293 nucleotides with 51 variable sites. *Myotis lucifugus* exhibited a comparable haplotype diversity of 0.927. The pairwise difference between sequences was greater in *M. lucifugus* (mean = 0.02 and max = 0.052), however this may be attributable to greater sample size (625 individuals) allowing for more variation to be captured and to the different gene region.

Table 3.1: Summary statistics for sequence and haplotype diversity for *Spinturnix americanus*, and *Myodopsylla insignis* collected from *Myotis lucifugus* at maternity sites in Atlantic Canada between 2010 and 2017 and *Myotis lucifugus* sampled by McLeod et al. (2015)

Summary statistics	<i>Myodopsylla insignis</i>	<i>Spinturnix americanus</i>	<i>Myotis lucifugus</i>
Number of sequences	87	223	625
Number of variable sites	51	25	57
Number of haplotypes	45	27	109
Haplotype diversity	0.940	0.833	0.927
Average number of nucleotide differences	4.001	2.406	5.573
Mean pairwise distance	0.006	0.004	0.020
Maximum pairwise distance	0.022	0.012	0.052

3.4.2 Genetic structure

The distance between roosts ranged from 2 km (Anne Marie Lake, Labrador from 2011 and Minipi Lake, Labrador from 2012) to 1227 km (Mill Village, Nova Scotia and Kaipokok River, Labrador). The Mantel test indicated a weak positive association between geographic distance and sequence divergence for *M. insignis* ($r = 0.105$, $p = 0.01$) whereas there is little to no association for *S. americanus* ($r = 0.017$, $p = 0.01$). This suggests that the fleas were more likely to have genetic structure among sites than the mites.

Variation within roosts accounted for the greatest proportion of molecular variation for both *M. insignis* and *S. americanus* (Tables 3.2 and 3.3). The ϕ statistics were significant ($p < 0.01$) for both species except for among roosts for *M. insignis* ($\phi_{SC} = 0.011$, $p = 0.328$). The low among roost variation for *S. americanus* and *M. insignis* suggests gene flow among roosts. Some

significant genetic differentiation is present for *M. insignis* and *S. americanus* between regions, 7.33% ($p < 0.001$) and 8.99% ($p=0.001$), respectively (Tables 3.2 and 3.3), suggesting some regional differentiation in genetic structure and more restricted gene flow.

Table 3.2: Analysis of molecular variance results for *Myodopsylla insignis* collected from *Myotis lucifugus* at 13 maternity sites in three regions (Nova Scotia, Newfoundland, and Labrador) within Atlantic Canada between 2010 and 2017.

Source of variation	Degrees of freedom	Sum of squares	Variance components	% Total variance	ϕ -statistics	p
Among regions	2	2.99	0.04	7.33	$\phi_{CT} = 0.073$	<0.001
Among roosts	10	4.68	0.01	0.98	$\phi_{SC} = 0.011$	0.328
Within roosts	74	32.76	0.44	91.69	$\phi_{ST} = 0.083$	<0.001

Table 3.3: Analysis of molecular variance for *Spinturnix americanus* collected from *Myotis lucifugus* at 23 maternity sites in four regions (Nova Scotia, Prince Edward Island, Newfoundland, and Labrador) within Atlantic Canada between 2010 and 2017.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation	ϕ -statistics	p
Among regions	3	8.43	0.04	8.99	$\phi_{CT} = 0.010$	0.001
Among roosts	20	14.74	0.04	10.19	$\phi_{SC} = 0.112$	<0.001
Within roosts	199	69.35	0.35	80.82	$\phi_{ST} = 0.192$	<0.001

For *M. lucifugus*, the greatest proportion of variation was also found within roosts (89.55%), followed by among roosts (6.60%), and among regions (3.85%, Table 3.4). The high within roost variance suggests that roost populations are well connected with gene flow between them and low inter-roost differentiation. The genetic differentiation of *M. lucifugus* was significant at all hierarchical levels ($p \leq 0.001$).

Table 3.4: Analysis of molecular variance for *Myotis lucifugus* sequences of the hypervariable region II (HVII) of the mtDNA control region from sampled McLeod et al. (2015) from bats in Quebec, Nova Scotia, Prince Edward Island, and Newfoundland and Labrador.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation	ϕ -statistics	p
Among regions	4	81.79	0.11	3.85	$\phi_{CT} = 0.039$	0.001
Among roosts	16	125.52	0.19	6.60	$\phi_{SC} = 0.069$	<0.001
Within roosts	604	1532.45	2.54	89.55	$\phi_{ST} = 0.105$	<0.001

Regional genetic differentiation is apparent for *S. americanus* between the island of Newfoundland and the mainland. Pairwise differentiation (F_{ST}) was significant ($p < 0.001$) between Salmonier Nature Park and all roost sites in Labrador and seven of the nine roost sites in Nova Scotia and the one site in Prince Edward Island (Supplemental Table 3.3). Pynn's Brook, Newfoundland, was significantly differentiated from seven of the eleven roost sites in Labrador but was not with any roost site in Nova Scotia. Pairwise differentiation was significant for 22 roost site pairs between Nova Scotia and Labrador. These results suggest that *S. americanus* in Newfoundland are experiencing genetic differentiation from the mainland, with some differentiation occurring between Labrador and Nova Scotia as well.

There is less evidence of regional genetic differentiation for *M. insignis*, but results suggested that Anne Marie Lake and Charlottetown Junction, Labrador were significantly differentiated from roost sites in Nova Scotia (Supplemental Table 3.4) and Anne Marie Lake, Labrador was differentiated from Salmonier Nature Park, Newfoundland ($p < 0.001$).

3.4.3 Demographic history

Across all roost sites in Atlantic Canada, Tajima's D was significant for *M. insignis* ($D = -2.056$, $p = 0.002$), but not for *S. americanus* ($D = -1.161$, $p > 0.10$). Tajima's D was significant

for two populations of *M. insignis*, Charlottetown Junction, Labrador ($D = -1.658$, $p = 0.01$) and Anne Marie Lake, Labrador ($D = -2.129$, $p = 0.00$), and approaching significance for the population from Rawdon, Nova Scotia ($D = -1.464$, $p = 0.06$). These negative Tajima's D results suggest that *M. insignis* may have undergone historical population expansion in these areas as a $D < 0$ can indicate a deviation from neutral theory, either as balancing selection or population growth (Tajima, 1989). Tajima's D was nonsignificant for all other roost groups of *M. insignis* and all roost groups of *S. americanus*. Fu's F_S was significant for *M. insignis* ($F_S = -42.25$, $p < 0.001$) and *S. americanus* ($F_S = -12.43$, $p = 0.002$). Fu and Li's D^* and F^* were significant for both *M. insignis* ($D^* = -3.926$, $p < 0.02$; $F^* = -3.808$, $p < 0.02$) and *S. americanus* ($D^* = -2.613$, $p < 0.05$; $F^* = -2.379$, $p < 0.05$). Negative values of Fu and Li's D^* and F^* indicate an excess of singleton haplotypes in the population which, similar to Tajima's D , suggests population expansion or selection (Fu and Li, 1993), with the significant negative results for Fu's F_S supporting population expansion (Fu, 1997). These results provide additional support for historical population expansion for *M. insignis* and suggest that it may have occurred for *S. americanus* as well.

Of the 87 *M. insignis* sequenced, 40.2% were assigned singleton haplotypes and 20.7% were assigned to the most abundant haplotype, XIII (Fig. 3.1A). The random minimum spanning tree for *M. insignis* exhibits starburst patterns around two haplotypes, XIII and XXVIII (Fig. 3.1A and 3.1B), suggesting population expansion in Labrador and Nova Scotia. The haplotypes branching from haplotype XIII are primarily present in Labrador and Newfoundland, while the haplotypes branching from XXVIII are only present in Nova Scotia. The higher frequencies of XIII and XXVIII and coupled with the starburst patterns around these haplotypes, support the contention that these haplotypes are ancestral in Labrador and Nova Scotia, respectively.

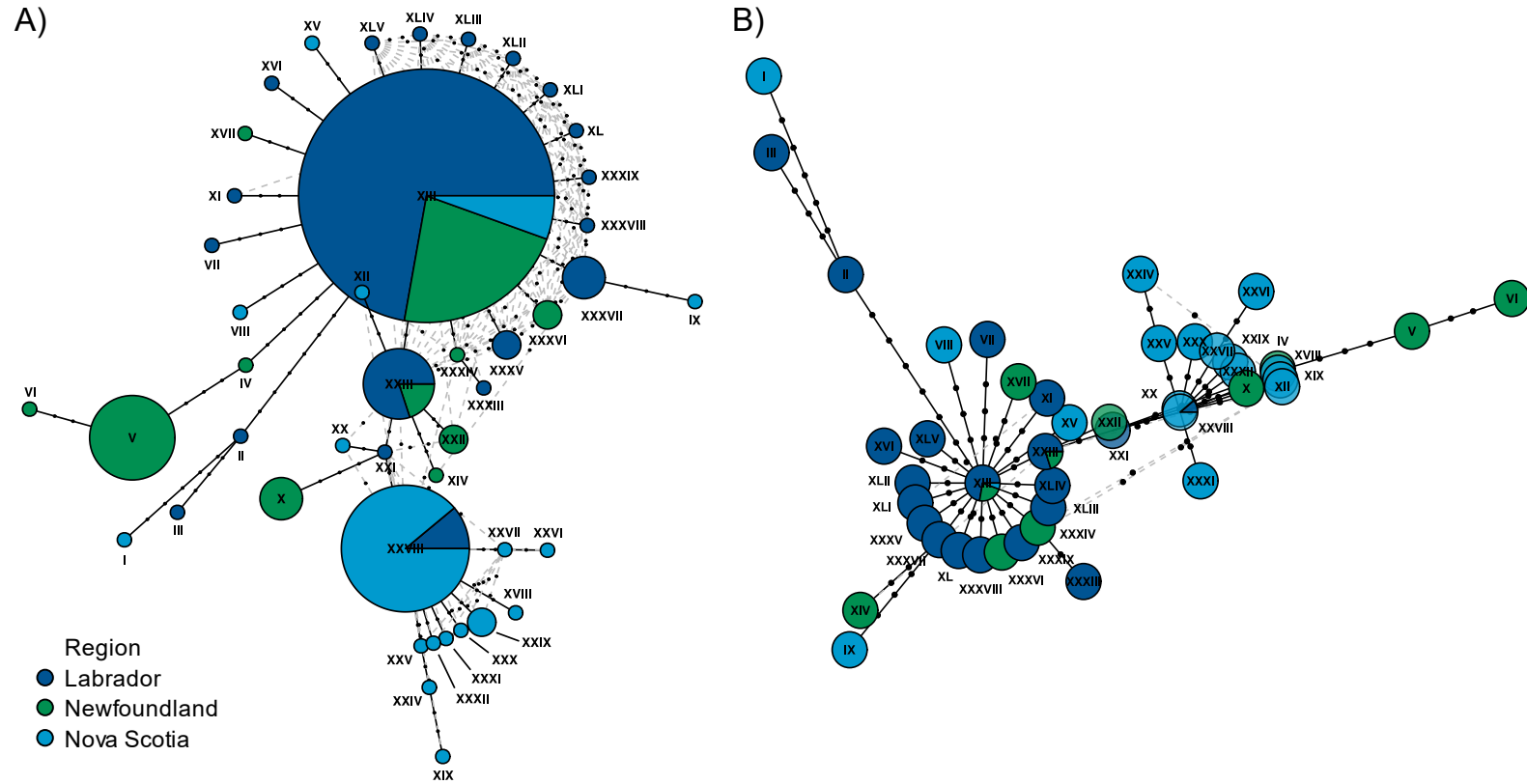


Figure 3.1: Visual representation of genetic relationships among *Myodopsylla insignis* individuals and geographic regions inferred using (a) maximum parsimony and (b) random minimized spanning tree algorithms. Individuals are colour-coded according to collection region and roman numerals correspond to haplotype numbers. Size of circles in (a) correspond to the frequency of each haplotype whereas circle sizes are standardized in (b) to allow for the visualization of the starburst patterns. Black dots on lines represent missing mutational steps between haplotypes with solid black lines representing primary links between haplotypes and grey dashed lines representing alternative links between haplotypes. The RMST algorithms produce fewer alternative links than the maximum parsimony method. Networks were calculated and visualized using *pegas* in RStudio (Paradis, 2010; R Core Team, 2023)

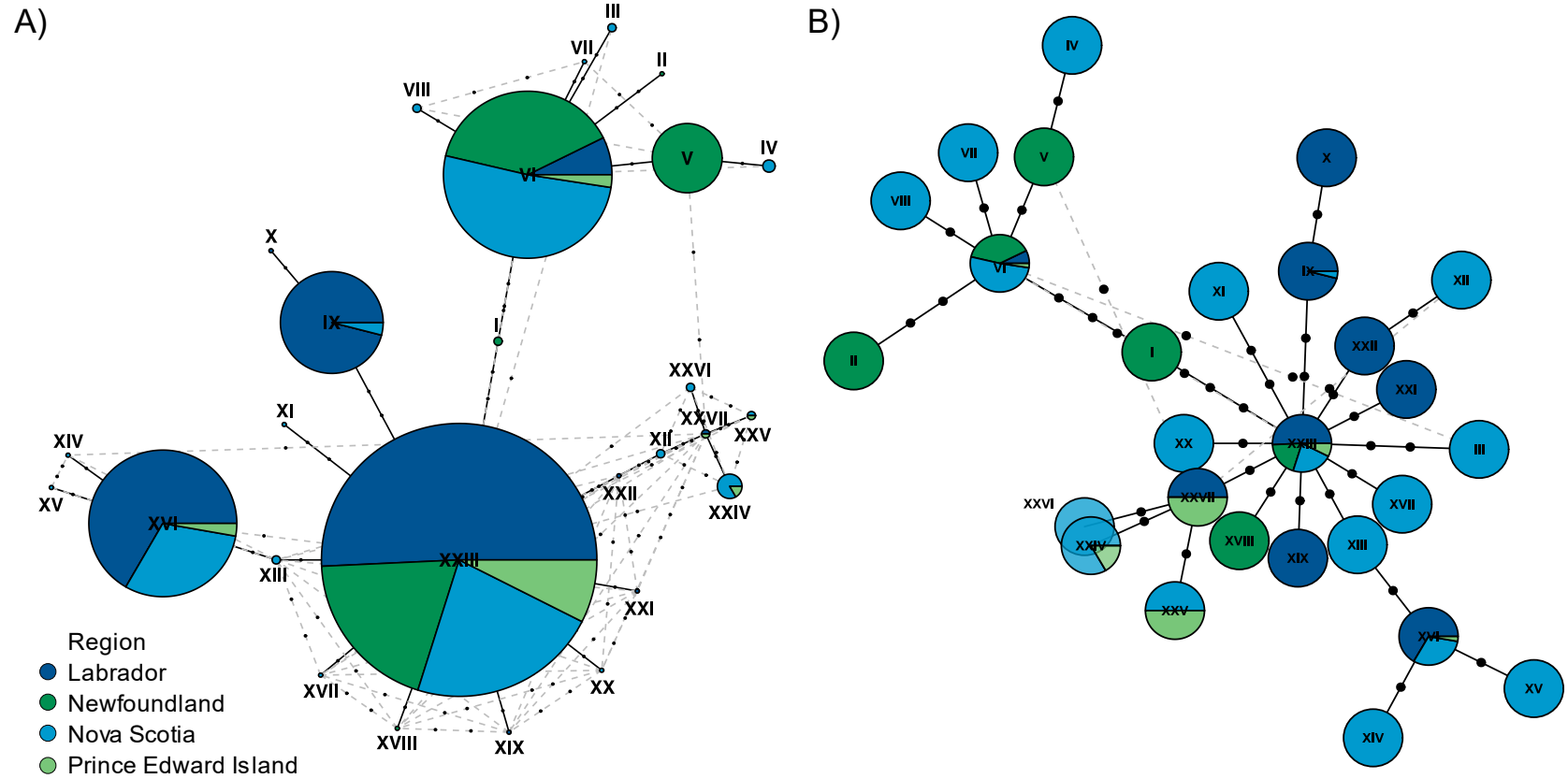


Figure 3.2: Visual representation of genetic relationships among *Spinturnix americanus* individuals and geographic regions inferred using (a) maximum parsimony and (b) random minimized spanning tree algorithms. Individuals are colour-coded according to collection region and roman numerals correspond to haplotype numbers. Size of circles in (a) correspond to the frequency of each haplotype whereas circle sizes are standardized in (b) to allow for the visualization of the starburst patterns. Black dots on lines represent missing mutational steps between haplotypes with solid black lines representing primary links between haplotypes and grey dashed lines representing alternative links between haplotypes. The RMST algorithms produce fewer alternative links than the maximum parsimony method. Networks were calculated and visualized using *pegas* in RStudio (Paradis, 2010; R Core Team, 2023).

Of the 223 *S. americanus* sequenced, 83% were assigned one of the five most abundant haplotypes, with 30% assigned to haplotype XXIII alone (Fig. 3.2A). Other haplotypes are represented by six or fewer individuals. Two of the haplotypes were present in all four regions, XXIII and VI, and with five other haplotypes present in more than one region (XVI, IX, XXIV, XXVII, and XXV). Although the presence of high frequency haplotypes in multiple regions suggests gene flow is occurring between regions and between islands and the mainland, the haplotypes are not evenly distributed between regions so there are limitations to the gene flow. The *S. americanus* haplotypes also exhibit a starburst pattern around from haplotype XXIII (Fig. 3.2B), but this did not coincide with any site-specific historical population expansion as per Tajima's D ($p > 0.05$).

Additionally, both ectoparasites exhibited a haplotype that was only present in Newfoundland. Seventeen specimens of *S. americanus* shared a haplotype that was only present in Newfoundland and shared between the four roost sites in the region (Fig. 3.2, haplotype V). Six specimens of *M. insignis* collected at Salmonier Nature Park, Newfoundland, also shared a haplotype only present at this site (Fig. 3.1, haplotype V). The presence of a haplotype solely present in Newfoundland may suggest that movement is primarily in the direction of Nova Scotia to Newfoundland or may represent the beginning of population expansion in Newfoundland.

Of the 625 *Myotis lucifugus* sequenced from McLeod et al. (2015), 54% of the were assigned to one of the five most abundant haplotypes, with 17% assigned to the most abundant haplotype (I). Of the 109 haplotypes assigned, 49 were singletons represented by only one sequence and 33 of the haplotypes are shared between regions. The *M. lucifugus* haplotypes exhibit starburst patterns around haplotypes I, III, VIII, and XXXI, four of the most abundant haplotypes (Fig. 3.3). The starburst cluster around XXXI consists mostly of haplotypes sampled

in Nova Scotia and Labrador whereas the clusters around I, III, VIII include more haplotypes sampled in Newfoundland and Quebec. These starbursts indicate the potential for historical population expansion in the little brown bat in this area of eastern Canada, however the tests of neutrality were non-significant for the overall population ($D = -0.934, p > 0.10$; $D^* = -1.091, p > 0.10$; $F^* = -1.226, p > 0.10$). Tajima's D was not significant any individual sites.

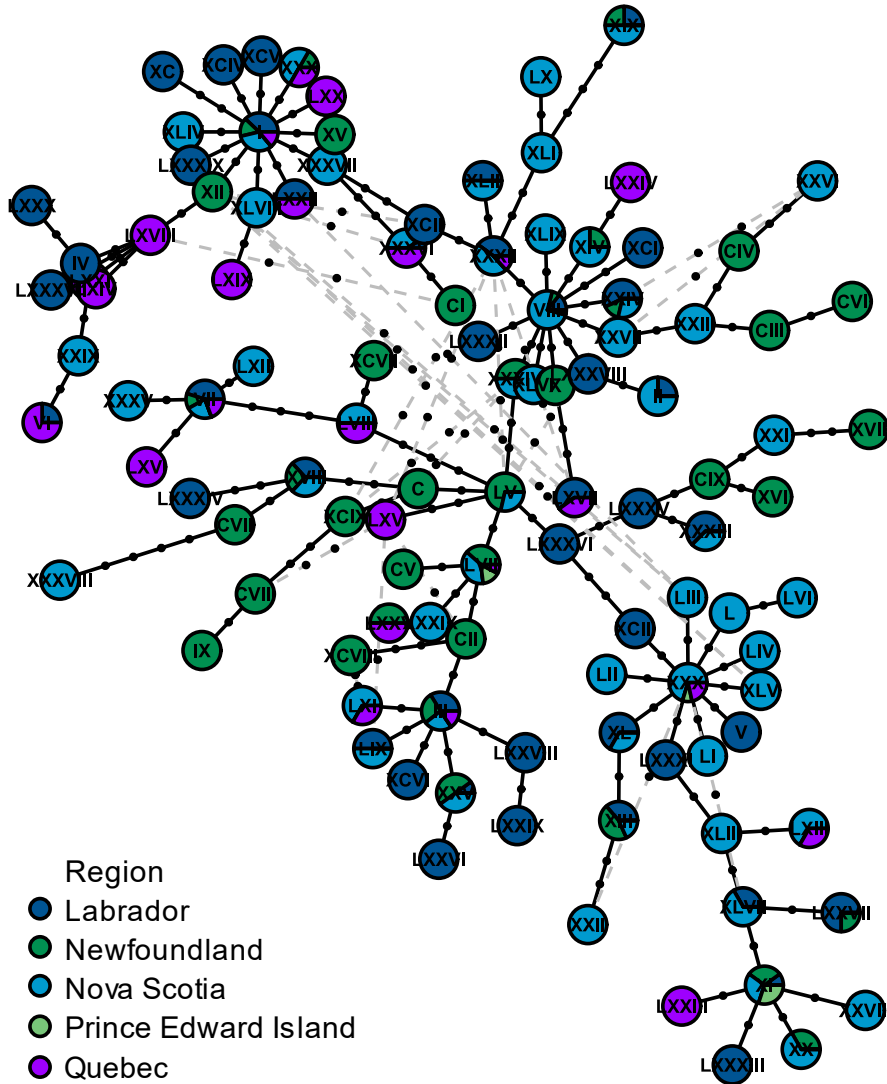


Figure 3.3: Visual representation of genetic relationships among *Myotis lucifugus* individuals and geographic regions inferred using a random minimized spanning tree algorithm. HVII sequence data from McLeod et al. (2015). Haplotypes are colour-coded according to collection region and roman numerals correspond to haplotype numbers. Circle sizes are standardized to allow for the visualization of the starburst patterns. Black dots on lines represent missing mutational steps between haplotypes with solid black lines representing primary links between haplotypes and grey dashed lines representing alternative links between haplotypes. Networks were calculated and visualized using *pegas* in RStudio (Paradis, 2010; R Core Team, 2023).

3.5 Discussion

By comparing the genetic diversity of two co-infecting ectoparasites, we can see the influence of their different reproductive strategies. Both ectoparasites are expected to synchronize their reproduction with that of their hosts (Marshall, 1982; Smith and Clay, 1988a; Christe et al., 2000; Orlova et al., 2018) but exhibit different modes of reproduction. *Myodopsylla insignis* are oviparous with females likely producing and laying many eggs a day and potentially hundreds in a lifetime, similar to other flea species (Marshall, 1982). Larvae and pupae then develop in the roost with only the adults parasitizing bats (Marshall, 1982; Smith and Clay, 1988). Conversely, *Spinturnix americanus*, like other Spinturnid mites, are viviparous where female Spinturnid mites embryonate eggs and larva internally before giving birth to the blood-feeding protonymph (Orlova et al., 2018). These differences in life history strategy are reflected in the genetic diversity of these ectoparasites. *Myodopsylla insignis* showed greater genetic diversity than *S. americanus* in terms of haplotype number, the number of variable sites, and the average number of nucleotide differences. The greater potential reproductive output of the fleas allows more opportunity for mutations to occur and build up in the species.

We identified varying levels of mtDNA genetic diversity in *M. insignis* and *S. americanus* in Atlantic Canada and low levels of genetic structure for both ectoparasites. The fleas were found to have higher genetic diversity than the mites. Our AMOVA and haplotype network results suggest gene flow is occurring for *S. americanus* between roost sites, however, regional differentiation (F_{ST}) is apparent between Newfoundland and the mainland. Whereas there is less evidence of regional differentiation in *M. insignis*, there is some evidence of isolation by distance and evidence for population expansion in Labrador (Tajima's D , Fu and Li's F^* and D^*). The genetic structure of both ectoparasites is reflective of the medium to low genetic structure previously found in their host *Myotis lucifugus* (Burns et al., 2014; Johnson

et al., 2015; McLeod et al., 2015) and was expected for *S. americanus* given its dependency on its bat hosts. Our hypothesis that *M. insignis* would exhibit greater genetic structure because of its roost dwelling life stages was not supported. Although neither species exhibited more than low levels of genetic structure between regions based on the AMOVA results, the greater number of *S. americanus* haplotypes across multiple regions suggests that the mites experience more dispersal with their bat hosts.

Parasites can act as biological tags for their host (Bruyndonckx et al., 2010; MacKenzie and Abaunza, 2013; Catalano et al., 2014) and investigating the genetic structure of *M. insignis* and *S. americanus* has provided important insight into the movement ecology of the little brown bat in Atlantic Canada. Landscape features, such as oceanic straits (Castella et al., 2000; Bildstein et al., 2009), mountains (Shepard et al., 2008; Beyer et al., 2016), and roadways (Zalewski et al., 2009; Atlas and Fu, 2019), can create movement barriers that restrict connectivity between populations. Previous work by McLeod et al. (2015) on *M. lucifugus* found evidence of regional differentiation in eastern Canada between Newfoundland and the mainland. The regional differentiation between Newfoundland and the mainland for *S. americanus* is consistent with these findings. This is particularly prevalent for bats roosting at Salmonier Nature Park, Newfoundland, which showed high regional differentiation when compared to roost sites in Labrador ($F_{ST} \geq 0.587$, $p < 0.001$) and low to medium levels of differentiation from most roost sites in Nova Scotia ($0.299 \leq F_{ST} \leq 0.455$, $p < 0.001$). Gene flow appears to be occurring between bats at Pynn's Brook, Newfoundland and bats in Nova Scotia, allowing for transmission *S. americanus* and gene flow between the mite populations. There is still low to medium levels of differentiation between mites at Pynn's Brook and most roost sites in Labrador ($0.263 \leq F_{ST} \leq 0.438$, $p < 0.001$). The connectivity of bats and their mites between Newfoundland and Labrador

may be restricted due to yet undetermined geographic, climatic, or behavioural barriers that are not present or are less restrictive between Nova Scotia and the western portion of Newfoundland (McLeod et al., 2015).

Host specific parasites and permanent parasites are expected to show higher levels of genetic structure as their dispersal and survival is tightly linked to their host (Nadler, 1995). Despite being generally considered host specific, the genetic structure of Spinturnid mites appears to be strongly dependent on the movement ecology and behaviour of their host species. For example, the Bechstein's bat (*Myotis bechsteini*) forms smaller roost groups than *M. lucifugus* with high levels of maternal philopatry and exhibits a greater level of population structuring (Bruyndonckx, Henry, et al., 2009). This is mirrored in their *Spinturnix bechsteini* ectoparasites which exhibit higher population structuring than *S. americanus*, likely due to the reduced contact between host roost groups (Bruyndonckx, Henry, et al., 2009). The spread of haplotypes across regions for *S. americanus* is consistent with gene flow or transmission of mites between roost sites and regions within Atlantic Canada. Although *S. americanus* populations are likely greatest during the spring and summer (Orlova et al., 2018), the mites have been identified from *M. lucifugus* and *Myotis septentrionalis* at swarming sites in Nova Scotia and New Brunswick (Poissant and Broders, 2008; Czenze and Broders, 2011). These locations where bats from multiple summer roosts congregate during the fall and winter (Fenton and Barclay, 1980; Burns and Broders, 2015) may provide opportunity for transfer of mites between bats from different summer roosts and potentially between different *Myotis* species. At least some female *M. lucifugus* are philopatric, where they return to the roosts they were born (Dixon, 2011), or show some combination of roost fidelity and social preference leading to the return of female bats to the same roosts year over year (Sunga et al., 2024). This consistent return of female bats

to maternity roosts provides a reliable resource for ectoparasites whereas the dispersal of other females and male bats provides an avenue for ectoparasite transmission to other areas (Dixon, 2011).

The fleas do not show as strong a regional differentiation between Newfoundland and the mainland as the mites, however, they do show evidence of structure and population growth. There appear to be two geographic clusters for haplotypes within Labrador and Nova Scotia, with some overlap between these two regions and with Newfoundland. Two roost sites in Labrador exhibited medium levels of regional differentiation with roost sites in Nova Scotia ($0.314 \leq F_{ST} \leq 0.556$, $p < 0.001$) which may, in part, be accounted for by isolation by distance (Mantel test $r=0.105$, $p = 0.01$). Although *M. insignis* adults are present at swarming sites (Czenze and Broders, 2011), reproduction of these fleas occurs during the summer and the pupa is proposed as the overwintering life stage (Smith and Clay, 1988). Adult fleas dispersing to swarming sites and hibernacula with their hosts may have limited effects on gene flow within this flea species, contributing to the regional differentiation. The population expansion of *M. insignis* in Labrador is particularly apparent, as represented by the starburst pattern around haplotype XIII and the Tajima's *D* results (Charlottetown Junction: $D = -1.658$, $p = 0.01$; Anne Marie Lake: $D = -2.129$, $p = 0.00$). This expansion is likely a result of *M. lucifugus* being restricted to a limited number of anthropogenic structures suitable for roosting. Ectoparasite infestations may be energetically costly for bats (Giorgi et al., 2001) and bats have been shown to change roosts to avoid ectoparasite infections (Bartonička, 2008). The lack of alternative roost options in Labrador prevents the bats from switching roosts to avoid ectoparasites, allowing the fleas to persist at larger population sizes. The differences in life history and reproductive strategy

between *M. insignis* and *S. americanus* likely means that the fleas are better situated to exploit this stable host supply.

Both ectoparasites likely underwent a population expansion in eastern Canada following the arrival of their host in the area after the Pleistocene deglaciation (Burns et al., 2014). All three species exhibit starburst patterns in their haplotype networks, suggesting historical population expansion. The tests of neutrality for all sampled *S. americanus* and *M. insignis* also support the hypothesis that these species exhibited past population expansion. The local population growth of *M. insignias* in Labrador was likely more recent, following the continued northward expansion of the range for *M. lucifugus*. The presence of medium abundance haplotypes in Newfoundland only for both ectoparasites may indicate the potential for population growth at those roost sites during the time of collection.

Myotis lucifugus and other hibernating bats in North America have experienced drastic declines in population numbers following the spread of the white nose syndrome causing fungus, *Pseudogymnoascus destructans* (Lorch et al., 2016; Environment Canada, 2018). Populations of *M. insignis* and *S. americanus* are likely experiencing pressures related to declines in *M. lucifugus* and other host species and there is the potential for significant genetic restructuring of these two ectoparasite species. The secondary effects of this disease on the bat ectoparasites are currently unknown but local extirpations and genetic bottlenecks are possible. If bat populations become more isolated and less connected, this will also reduce the gene flow between ectoparasite populations and future generations may exhibit greater population structure. Both *S. americanus* and *M. insignis* have previously been recorded from *E. fuscus* (Phillips, 1966; Dick et al., 2003) and related species *Myodopsylla borealis* and *Spinturnix bakerii* have previously been found on the big brown bat (*Eptesicus fuscus*) which appears to be less susceptible to white

nose syndrome (Pearce and O'Shea, 2007; C.L. Frank et al., 2014). If *E. fuscus* is a viable alternative host for *S. americanus* and *M. insignis*, it may act as reservoir for these species where their ranges overlap. The survival of these ectoparasites is dependent on the long-term viability of their *Myotis* spp. hosts and the potential for reservoir populations on alternative hosts like *E. fuscus*.

3.6 Conclusion

The results of our study highlight the importance of considering host-parasite dynamics and parasite life history when investigating the genetic structure of parasites. The differences in host-parasite dynamics between *M. insignis* and *S. americanus* and their host likely contributed to their varying levels of genetic diversity while the movement ecology of *M. lucifugus* maintained gene flow between populations. This research highlights the importance of host mobility and sociality in the maintenance of gene flow between parasite populations at large scales. If this pattern of mirroring of host genetic structure is consistent for other threatened or endangered host species, parasites may provide additional insight into the behaviours and movements of the hosts that can help inform conservation and management decisions.

Additionally, understanding how aspects of both parasite and host biology influence the host-parasite relationship at multiple scales is necessary for being able to predict how these dynamics may be affected by disturbances such as climate change, disease and species introductions, and land use changes.

Chapter 4: A meta-analysis of arthropod ectoparasites of North American bats (Chiroptera) and their taxonomic and conservation challenges

4.1 Abstract

Climate change and habitat loss pose substantial threats to many bat species with the potential for cascading effects on their parasites. North American bats are host to a variety of ectoparasites, many of which are bat specialists. In this meta-analysis, we provide a synthesis of the currently described bat ectoparasites in North America and an analysis of how host characteristics, environmental, and geographic factors influence the ectoparasite richness present on bat species and the geographic distribution of ectoparasites across North America. We conducted a systematic review of the literature for ectoparasites infecting bats in Canada, the USA, and Mexico that included species descriptions, occurrence reports, and analytical ectoparasite studies. Ectoparasite records were available for 53% of bat species (81/152) with more abundant and widespread bat species better represented. Estimated ectoparasite species richness was not significantly different among bat families but did vary widely between species. Bat ectoparasite diversity was consistent with the predictions of the latitudinal diversity hypothesis with a 3.4% decrease in species richness for every degree increase in latitude from latitude 16.5° to 50.2°. More research is needed to parse out the climate and host factors that influence ectoparasite richness and distributions. We suggest multidisciplinary collaborations between bat biologists, parasitologists, and taxonomists are necessary to collect ectoparasites and catalogue bat-ectoparasite associations. The coinciding increase in threats of environmental

change and the decline in taxonomic experts poses a substantial challenge for describing and conserving bat ectoparasites before they disappear.

4.2 Introduction

Bats (Chiroptera) are the second most speciose mammal order with over 1400 described species (Simmons and Cirranello, 2024). The order exhibits a global distribution and represents the only mammals capable of sustained flight. Bats have exploited a variety of dietary niches, from nectarivore to carnivore (Barclay and Brigham, 1991; Moosman et al., 2012; Clare et al., 2014; Santana and Cheung, 2016; Oelbaum et al., 2019; Gual-Suárez and Medellín, 2021; Oelbaum et al., 2022), and roost types, both natural and anthropogenic (Niu et al., 2007; Pearce and O'Shea, 2007; Postawa et al., 2014; Deleva and Chaverri, 2018; Herrera-Victoria et al., 2018).

This diversity of taxa and niche has coincided with the evolution of several bat specialist ectoparasites within Insecta and Acari (Marshall, 1982), including families of fleas (Ischnopsyllidae; Lewis and Lewis, 1994), mites (Spinturnicidae; Baulechner et al., 2013), and bat flies (Nycteribiidae and Streblidae; Dittmar et al. 2015). Research on bat ectoparasites is expanding to include hosts and ectoparasites from diverse geographic locations, including bat flies in Madagascar (Rajemison et al., 2017) and Southeast Asia (Olival et al., 2013; Gay et al., 2014), ectoparasites from Vespertilionidae and Rhinolophidae bats in Europe (Zahn and Rupp, 2004; van Schaik et al., 2011; Sándor et al., 2019), and ectoparasites from many bat families in Algeria (Bendjeddou et al., 2017), Mexico (Martínez et al., 2016; Najera-Cortazar et al., 2023; Ramírez-Martínez and Tlapaya-Romero, 2023), and the Orinoquia region of South America (Ospina-Pérez et al., 2023). The accessibility of sequencing technology has allowed for more

molecular studies of bat ectoparasites (Van Schaik et al., 2014; Talbot et al., 2016; Speer et al., 2019; Najera-Cortazar et al., 2023). Researchers are also increasingly interested in the potential for the bat ectoparasites to harbour and transmit pathogens (Gay et al., 2014; McKee et al., 2016; Reeves et al., 2016; Abundes-Gallegos et al., 2018; Hornok et al., 2019).

As of 2023, there were 152 bat species recorded in North America from six families (Emballonuridae, Molossidae, Mormoopidae, Natalidae, Phyllostomidae, and Vespertilionidae; (Bat Conservation International, 2023; Simmons and Cirranello, 2024). A diversity of ectoparasites have been recorded from many of these bats, including bat flies (Abundes-Gallegos et al., 2018; Bolívar-Cimé et al., 2018; Trujillo-Pahua and Ibáñez-Bernal, 2019), bat bugs (Bowles et al., 2013; Talbot et al., 2016; Najera-Cortazar et al., 2023), mites and ticks (Czenze and Broders, 2011a; Herrera-Mares et al., 2021; Zamora-Mejías, Trejo-Salazar, et al., 2022). The State of the Bats 2023 North America (Bat Conservation International, 2023) report estimates that 82% of North American bat species are at risk from climate change over the next 15 years, particularly by severe droughts and extreme heat, and that 98% of bat species are losing habitat due to logging, fire regimes, and ranching, among other factors (Bat Conservation International, 2023). Some species of bats are already listed as federally endangered in Canada (Environment Canada, 2018; Bat Conservation International, 2023) and the USA (National Park Service, 2023; U.S. Fish & Wildlife Service, 2024) where extinction also threatens the continued survival of their parasites as co-extinctions are predicted to be the most severe in mutualistic and parasitic interactions (Dunn et al., 2009).

The literature on North American bat ectoparasites encompasses a variety of forms with increasing insight into the associations between host and parasite. Historically, literature on North American bat ectoparasites primarily consisted of species descriptions, occurrence reports,

and natural history papers (Phillips, 1966; Usinger, 1966; Bernath and Kunz, 1981; Durden et al., 1992; Guzmán-Cornejo et al., 2004) but there is an increasing proportion of more recent literature that includes new and updated morphological species descriptions (Crossley and Clement, 2015; Guzmán-Cornejo et al., 2016; Morales-Malacara et al., 2018; Morales-Malacara and López-Ortega, 2023). Beyond the descriptive literature, ectoparasite studies often characterize infection prevalence and intensity (Ritzi and Whitaker, 2003; Ritzi and Munzer, 2009; Czenze and Broders, 2011a; Tlapaya-Romero, L., A. Horváth, S. Gallina-Tessaro, E. J. Naranjo, 2015), effects of host sex and host life stage on infection status (Lewis, 1996; Webber, Czenze, et al., 2015; Salinas-Ramos et al., 2018; Zamora-Mejías, Morales-Malacara, et al., 2020), and seasonal or habitat variation in ectoparasite diversity or abundance (Pearce and O'Shea, 2007; Bolívar-Cimé et al., 2018; Salinas-Ramos et al., 2018; Salinas-Ramos et al., 2019). In Chapter 2 of this thesis, I investigate prevalence and intensity of infection on *Myotis lucifugus* and *M. septentrionalis* and the effect of host characteristics on ectoparasite infection. Molecular studies have also been completed on select bat ectoparasites, examining population structure, historical demographics, phylogeography, and cryptic lineages (Lack et al., 2011; Talbot et al., 2017; Zamora-Mejías, Trejo-Salazar, et al., 2022; Najera-Cortazar et al., 2023). Several studies have also tested bat ectoparasites for potential zoonotic pathogens, including flaviviruses and the bacteria *Borrelia*, *Bartonella*, and *Rickettsia* (Abundes-Gallegos et al., 2018; Moskaluk et al., 2018; Banerjee et al., 2020; Nadolny et al., 2021). The increase in analytical bat ectoparasite studies has provided a greater understanding of the factors shaping evolution and ecology of bat-ectoparasite associations.

The ecology and evolution of both hosts and ectoparasites influences ectoparasite community diversity and the presence of specific ectoparasite taxa on hosts (Kamiya et al., 2014;

Fagir et al., 2015). Ectoparasite diversity is expected to follow the latitudinal diversity gradient with environmental conditions at lower latitudes driving ectoparasite speciation and diversity (Rohde and Heap, 1998; Poulin, 2004). The distribution of ectoparasite taxa can be limited by their environmental tolerances (Benoit and Denlinger 2010, Mize et al. 2011) but the extent to which environmental factors influence ectoparasites depends on whether they are permanent, remaining on the host throughout their life cycle, or temporary, living off the host for one or more life stages (Froeschke et al., 2013). Aspects of a host ecology and behaviour can influence their encounter rate and susceptibility to ectoparasites. Hosts with large geographic ranges or those with ranges that overlap with many other potential host species may encounter more ectoparasites, increasing the diversity of their ectoparasite communities (Dick and Patterson, 2007; Kamiya et al., 2014). Host species that form larger groups can experience higher transmission rates of ectoparasites, allowing for increased ease of mate finding for ectoparasites and coinciding with higher ectoparasite diversity (Dick and Patterson, 2007; Kamiya et al., 2014). The factors that influence ectoparasite distributions are varied and differ among host-parasite systems.

The goal of this review is to summarize and assess current knowledge of the ectoparasite species infecting bats of North America and evaluate hypotheses to explain the species richness and distribution of these ectoparasites. If bat ectoparasite diversity is consistent with the latitudinal diversity hypothesis (Rohde and Heap, 1998; Poulin, 2004), we predict ectoparasite richness will be greater on bats at lower latitudes and that bat families with primarily tropical distributions, such as Phyllostomidae, will have greater average species richness across the family than bat families that include more species at higher latitude, such as Vespertilionidae. We hypothesize that regional differences in ectoparasite community composition will be a result

of a combination of factors related to regional host composition, climate, and geography. Since transmission of ectoparasites and maintenance of infections are hypothesized to be more successful in areas with high host diversity and density (Dick and Patterson, 2007; Kamiya et al., 2014), we predict that ectoparasite dissimilarity will be greater between regions of high and low host diversity. We also predict that the regional ectoparasite composition will vary with climate variables (e.g., annual temperature and precipitation) as differences in the life histories and environmental constraints of ectoparasites limits their geographic distribution (Benoit and Denlinger 2010, Mize et al. 2011). This review will provide background knowledge of these host-parasite relationships to future researchers, create new understanding of the ecological and evolutionary factors effecting the ectoparasite richness, and provide directions for future study.

4.3 Methods

The list of current bat species recorded in Canada, the United States of America (USA), and Mexico were retrieved from Bat Names of the World (www.batnames.org; (Simmons and Cirranello, 2024). The list of bat species was used to create search strings for Web of Science, Scholars Portal, and Wiley Online Library to search for literature regarding ectoparasites or parasites of those bats occurring in the three target countries. An example search string for Web of Science would be: TS=((ectoparasit* OR parasit*)) AND TS=(("Antrozous pallidus")) AND TS=((Canada OR "United States" OR Mexico OR "North America" OR Canadian OR Mexican OR American)). Ectoparasit* and Parasit* were used to capture any papers that investigate both ecto- and endoparasites and referred to parasites generally in the title, abstract, and keywords. Covidence (Veritas Health Innovation, 2023) was used to filter search results, removing any literature not pertaining to ectoparasites or studies that occurred outside of Canada, the USA, or Mexico.

The following data was extracted from the literature meeting the search requirements: bat species, ectoparasite species (or higher taxon if not identified to species), location (region/state or province/country) and geographic coordinates (if given). When geographic coordinates were not available, coordinates were estimated based on the location description (e.g., city, county, or state/province). Bat species names and ectoparasite species names were updated to currently accepted name according to Bat Names of the World (Simmons and Cirranello, 2024) and Global Biodiversity Information Facility (www.gbif.org; (GBIF.org, 2024) as applicable. We noted the type of article including if it was a species description, occurrence report, or study examining some aspect of ectoparasite ecology or evolution. We also noted if infection parameters were reported (e.g., prevalence and intensity) and whether additional analyses were conducted, such as comparing infection status between sexes or seasons or if the authors tested for potential zoonotic pathogens.

We used R to conduct statistical tests and create graphics (R Core Team, 2023). The ‘ggscatter’ and ‘stat_cor’ functions in *ggpubr* were used to plot the correlation between ectoparasite species richness and number of papers that included bat species (Kassambara, 2023; R Core Team, 2023).

4.3.1 Bat-ectoparasite network

Using a network of bat-ectoparasite associations, we examined the species richness of ectoparasite faunas and the host ranges of the ectoparasites. We mapped connections between ectoparasites and bat species using *igraph* (Csardi and Nepusz 2006, Team 2020, Csardi et al. 2024). We selected the layout option ‘layout_with_graphopt’ to visually display the connections between bat and ectoparasite species (Csardi et al. 2024). The network included only those ectoparasites that were reported at the species level. We calculated the degree centrality of each

node in the network (Csardi and Nepusz, 2006; Csardi et al., 2024). Since degree centrality is sum of the number of connections of a network node (Golbeck, 2015), uninfluenced by node position within the network, it can be used as a proxy for ectoparasite species richness on bat species (Dáttilo et al., 2020) and for host range of ectoparasite species, the number of host species a parasite species is known to infect (Dallas et al., 2017). We conducted pairwise t-tests using ‘pairwise_t_test’ in *rstatix* with Bonferroni correction to determine if pairs of bat families or ectoparasite orders exhibited significant differences in ectoparasite species richness or host range, respectively (Kassambara, 2023).

4.3.2 Ectoparasite maps

Insect and acarine ectoparasites were mapped at the order level in conjunction with the North American ecoregions (Commission for Environmental Co-operation, 2021). North American ecoregions are 15 broad ecological regions that reflect areas of general similarity in ecosystems and environmental resources and incorporate air, water, land, and biota (Commission for Environmental Co-operation, 2021). Violin plots were created to represent the density of ectoparasite observations across latitude at the order level.

4.3.3 Modelling ectoparasite species richness with general linear regression models (GLMs)

We evaluated the effect of geography and host taxonomy on species richness of the ectoparasite faunas using the degree centrality from the bat-ectoparasite network as a proxy for species richness. Based on the latitudinal diversity hypothesis, we predict that species richness would increase at lower latitudes and bat families with primarily tropical and sub-tropical distributions would have higher species richness relative to other bat families. To characterize the variation of species richness, we used regression models with Poisson distributions with species richness as the response variable. Candidate models investigated the effect of bat

characteristics and geography on ectoparasite species richness (Table 4.1). Host characteristics included are bat family as categorical explanatory variable, forearm length as a measure of bat size based on forearm ranges available from the literature, and bat diet as a binary variable 0 – primarily plant based (e.g., pollen, nectar, fruit) and 1 – primarily animal based (e.g., insects, vertebrates, blood). Geographic explanatory variables include the area (km²) of bat species range in North America which were obtained from the IUCN Red List (IUCN, 2022) and the latitudinal midpoint of the range. Since species richness may be correlated with sampling effort, the number of papers including each bat species was included as an offset to account for variation in sampling effort. The global model is:

$$\text{species richness} \sim \text{area} + \text{latitudinal midpoint} + \text{diet} + \text{forearm} + \\ \text{family} + \text{offset}(\log(\text{no. papers}))$$

We fit GLMs using the ‘glm’ function in the package *lme4* (Bates et al., 2015) in R (R Core Team, 2023) and assessed global and candidate models using AIC_c to account for small sample sizes (Burnham and Anderson, 2002). Model ranking was done using the function ‘model.sel’ from the *MuMIn* package (Bartoń, 2023). We averaged the models in the 95% confidence set using ‘model.avg’ from the package *MuMIn* (Burnham and Anderson, 2002; Bartoń, 2023) and calculated the 95% confidence intervals of the b values using ‘confint’ (R Core Team, 2023) on the model average, which reports values based on the conditional average.

4.3.4 Modelling ectoparasite dissimilarity with multiple regression on distance matrices (MRM)

A subset of the data was used in the MRM analysis to characterize the effect of bat community composition, climate, latitude, and geographic distance on ectoparasite dissimilarity between regions. MRM analysis enables researchers to test for spatial patterns in species abundances related to the environment or spatial process related to disturbance or dispersal

(Lichstein, 2007). MRM involves multiple regression of a response matrix on two or more explanatory distance matrices, such as environmental or climatic variables (Lichstein, 2007). Tests of significance for the explanatory variables are performed by permutation (Lichstein, 2007). For this analysis, we extracted the number of ectoparasite individuals collected at the species level and the number of individual bats examined from the articles in the review that provided this information. Abundances were grouped into regions at the state or province level and the central latitude and longitude for each region was calculated from the collection areas. Distance matrices were calculated using the ‘vegdist’ function in *vegan* (Oksanen et al., 2018) for ectoparasite, host, climatic, and latitudinal distances while the geographic distance matrix was calculated using the ‘dist’ function in *geodist* (Padgham, 2021). We tested the effects of the explanatory matrices on the Bray-Curtis dissimilarities between regions for all ectoparasite species. Our explanatory variables were host dissimilarity, geographic, latitudinal, and climatic distances. Ectoparasite and host counts were standardized using the Hellinger transformation. Bray-Curtis host dissimilarity between regions was calculated using ‘vegdist’ function in *vegan* (Oksanen et al., 2018). Euclidean distances were calculated for the central geographic coordinates of the regions and the latitudes. Our climatic variables (elevation, annual temperature range, annual mean temperature, and annual precipitation) provide an overview of the climate in the chosen regions in terms of the temperatures and precipitation that ectoparasites would encounter and were obtained from the WorldClim database (<https://www.worldclim.org/data/index.html>) using the 30-arcsec grids (approximately 1 km resolution). Climatic variables were extracted for the central coordinates of each region and standardized to a mean = 0 and variation = 1 (Krasnov et al., 2010). The Euclidean distance was computed between regions to provide a measure of climatic distance (Krasnov et al., 2010). The

‘varpart’ function in *vegan* was used to determine variance fractions for the different explanatory distance matrices (Oksanen et al., 2018). Generalized dissimilarity modelling (GDM) was used as a secondary check of model and data fit. The function ‘formatsitepair’ from package *gdm* was used to format the dissimilarity data and the untransformed geographic and environmental data to run the model using the ‘gdm’ function. The function ‘dgm.partition.deviance’ was used to partition the deviance from the host dissimilarity, environmental and spatial variables.

4.4 Results

Our review of the literature included 78 journal articles published between 1947 and 2023 and the data from Chapter 2 of this thesis. Ectoparasite records were available for 192 ectoparasites species from 79 species of bats in North America (Supplemental Tables 4.1-4.4, in Appendix A). Two bat species (*Myotis peninsularis* and *Natalus stramineus*) were included in the literature with ectoparasites collected but not identified to species for a total of 81 bat species. Available literature varied between bat species with a range of 1 to 21 papers per species and a median of 2 papers per species. Estimated ectoparasite species richness for a bat species was correlated with the number of papers per bat species ($R^2 = 0.64$, $p < 0.001$; Fig 4.1). Bat ectoparasite literature is more abundant for bat species in the USA and Mexico (37 and 33 studies, respectively), corresponding to a better distribution of records across those countries, while there are limited ectoparasite records in the literature from bats in Canada (8 studies). Ectoparasites were recorded from bats in British Columbia, Manitoba, New Brunswick, Prince Edward Island, Nova Scotia, and Newfoundland and Labrador.

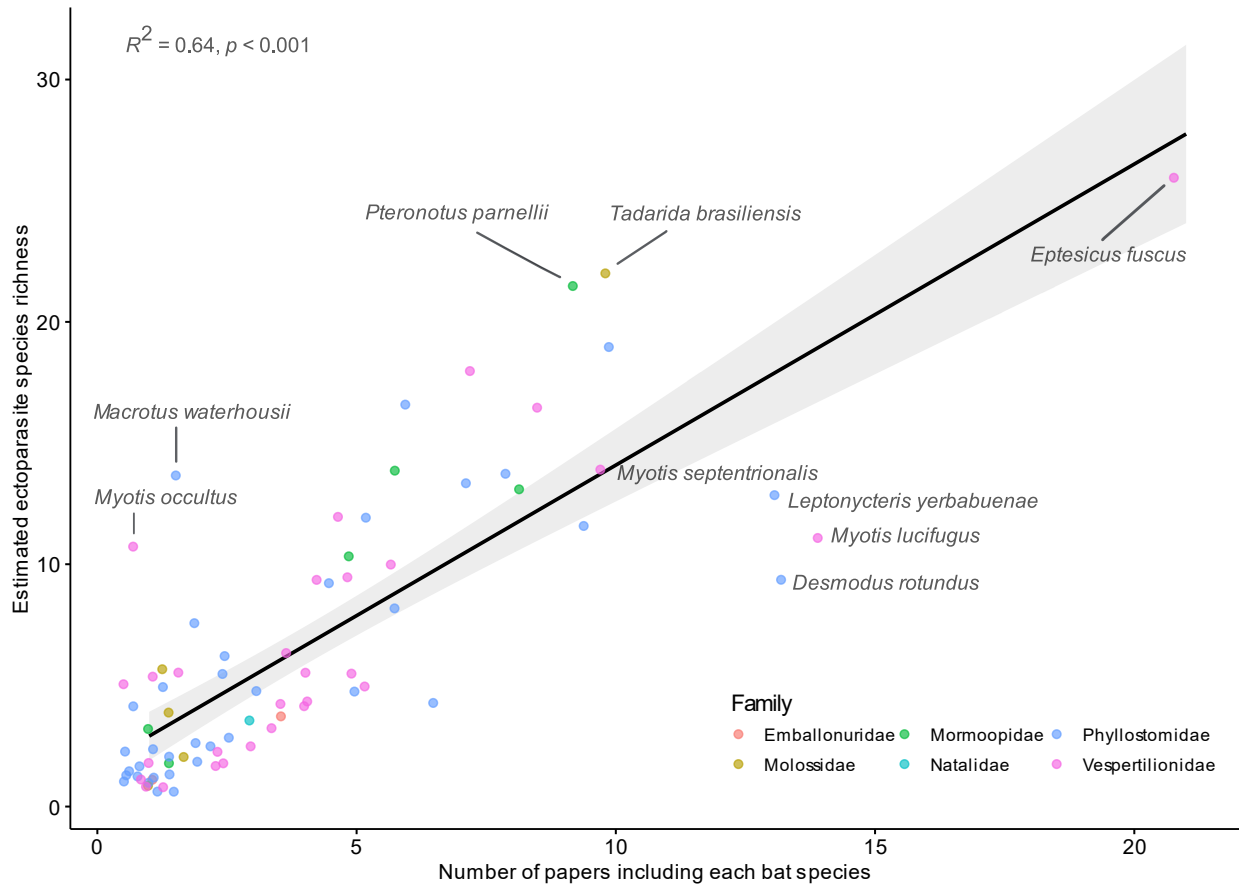


Figure 4.1: Correlation between estimated ectoparasite species richness per bat species and the number of papers each bat species appears in. The black line represents to the regression line with the 95% confidence interval in grey. Points represent each of 79 bat species with at least one ectoparasite identified to the species level and are coloured according to bat family. Points are jittered to account for high levels of overlap.

The articles in this review included a variety of article types from species descriptions (Morales-Malacara and López-W, 1998; Guzmán-Cornejo et al., 2004; Crossley and Clement, 2015) and species occurrence reports (Bernath and Kunz, 1981; Durden et al., 2012; Bowles et al., 2013; Eckerlin and Gardner, 2021) to analytical ectoparasite studies (Czenze and Broders, 2011a; Talbot et al., 2016; Bolívar-Cimé et al., 2018; Salinas-Ramos et al., 2019; Zamora-Mejías, Morales-Malacara, et al., 2020). Many articles focused on a single bat species, such as *Eptesicus fuscus* (Pearce and O'Shea, 2007; McKee et al., 2018; Nadolny et al., 2021; Occi et al.,

2022), *Leptonycteris yerbabuenae* (Zamora-Mejías, Herrera-Mares, et al. 2020, Zamora-Mejías, Morales-Malacara, et al. 2020, Zamora-Mejías, Ojeda, et al. 2022) and *Tadarida brasiliensis* (Foster and Mertins, 1996; Guzmán-Cornejo et al., 2003; McAllister et al., 2006). Other papers included a small number of bat species (Villegas-Guzman et al., 2005; Poissant and Broders, 2008; Czenze and Broders, 2011a; Herrera M et al., 2016; Bolívar-Cimé et al., 2018) or a wider community of bat species (Whitaker, 1973; Chilton et al., 2000; Steinlein et al., 2001; Trujillo-Pahua and Ibáñez-Bernal, 2019; Najera-Cortazar et al., 2023). In terms of the ectoparasites, the articles either focused on specific ectoparasite taxa or included a broad survey of bat ectoparasites (Chilton et al., 2000; Ritzi et al., 2001; Czenze and Broders, 2011a; Martínez et al., 2016; Najera-Cortazar et al., 2023). Bat flies (Abundes-Gallegos et al., 2018; Bolívar-Cimé et al., 2018; Moskaluk et al., 2018; Salinas-Ramos et al., 2018; Ramírez-Martínez and Tlapaya-Romero, 2023), mites (Durden et al., 1992; Herrera-Mares et al., 2021; Zamora-Mejías, Ojeda, et al., 2022), and ticks (Steinlein et al., 2001; Guzmán-Cornejo et al., 2017; Colín-Martínez and García-Estrada, 2018) appear to be of particular interest. Two papers focused on the bat bug, *Cimex adjunctus* (Talbot et al., 2016; McKee et al., 2018), with a third collating occurrences of *C. adjunctus* and the soft tick *Carios kelleyi* (Bowles et al., 2013). No papers focused on bat fleas specifically, but bat fleas were included as part of ectoparasite community studies (Ritzi et al., 2001; Czenze and Broders, 2011a; Webber, Czenze, et al., 2015) or inventories of mammal fleas generally (Durden et al., 2012; Eckerlin, 2016; Eckerlin and Gardner, 2021).

Ectoparasitic insects in North America belonged to four orders: Diptera, Hemiptera, Psocodea, and Siphonaptera. Of the identified Diptera, two were mosquitoes (*Culex restuans* and *Aedes quadrivittatus*, Culicidae) and 53 were bat flies. The Streblidae family was represented by 49 species whereas all four of the Nycteribiidae bat flies belonged to the genus *Basilia* (the

phylogenetic status of Streblidae and Nycteribiidae is in flux and bat fly genera are accepted under Hippoboscidae in GBIF; (GBIF Taxonomy Backbone). Of the identified Hemiptera, one was a Polyctenidae (*Hesperoctenes eumops*) and three were Cimicidae, including two species of bat bugs (*Cimex adjunctus* and *C. pillosellus*) and one swallow bug (*Oeciacus vicarius*). Twelve species of fleas (Siphonaptera) were identified, six belonging to the bat flea family, Ischnopsyllidae, and six belonging to other flea families. One individual *Tadarida brasiliensis* bat was infected with an unidentified bark louse (Psocodea) in Florida, USA (Foster and Mertins, 1996).

Ectoparasitic Acari in North America belonged to four orders: Ixodida, Mesostigmata, Sarcoptiformes, and Trombidiformes. The ticks (Ixodida) were represented by one hard tick (*Ixodes scapularis*, Ixodidae) and 10 species of soft tick, eight of which belonged to the genus *Carios* (Argasidae) and two to the genus *Antricola* (Argasidae). The identified Mesostigmata mites belonged to four families, with the majority belonging to Macronyssidae or Spinturnicidae with 16 and 17 species, respectively. The identified Sarcoptiformes mites belonged to four families and 11 species, with the family Chrisodiscidae represented by six species. Of the Acari, the Trombidiformes chiggers were the most species rich with 61 species identified from 7 families. The Myobiidae and Trombiculidae families were the most represented of the Trombidiformes with 39 and 15 species, respectively.

4.4.1 Geographic distributions

The mites of Mesostigmata and Trombidiformes appear to be the most widely distributed Acari orders, infecting bats from southern Mexico into Canada (Fig. 4.2 and 4.3). The ticks (Ixodida) and Sarcoptiformes mites appear to be more restricted, with most observations occurring in the USA and Mexico and being absent from the cooler climate of Atlantic Canada,

highlighting a preference for warming climates. Ticks have been identified from bats in northern regions of the USA so there is potential that bat ticks in the genus *Carios* are parasitizing bats in southern Canada but have not been recorded yet (Dick et al., 2003; Bowles et al., 2013). The bat flies (Diptera) are more geographically restricted, occurring throughout Mexico and in the warmer, western regions of the USA and Canada. The highest density of observations of bat flies is at lower latitudes. The fleas (Siphonaptera) and bat bugs (Hemiptera) are absent from the lower latitudes of Mexico where the climate is more tropical but are widely distributed across the USA and show a greater density of observations at mid-latitudes.

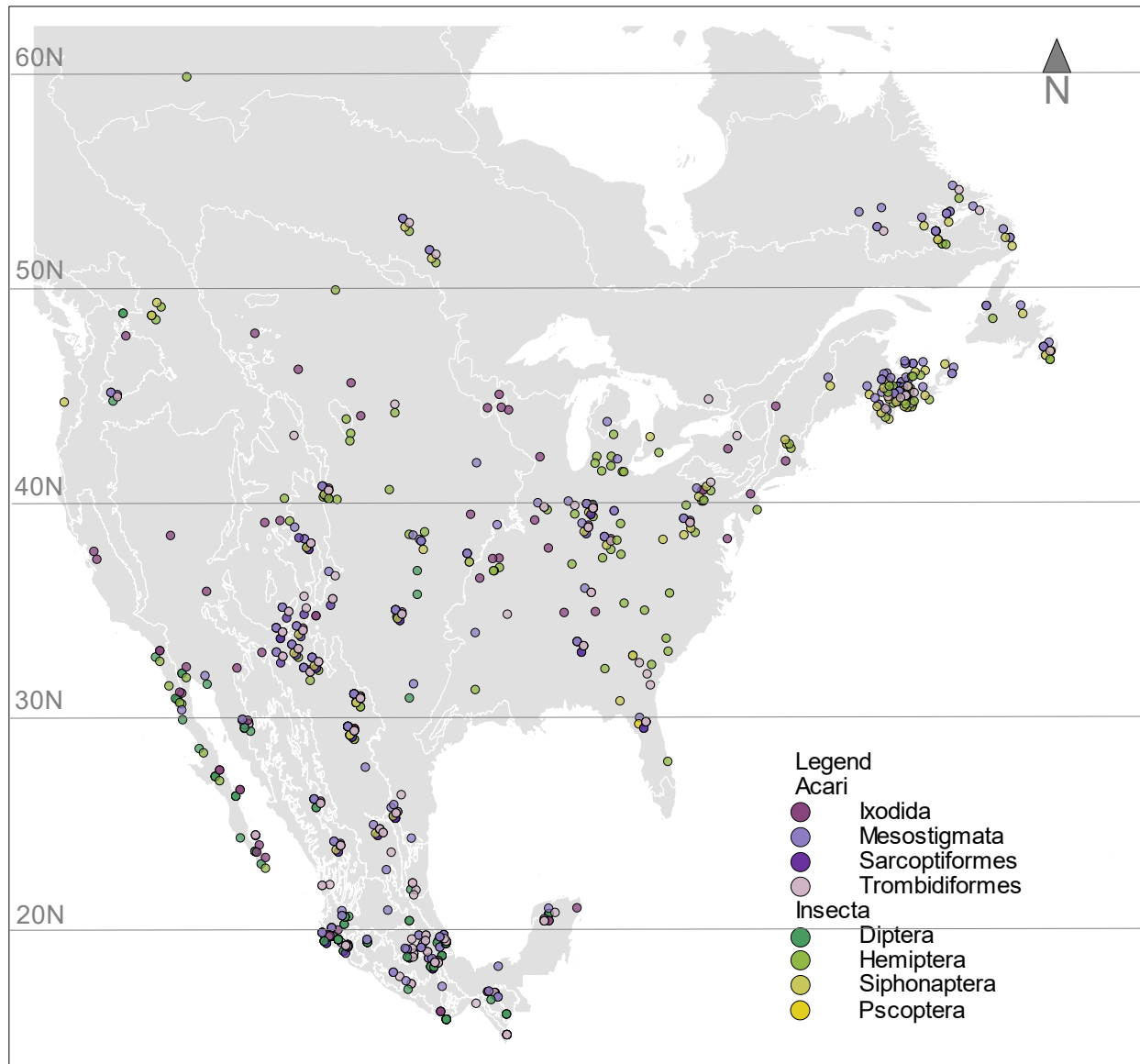


Figure 4.2: Mapped records of Acari and Insecta orders of bat ectoparasites illustrating their distributions across North America. Points are offset from geographic coordinates where multiple orders were collected. Ectoparasite order identifications and collection locations were pulled from the literature used for the review. Latitude was taken directly from literature where available or estimated based on collection location descriptions. The map of North American level 1 ecoregions (separated by the white lines) is from the Commission for Environmental Co-operation (2021)

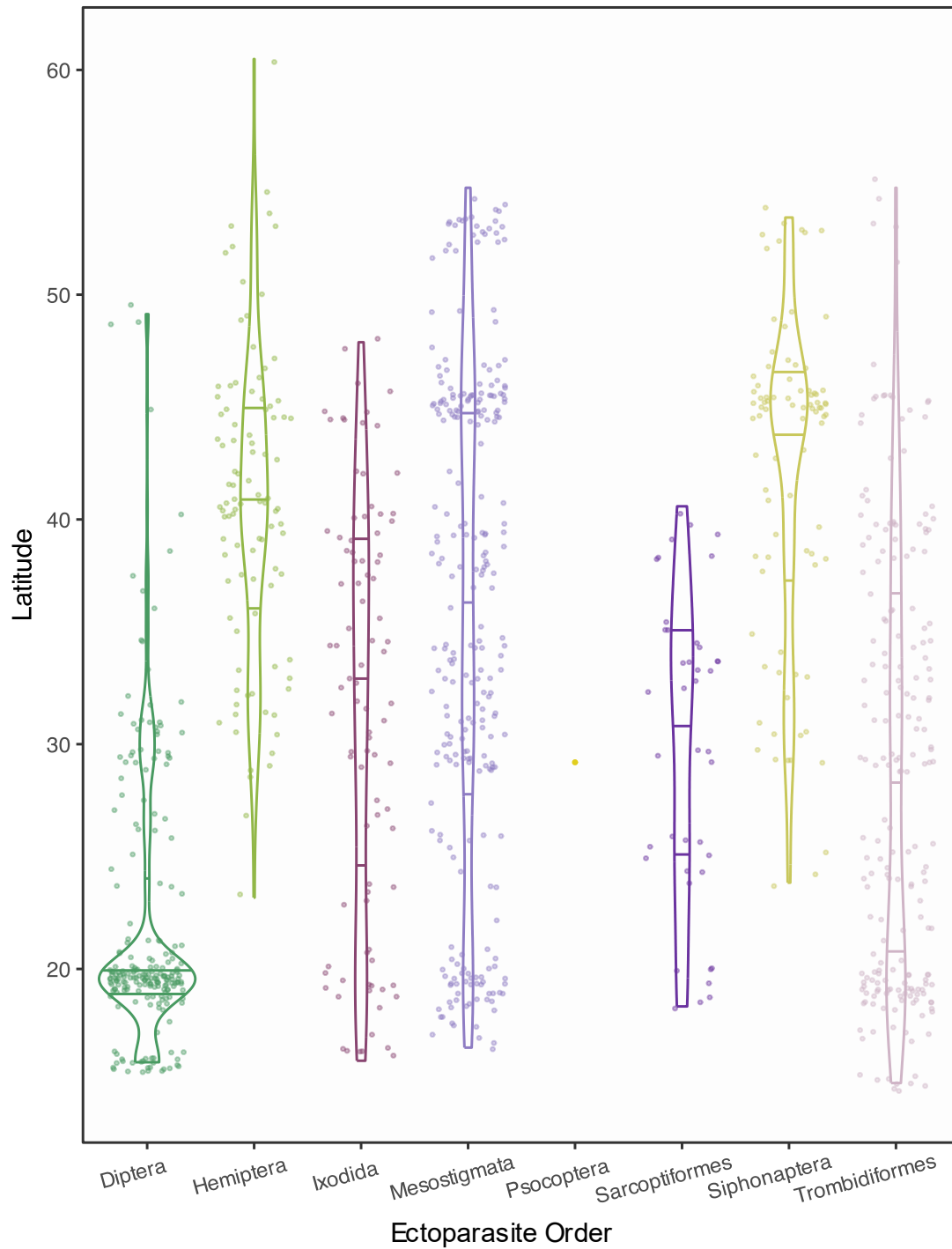


Figure 4.3: Density of ectoparasite observations distributed across latitude for each ectoparasite order. First, median, and third quartiles are represented by the horizontal lines on each violin plot. Ectoparasite order identifications and collection locations were pulled from the literature used for the review. Latitude was taken directly from literature where available or estimated based on collection location descriptions.

4.4.2 Ectoparasite richness

Ectoparasite species richness of bat species varied within and between bat families but was not significantly different ($p > 0.05$, Fig. 4.4). Mormoopidae exhibited the highest median ectoparasite species richness (11.5 species) of any bat family. Of the 81 species, *Eptesicus fuscus* (Vespertilionidae) and *Tadarida brasiliensis* (Molossidae) had the most speciose ectoparasite faunas, with species richness values of 26 and 22, respectively, across their distributions. This may in part be due to the number of papers reporting ectoparasites from each species as there is a relationship between estimated ectoparasite species richness and the number of papers reporting on each bat species (Fig. 4.1).

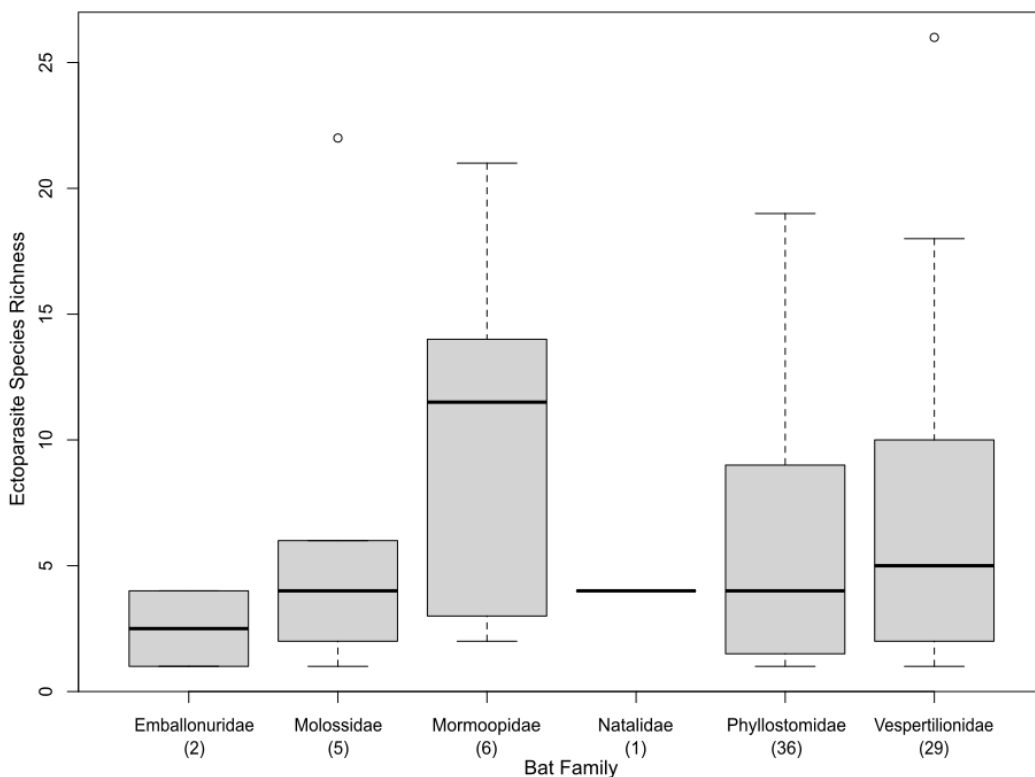


Figure 4.4: Ectoparasite species richness across the six bat families present in contiguous North America. Ectoparasite species richness was estimated from the degree centrality for each species in the bat-ectoparasite species network. Box plots display the median ectoparasite species richness (black line), inter quartile range (grey boxes) and minimum and maximum ectoparasite species richness (whiskers) for each bat family. Number of bat species included are listed below each family. Outliers are *Tadarida brasiliensis* (Molossidae) and *Eptesicus fuscus*

(Vespertilionidae). Only one species of Natalidae, *Natalus mexicanus*, was reported with ectoparasites identified to the species level. No pairs of bat families exhibited significantly different ectoparasite species richness when adjusted for multiple t tests.

Through model selection with AICc, model 6 with bat range latitudinal midpoint and bat family best explained ectoparasite richness ($w = 0.54$, Table 4.1). Model-averaged parameter estimates were calculated for the models in the 95% confidence sets which include models 6, 9, 2, and the global model which included the explanatory variables of North American bat range area, latitudinal midpoint, and bat family (Table 4.2). The global model also included additional parameters of forearm length and diet, however the 95% confidence interval for these parameters crossed 0. Parameter estimates were consistent among models included in the 95% confidence set. The latitudinal midpoint of a bat species range was significantly negatively associated with ectoparasite richness, such that for every one degree increase in latitude, ectoparasite species richness was 3.4% lower (with data representing from latitude 16.5° to 50.2°). Bat range area also showed weak negative associations with ectoparasite species richness (Table 4.2). The bat family Molossidae appears to have a positive relationship to estimated ectoparasite richness relative to Emballonuridae, the reference family. No other bat families showed a significant relationship in the GLM but the families of Mormoopidae, Phyllostomidae, and Vespertilionidae did show greater species richness when compared to Emballonuridae. The 95% confidence interval for the intercept crossed 0, suggesting that ectoparasite species richness may not be linearly related with geographic and host factors.

Table 4.1: Models explaining ectoparasite fauna species richness of North American bat species. Data was included for the subset of 70* bat species with at least one ectoparasite identified to species and with range data available from IUCN Red List (IUCN, 2022). Models in the 95% confidence set are highlighted. K = number of parameters; AICc = Akaike Information Criterion for small sample sizes; ω_i = Akaike weight; $\Sigma\omega_i$ = sum of Akaike weights.

Model		K	AICc	Δ AIC	w_i	$\Sigma\omega_i$
Model 6	family + latitudinal midpoint + offset(log(no. papers))	6	364.0	0.0	0.54	0.54
Model 9	family + area + offset(log(no. papers))	6	365.2	1.2	0.30	0.84
Model 2	area + offset(log(no. papers))	2	367.3	3.3	0.10	0.94
Global model	family + latitudinal midpoint + area + forearm length + diet + offset(log(no. papers))	9	368.9	4.9	0.05	0.99
Model 3	latitudinal midpoint + offset(log(no. papers))	2	371.6	7.6	0.01	1.00
Model 1	family + offset(log(no. papers))	5	376.6	12.6		
Model 5	diet + offset(log(no. papers))	2	377.8	13.7		
Model 4	forearm length + offset(log(no. papers))	2	378.6	14.6		
Model 7	family + forearm length + offset(log(no. papers))	6	378.8	14.8		
Model 8	family + diet + offset(log(no. papers))	6	378.9	14.9		

*Data from 81 bat species are included in the review. Two bat species did not have ectoparasites identified to the species level and nine bat species did not have range data available and so were not included in this analysis.

Table 4.2: Model-averaged parameter estimates, standard errors, and the 95% confidence interval for variables affecting ectoparasite species richness of North American Bats. Emballonuridae is the reference family. Data was included for 70 bat species with at least one ectoparasite identified to species and with range data available from IUCN Red List (IUCN, 2022).

Parameter	Estimate	Standard Error	Lower CI	Upper CI
intercept	0.469	0.534	-0.596	1.522
latitudinal midpoint	-0.035	0.010	-0.055	-0.015
family – Molossidae	1.229	0.500	0.231	2.226
family – Mormoopidae	0.778	0.476	-0.173	1.729
family – Phyllostomidae	0.537	0.455	-0.371	1.446
family - Vespertilionidae	0.946	0.508	-0.066	1.958
area	-0.0005	0.0002	-0.0008	-0.0001
diet	-0.016	0.154	-0.325	0.292
mass	-0.003	0.005	-0.013	0.008

4.4.3 Host range

The host range, or number of host species infected by a parasite, varied between acarine and insect orders. Acarine host range was low with all four orders having a median number of

hosts of 1 or 2 species (Fig. 4.5A), suggesting that acarine bat ectoparasites often have high host specificity. Pairwise comparisons of host ranges were significant between three pairs of Acarine orders when adjusted for multiple t tests ($p < 0.05$, Fig. 4.5A). *Carios kelleyi* (Ixodida) and *Spinturnix americanus* (Mesostigmata) exhibited the largest host ranges (15 and 12 host species, respectively), suggesting these two species are more generalist in terms of their host compatibility. Host range was more variable for the insect orders with medians ranging from 1 to 5.5 (Fig. 4.5B). Pairwise comparisons of host ranges were not significant between Hemiptera and Siphonaptera when adjusted for multiple t tests ($p = 0.12$). *Cimex adjunctus* (Hemiptera) and *Myodopsylla gentilis* (Siphonaptera) exhibited the largest host ranges at 11 host species each while *Cimex pilosellus* (Hemiptera) had a host range of 10 species.

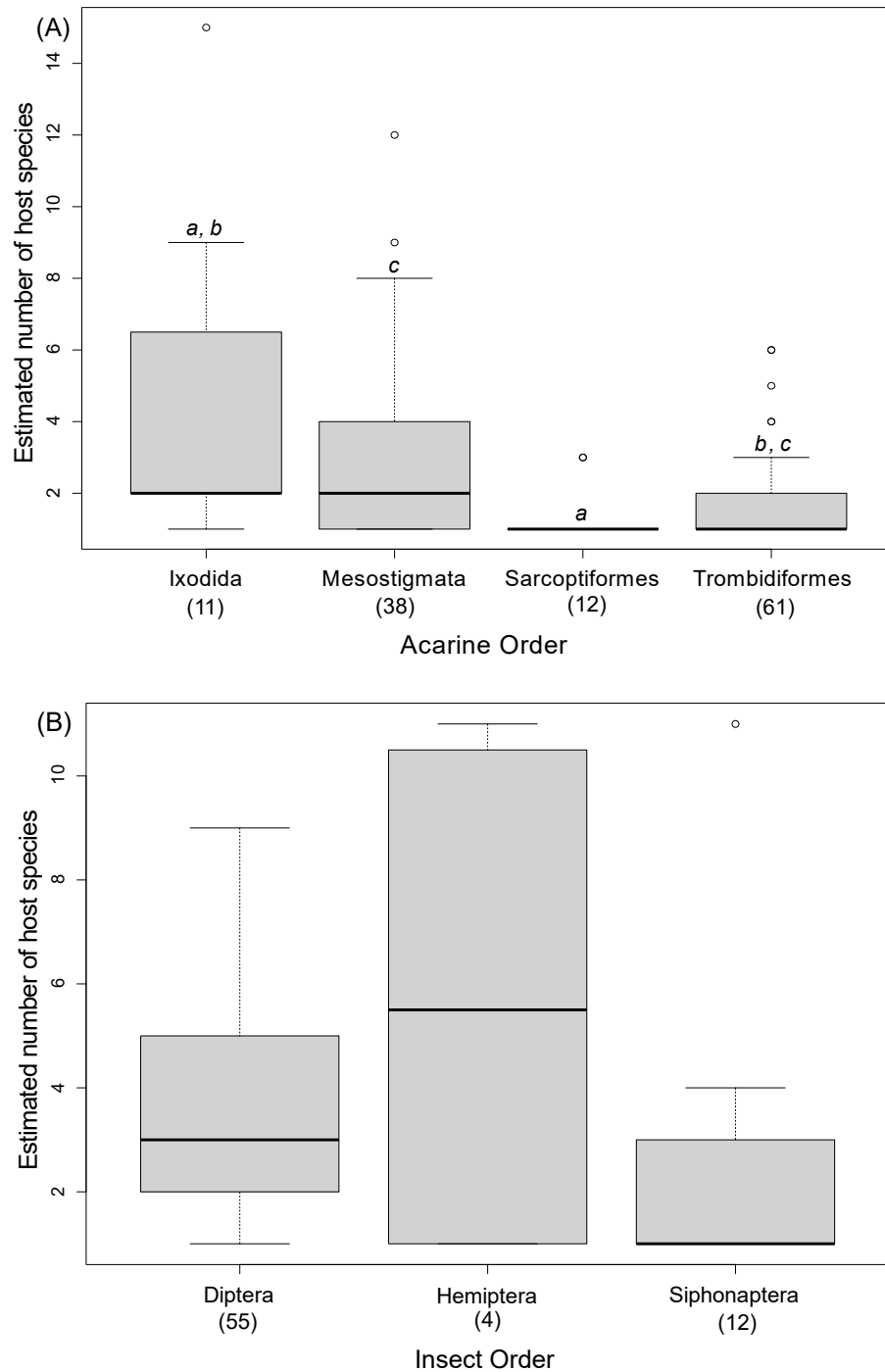


Figure 4.5: Estimated host range of ectoparasite orders infecting bats in North America: (A) acarine orders (Ixodida, Mesostigmata, Sarcoptiformes, and Trombidiformes) and (B) insect orders (Diptera, Hemiptera, and Siphonaptera). Host range is the number of host species infected by a parasite and was estimated from the degree centrality for each species in the bat-ectoparasite species network. Box plots display the median host range (black line), inter quartile range (grey

boxes) and minimum and maximum host ranges (whiskers) for each ectoparasite order. Number of species included is listed below each order. Outliers for Acari are *Carios kelleyi* (Ixodida); *Spinturnix americanus* and *Macronyssus crosbyi* (Mesostigmata); *Lawrenceocarpus chilonycteris* and *Olabidocarpus whitakeri* (Sarcoptiformes); *Leptotrombidium myotis*, *Eudusbabekia viguerasi*, and *Euschoengastia pipistrelli* (Trombidiformes). The Insecta outlier is *Myodopsylla gentilis* (Siphonaptera). Three pairs of Acarine orders exhibited significantly different host ranges when adjusted for multiple t tests: (a) $p = 0.003$, (b) $p < 0.001$, and (c) $p = 0.02$. No pairs of insect orders exhibited significantly different host ranges when adjusted for multiple t tests.

4.4.4 Bat-ectoparasite network

The network of bat-ectoparasite associations illustrates the differences in ectoparasite faunas between the two most represented bat families, Phyllostomidae and Vespertilionidae (Fig. 4.6). Most of the vespertilionid bats are situated close together in the network in comparison to the more diffuse arrangement of the Phyllostomid bats, suggesting more overlap in the ectoparasite faunas of the vespertilionid bats. The ectoparasite faunas of the more southerly distributed bat families (Molossidae, Mormoopidae, and Phyllostomidae) were dominated by bat flies (Diptera) followed by mites in the Mesostigmata and Trombidiformes orders. The more northerly distributed vespertilionid bats had fewer associations with bat flies and an increase in associations with fleas (Siphonaptera), ticks (Ixodida), and Sarcoptiformes mites. The bat families Natalidae and Emballonuridae are represented by only two species.

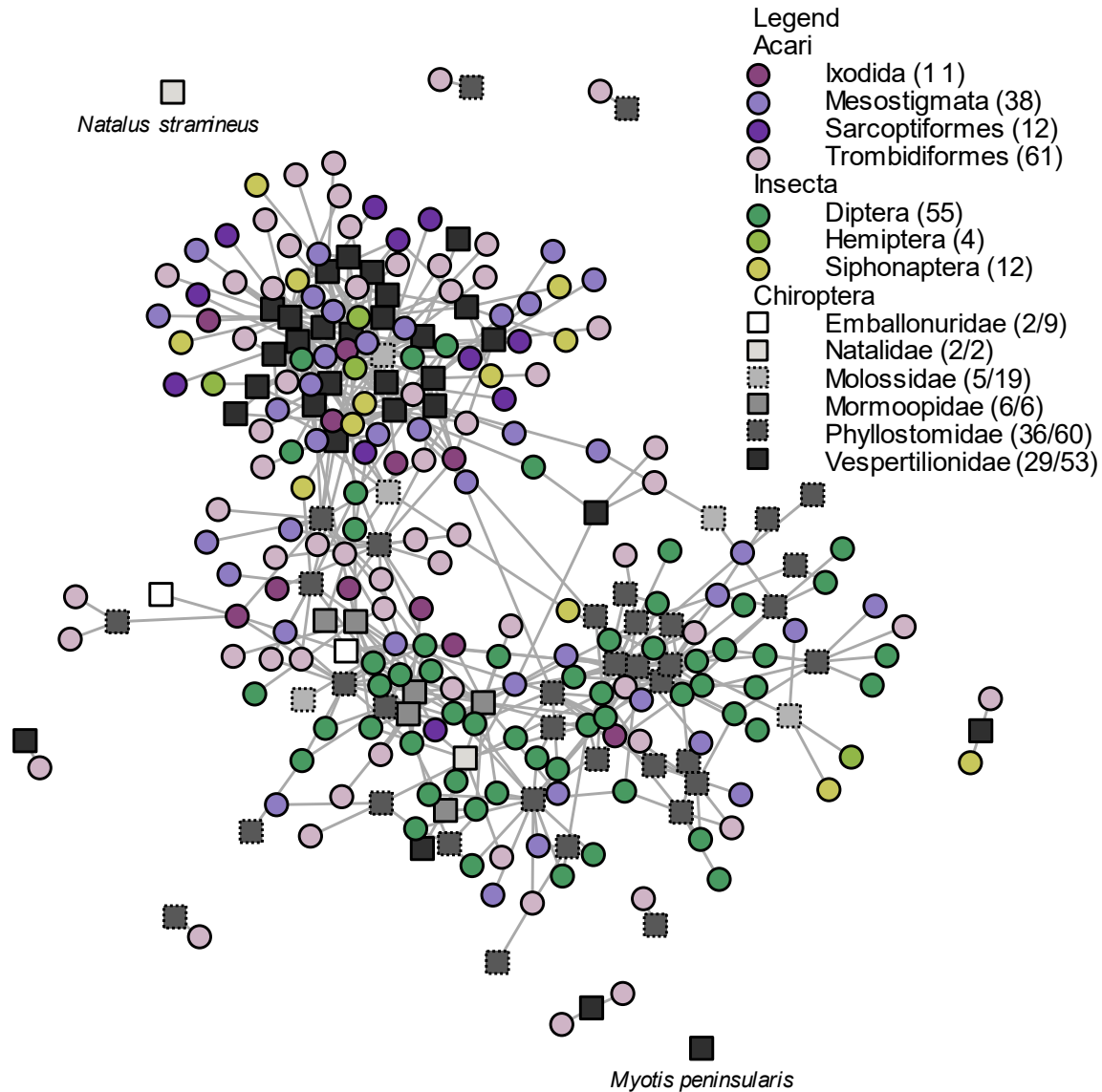


Figure 4.6: Bat-ectoparasite network of all species-level relationships within the literature. Bat species are represented by the squares and coloured by family while ectoparasite species are represented by the circles and are coloured based on their order within the Acari or Insecta. Bat species with two or fewer recorded ectoparasite species are arranged on the outskirts of the network, including *Myotis peninsularis* and *Natalus stramineus* which appear as independent squares as no ectoparasites identified to the species level were captured in the purview of this review. Number of species included in each ectoparasite order are listed next to the order names in the legend. The number of bat species included in the network for each family that are present in North America are listed next to the families in the legend. No species from the families Noctilionidae and Thyropteridae were included in the review.

4.4.5 Ectoparasite dissimilarity

The MRM analysis was run on a subset of the data from 25 articles that included bat and ectoparasite capture numbers from six states in each of USA and Mexico. The model had a moderate fit to the data with an $R^2 = 0.448$ ($p < 0.001$). Host dissimilarity and latitude dissimilarity were identified as significant factors ($p = 0.004$ and $p = 0.002$, respectively). This result is consistent with our findings that while some ectoparasites have a more generalist with a wide host range, many ectoparasites are host specific and this reflective in the different compositions of ectoparasite communities in different regions. Like the earlier modelling findings regarding ectoparasite species richness and latitude, these results support that ectoparasite community composition changes with latitude. The explanatory variables were determined to be collinear by the variance partitioning analysis and further partitioning of the variance was not possible. The GDM analysis was similarly unable to partition deviance between the explanatory variables. The large geographic spread of the data and the high species dissimilarity between regions likely contributed to the collinearity of the explanatory variables and the inability to split variance between them. More ectoparasite collections from mid-latitude locations may exhibit more incremental changes in species composition that would allow for better assessment of the environmental factors influencing ectoparasite distributions.

4.5 Discussion

The richness of the ectoparasite faunas of the bats included in this meta-analysis is strongly correlated with the number of papers that study each bat species. The more well-studied species, e.g., *Artibeus jamaicensis*, *Eptesicus fuscus*, *Myotis lucifugus*, and *Tadarida brasiliensis*, have higher reported estimated ectoparasite richness values. When controlling for sampling effort, species richness was only significantly greater for the bat family Molossidae.. The

latitudinal midpoint of bat species ranges was negatively associated with ectoparasite species richness, such that for every degree increase in latitude, there was a 3.4% decrease in species richness. This suggests that bats inhabiting lower latitudes have greater species richness of ectoparasites than those at higher latitudes, but more data is needed from bats in northern latitudes, particularly Canada, to fully characterize the latitudinal gradient. This higher species richness on bats in lower latitudes may also relate to environmental conditions increasing speciation rates in the tropics (Rohde and Heap, 1998; Poulin, 2004), however, geographic and environmental conditions could not be assessed through the MRM analysis.

Chiroptera is a diverse order with varied life history strategies and social structures that can influence their susceptibility to ectoparasites. Bats whose ranges overlap with many other bat species, such as in the species rich tropics, may encounter more ectoparasites, increasing the diversity of their ectoparasite communities (Dick and Patterson, 2007; Kamiya et al., 2014). Dáttilo et al. (2020) found the co-occurrence of bat species to be a significant predictor of ectoparasite richness in Mexico. Sharing roosts with conspecifics (Flores et al., 2020; Sunga et al., 2024) and even other bat species (Kelm et al., 2021; Jackson et al., 2023) is common for some bat species which likely facilitates transmission between host individuals and host switching between bat species (McKee et al., 2016). Additionally, group sizes reach considerably greater numbers at lower latitudes, for example roost groups of *Tadarida brasiliensis* and *Leptonycteris yerbabuenae* can number in the tens to hundreds of thousands (Cole and Wilson, 2006; Hristov et al., 2010) whereas the more temperate *Myotis lucifugus* and *Eptesicus fuscus* may gather in groups of up to a few hundred during the maternity season (Fenton and Barclay, 1980; Kurta and Baker, 1990). The seasonality of reproduction also varies between temperate and tropical regions with temperate bats experiencing monoestry (one birth a year)

interspersed with either hibernation or migration (Fenton and Barclay, 1980; Kunz, 1982; Shump and Shump, 1982; Kurta and Baker, 1990). Tropical bats may time breeding around rainy seasons or the availability of fruit, with many species having bimodal polyestry (Molinari and Soriano, 2014). These variations in bat group sizes and reproduction may coincide with patterns of diversity and abundance of their ectoparasites.

Uneven sampling effort can create the appearance of patterns in host-parasite relationships and needs to be considered when comparing ectoparasite faunas (Poulin, 1997; Dáttilo et al., 2020). Ectoparasites generally exhibit an aggregated distribution where a small number of host individuals are infected by the majority of parasites (Poulin, 2007). This distribution across the host population can require a large number of host individuals to be examined to capture the whole parasite community (Poulin and Morand, 2000; Poulin, 2007). Some bat species naturally form large gregarious groups while others roost individually or in small groups (Kerth, 2008; Hristov et al., 2010; Klug and Barclay, 2013). These differences in bat behaviour as well as how accessible each species is for research (*e.g.*, has known, physically accessible roosts or flyways), contributes to the discrepancy the number of studies between species. Less accessible species, including those absent from the literature and this review, may have robust ectoparasite faunas yet to be identified and described.

4.5.1 Geographic trends

Observations of ectoparasites within the Insecta and Acari across North America suggest different geographic trends in the distribution at the order level. The ticks and mites appear to be evenly distributed latitudinally, with observations tapering off approaching 50°. More ectoparasite collection is needed from bats in western and central Canada to determine if bat ticks and Sarcoptiformes mites are infecting Canadian bats and where the northernly limit is for

these ectoparasites. Flea and bat bug observations have a higher density of observations in mid-latitudes which is expected for fleas based on their environmental constraints (Medvedev and Krasnov, 2006). For example, few fleas were collected by (Najera-Cortazar et al., 2023) Baja California, Mexico in comparison to high abundance of fleas in Atlantic Canada (Chapter 2). The records include relatively few species of bat bugs; however, recent research suggests the presence of cryptic lineages in parts of Mexico (Najera-Cortazar et al., 2023). The greater density of bat flies at lower latitudes is also expected based on previous latitudinal patterns for these ectoparasites in the Western hemisphere (Dick and Patterson, 2006). The most northerly observations of bat flies occurred in British Columbia with *Basilia antrozoi* on *Antrozous pallidus* and *Basilia forcipata* on four species of *Myotis* (Chilton et al., 2000).

4.5.2 Sex-biased parasitism

Several of the papers examined the potential for host sex as a driver of ectoparasite infection. Female biased parasitism was evident for some species but not for others. For example, adult female *Myotis lucifugus* and *Myotis septentrionalis* consistently exhibited either higher prevalence or density of infection than males (Dick et al., 2003; Poissant and Broders, 2008; Czenze and Broders, 2011a; Webber, Czenze, et al., 2015). Czenze and Broders (2011) also found that young of year exhibited the highest prevalence of infection regardless of sex. Variation in apparent sex biases in parasitism can vary between ectoparasite species as (Reisen et al., 1976) found greater numbers of *Spinturnix carloshoffmanni* (=americanus) and *Macronyssus crosbyi* on female *Myotis velifer* but greater numbers of *Paraspinturnix globosus* on males. Similarly, (Salinas-Ramos et al., (2018) found that the average number of bat flies per host was higher for inactive males than females in the wet season for *Pteronotus davysi* and *P. personatus* but no pattern in ectoparasite load between inactive females and males in any bat species. In

comparison, (Zamora-Mejías, Morales-Malacara, et al., (2020) found no significant difference in ectoparasite prevalence between males and females of *Leptonycteris yerbabuenae*, however, abundance of the wing mite *Periglischrus paracaligus* was found to be higher on migrant females than resident females. Sex-biased parasitism is present for some bat species but whether that bias is towards higher infection in males or females appears to be dependent on the bat and ectoparasite species as well as ecological or behavioural factors.

4.5.3 Taxonomic challenges

Historically, parasitology has been focused on parasites of medical, veterinary, or agricultural concern, creating a bias in parasite discovery and description (Gómez and Nichols, 2013; Bordes and Morand, 2015). Describing parasite diversity is challenging due to the size of parasites, their location on or in their hosts, and their aggregated distribution on a small number of hosts (Poulin and Morand 2000). New species of bat ectoparasites continue to be described, such as the Spinturnid mite *Periglischrus calcariflexus* found on the Greater Long-tongued bat *Leptonycteris nivalis* in Mexico (Morales-Malacara and López-Ortega, 2023) and the Trombiculid chigger *Hoffmanniella solickiana* found on Rafinesque's Big-Eared Bat (*Corynorhinus rafinesquii*) in the USA (Crossley and Clement, 2015). DNA-based identification methods can assist in taxonomic and ecological studies of parasites whose size or overlapping morphological features make them difficult to distinguish. For example, phylogenetic research from (Najera-Cortazar et al., 2023) uncovered several undescribed lineages of bat bugs (Cimicidae), bat flies (Nycteribiidae and Streblidae), and ticks (Argasidae), suggesting that there are many more species awaiting description. (Najera-Cortazar et al., 2023) also noted that the disconnect between species with formal morphological descriptions and species with molecular data adds an additional challenge when identifying ectoparasites. Identifications based largely on

DNA are controversial (Wheeler, 2007; Meier et al., 2021) and should be combined with taxonomic and systematic work. However, parasitology, like many fields, suffers from the taxonomic impediment and the lack of taxonomic experts (Hoberg, 2002; Carlson et al., 2020).

4.5.4 Bat ectoparasites as disease vectors

The potential for the bat ectoparasites to harbour and transmit pathogens has been a focus of study globally for at least the past decade (Gay et al., 2014; McKee et al., 2016; Reeves et al., 2016; Abundes-Gallegos et al., 2018; Hornok et al., 2019). Ectoparasites can carry a variety of pathogens, including *Borrelia* (Banerjee et al., 2020), *Bartonella* (Brook et al., 2015; McKee et al., 2016; Reeves et al., 2016), and *Rickettsia* (Reeves et al., 2016; Nadolny et al., 2021). These pathogens can illicit costly immune responses (Lilley et al., 2014; Brook and Dobson, 2015; Szentiványi et al., 2020) and contribute to bats acting as reservoirs for zoonotic diseases (Luis et al., 2013; Brook and Dobson, 2015; Szentiványi et al., 2020). In North America, crossover of bat ectoparasites to humans is an area of concern for bat ticks (*Carios* spp.; Nadolny et al. 2021, Sullivan et al. 2022) and bat bugs (*Cimex* spp.; McKee et al., 2018) when bats roost in human homes. As bat populations continue to experience stressors from climate change and habitat loss, they and their ectoparasites may come into closer proximity to humans, increasing the risk of zoonotic transfer. The potential for bat ectoparasites to act as vectors of zoonotic pathogens is an on-going field of study and will require an understanding of the ecology of bat-ectoparasite relationships and the competency of bat ectoparasites to spread pathogens between hosts. Further study of bat ectoparasite faunas could provide a starting point to build hypotheses about which ectoparasites might be most likely to encounter humans.

4.5.5 Conservation challenges

The landscapes in which bats and their ectoparasites reside continue to change in the face of both anthropogenic habitat loss and climate change, both of which pose substantial risk to bat populations (Bat Conservation International, 2023). For example, three bat species were listed as endangered in Atlantic Canada after white nose syndrome caused the catastrophic collapse of colonies already under strain from habitat loss (Environment Canada, 2018). The status of the ectoparasites that infected these bats is currently unknown. The high host specificity of some bat ectoparasites would likely result in co-extinctions if their bat host were to go extinct.

Additionally, previous work by Dáttilo et al. (2020) found that while the ectoparasite faunas many mammals orders in Mexico overlap, largely due to rodent facilitated transmission, bat ectoparasite faunas overlap very little with others. This is not surprising given the long history of co-evolution between bats and their ectoparasites. If the lack of overlap in suitable hosts in other mammal orders is consistent with bat ectoparasites outside of Mexico, bat ectoparasites may not be able to switch to other mammals if bat numbers continue to decline. As this work shows, there are many bat-ectoparasite associations that we know little about and potentially hundreds more waiting to be described, with the risk that some of these ectoparasites may disappear before we have a chance to study them. These ectoparasites likely have interactions with other organisms, like fungi (Haelewaters et al., 2017; de Groot et al., 2020), and may have yet unknown important roles in food webs and ecosystems. Understanding the diversity and ecology of bat ectoparasites is integral for predicting how future environmental changes or threats to the hosts will have cascading effects on the ectoparasites and the food webs they are a part of .

4.6 Conclusion

Ectoparasite information is available for just over half of the bat species that reside in North America. The majority of ectoparasite studies were completed in Mexico and the USA where bat richness is greater. The overlap in bat species in Canada and the USA may allow for some extrapolation as per the types of ectoparasites present but more research is needed to identify species of bat ectoparasites in Canada and the different climatic factors that influence their distribution across the continent. As well, the depth of ectoparasite knowledge varies heavily between bat species, with some species having well studied ectoparasite faunas and others only having a few described parasites from a small number of publications. This variation is likely a product of bat ecology and behavioural factors that affect how accessible each species is to research, such as their group size and roosting locations. Coupled with the taxonomic difficulties in studying ectoparasites, it is unlikely that we will have a fully described ectoparasite fauna for every bat species. Nevertheless, gaining a greater understanding of the diversity of bat-ectoparasite relationships in North America is important for predicting how these interactions will be affected by climate change and habitat loss and how that will coincide with the vector potential of the ectoparasites. An increase in the collection and identification of bat ectoparasites is needed to create a more comprehensive catalogue of bat-ectoparasite associations and to continue testing hypotheses related to species richness and distribution. Multidisciplinary collaborations between bat biologists, parasitologists, and taxonomists may better provide the resources and expertise to continue this work. Passive sampling of bat ectoparasites during bat focused research could provide ample specimens for description and study if a large number of bats are available for surveying or if ectoparasites can be collected at long term study sites over many seasons. More targeted approaches to sampling will likely be required for bat species with poorly studied parasite faunas or those that are difficult to capture and study.

Chapter 5:

Synthesis and Discussion

Through an analysis of bat ectoparasite communities at multiple scales, I have provided evidence supporting the role of evolutionary and ecological forces, including host and parasite life history traits, on shaping ectoparasite communities. Looking at the regional scale, I found that while *Myotis lucifugus* and *M. septentrionalis* in Atlantic Canada have similar ectoparasite faunas overall, the prevalence and abundance of infections of a wing mite (*Spinturnix americanus*) and a flea (*Myodopsylla insignis*) differ by a combination of host and ectoparasite life history traits (Chapter 2). *Myotis lucifugus* females and their young typically roost in large maternity colonies over the summer, often in anthropogenic structures, whereas *M. septentrionalis* females and their young form smaller colonies that more often switch between tree roosts (Fenton and Barclay, 1980; Caceres and Barclay, 2000; Arnold, 2007; Sunga et al., 2022). These differences in group size and roosting ecology interact with life history strategies of their ectoparasites. *Spinturnix americanus* mites are permanent ectoparasites that gestate the non-feeding immature stages, allowing them to maintain their close association with their hosts, regardless of how often the host may switch roosts (Dowling, 2006; Orlova et al., 2018). This life history strategy allowed the mites to achieve a 90% increase in presence and 89% increase in abundance on *M. septentrionalis* relative to *M. lucifugus* (Chapter 2). Infections of *S. americanus* on *M. lucifugus* were still at or above 60% prevalence and was 46% higher on juvenile bats than adults, suggesting that mites preferentially choose hosts in the larger, more stable *M. lucifugus* groups. In comparison, early life stages of *M. insignis* fleas develop in the roost, requiring them to have a host that more consistently uses the same roost to allow new generations to continue (Smith and Clay, 1988a; Medvedev and Krasnov, 2006). This very different approach resulted in

a 79% decrease in prevalence and an 82% decrease in abundance of fleas on *M. septentrionalis* relative to *M. lucifugus* (Chapter 2), further supporting that *M. lucifugus* is the preferred host species (Smith and Clay, 1988).

In Chapter 3, I conducted a genetic analysis of these two common ectoparasites, investigating their genetic diversity and structure relative to *M. lucifugus*. I found that the differences in lifecycles and life history traits between these two ectoparasites continued to influence the dynamics of their host-parasite relationship. *Spinturnix americanus* showed similar regional genetic structure to *M. lucifugus* due to the permanency of its association, including evidence of biogeographic effects as *S. americanus* are genetically differentiated between the mainland of Labrador and the island of Newfoundland, consistent with previous findings for *M. lucifugus* (McLeod et al., 2015). Contrary to my predictions, *M. insignis* did not show statistically higher levels of genetic structure despite the separation of early life stages from the host. I did find that the higher reproductive output of *M. insignis* allowed it to exploit the lack of available roosts in Labrador and undergo a population expansion (Chapter 3). A historical population expansion of *S. americanus* likely occurred after bats moved into the regions following the last deglaciation (Burns et al., 2014), however, the viviparous reproductive method of the mites would have prevented them being able to exploit available hosts as quickly as the fleas. This work further highlights that host-parasite dynamics can vary widely, even between two co-infecting parasites on the same species, and it is important to understand both host and parasite ecology and natural history to fully understand host-parasite dynamics.

By examining ectoparasite faunas at a continental level in Chapter 4, I was able to investigate broader evolutionary and ecological factors affecting bat ectoparasites. I found that ectoparasite species richness varies between bat families and varies significantly with latitude

such that a one degree increase in latitude corresponds to a 3.4% decrease in ectoparasite richness (Chapter 4). This is consistent with the latitudinal diversity hypothesis that diversity is greater near the equator and reduces out to the poles (Rohde and Heap, 1998; Poulin, 2004), however, more ectoparasite collection is needed from bats in Canada to see how this trend continues at higher latitudes. The available literature with ectoparasite and bat capture numbers was not sufficient to determine how climate affects ectoparasite distributions, although there are clear patterns of ectoparasite distribution at the order level (Chapter 4). These patterns are particularly prevalent for the bat flies, who exhibit higher numbers at lower latitudes, and the fleas and bat bugs that are more prominent at mid-latitudes. Since ectoparasite information was only available for 53% of the bat species across Canada, the United States of America, and Mexico, more collaborative research between bat biologists, parasitologists, and taxonomists is needed to collect and catalogue ectoparasites from the underrepresented bat species. While a full catalogue of all bat ectoparasites in North America is unlikely without many decades of dedicated research, more comprehensive sampling during bat research projects could fill the gaps. This would allow future researchers to better study how the ecology and behaviour of each bat species, such as their sociality and roosting preferences, influences their individual ectoparasite faunas as well as how biogeographic phenomena influence distribution and speciation of ectoparasites across the continent.

Our understanding of the species richness of ectoparasites in Canada is limited for many host species, not only bats (Galloway and Danks, 1991). Some groups, such as the chewing lice and the mites, are especially poorly studied (Galloway and Danks, 1991). Hosts can be parasitized by a variety of ectoparasites leading to diverse assemblages living on one host, but these faunal relationships have not been identified for several parasites and hosts. Nor have the

lifecycles and demographic life history strategies of many ectoparasites (Galloway and Danks, 1991). The 20 years of ectoparasite collection by the Broders group that culminated in Chapter 2 provides an extensive look at ectoparasites of two bat species in Atlantic Canada. Previous work has also been completed on several species in British Columbia (Chilton et al., 2000) and the little brown myotis in Manitoba (Webber, Czenze, et al., 2015; Webber, McGuire, et al., 2015). Bat researchers, conservationists, and wildlife rehabbers across the other provinces and territories where bats reside could fill in the gaps by collecting ectoparasites from captured or rescued bats.

Differences in parasite life cycle and mode of transmission can have implications for host-parasite dynamics. This has been found with Bechstein's bats (*Myotis bechsteinii*) and their wing mite (*Spinturnix bechsteinii*) and bat fly (*Basilina nana*) ectoparasites (Reckardt and Kerth, 2009). Like the wing mite and bat flea system on *Myotis lucifugus* in Atlantic Canada (Chapter 3), *S. bechsteinii* is a permanent ectoparasite that requires direct host contact for transmission whereas *B. nana*, a temporary ectoparasite, does not (Reckardt and Kerth, 2009). These contrasting transmission routes may have allowed for the bat flies to choose higher quality bat hosts, having greater abundance on bats with good body condition whereas the mites show higher abundance on bats with lower body condition and reproductive females and their offspring (Reckardt and Kerth, 2009). Whether the bat flea *Myodopsylla insignis* is similarly able to choose higher quality of hosts after emerging as adults is an avenue for future study. Demographic differences in infection were found for *M. lucifugus* and *M. septentrionalis* (Czenze and Broders, 2011) and it would be interesting to see if this host-parasite system allows for parasite choice. Host characteristics do not always influence parasite infections, as is the case with the fishing bat (*Noctilio leporinus*) and its bat flies (Moura et al., 2003). Thus, patterns of

host-parasite dynamics may show consistency between species pairs with similar life histories while others may be more heavily influenced by external factors.

Where animals spend their time, whether it be foraging, resting, or simply moving through the landscape, can influence the composition of their parasite community (Mize et al., 2011; Hoken et al., 2017). Parasites must overlap with their potential hosts spatially and temporally and must attach to (ectoparasites) or enter the host (endoparasites) to successfully parasitize the host (Combes, 2001; Gómez-díaz et al., 2008). This encounter filter has been found for two species of lemurs (*Avahi occidentalis* and *Lepilemur edwardsi*), whose risk of parasitism differed between sleeping locations (Hoken et al., 2017). *Avahi occidentalis*, which slept on branches in the open, were at greater risk of mosquitoes and blood parasites whereas *L. edwardsi*, which slept in tree hollows, were more protected from mosquitoes but at greater risk from mites and ticks (Hoken et al., 2017). Where bats roost could similarly influence their encounters with ectoparasites. The tri-coloured bat (*Perimyotis subflavus*) roosts in trees with Deadman's beard lichen (*Usnea trichodea*) in Nova Scotia (Poissant et al., 2010). This lichen has anti-insect and anti-microbial properties (Ingolfssdottir, 2002) which could provide some protection from the ectoparasites that are otherwise found on sympatric *M. lucifugus* and *M. septentrionalis* (Chapter 2). (Saldaña-Vázquez et al., 2019) similarly found that roosting ecology influences bat fly interactions in the Neotropics, with bat fly niche overlap being greater in cave-roosting bats than tree-roosting bats. The landscape ecology of hosts has important consequences for their parasite communities.

Wildlife habitat is increasingly fragmented, and the loss of habitat is significant concern for many bat species in North America (Bat Conservation International, 2023). Bat preferences for roosting and foraging sites as well as parasite transmission routes may mediate the effects of

fragmentation on bat ectoparasites. However, like other factors influencing the biology of parasites, the effects of habitat fragmentation are not consistent as it appears to increase infections of some parasites and decrease infections of others (Froeschke et al., 2013; Kiene et al., 2020; Bitters et al., 2022; Perrin et al., 2023). Froeschke et al., (2013) found that parasite richness and abundance was greater in fragmented habitat, particularly for generalist parasites with free-living life stage. In contrast, fragmentation was found to cause population bottlenecks for parasites with complex lifecycles (Bitters et al., 2022) and reduced ectoparasite abundance at forest edges (Kiene et al., 2020). The lack of alternative habitat locations is also an important factor when considering host-parasite interactions. Little brown bats in Labrador are limited to a select number of cabins for roosts, preventing them from switching roosts when populations of *M. insignis* flea populations reach high intensities (Chapters 2 and 3). This case may represent the likely outcome for other bats whose roosting habitat is reduced due to habitat loss or fragmentation but maintain inter-specific interactions with some of their parasites.

Bats are facing several threats related to climate change and habitat degradation (Bat Conservation International, 2023), putting their specialized parasites at risk. While future predictions for ectoparasites are bleak (Carlson et al., 2017; Bellay et al., 2020), we cannot accurately estimate changes to distributions or record extirpations and extinctions without first knowing what ectoparasites currently infect bats. While discovering parasites is difficult and near impossible if large numbers of hosts are not examined (Poulin and Morand 2000), our research in Atlantic Canada shows that long term passive sampling of ectoparasites is effective for capturing ectoparasite diversity (Chapter 2). Some aspects of parasite biology may be difficult to study with passive sampling, such as determining seasonal changes in abundance due to climate or host reproduction as is lacking here. If the goal is to discover and monitor bat ectoparasites, passive

sampling in conjunction with ongoing bat trapping could be an effective solution at long term study sites. There is limited research on ectoparasites for several bat species, particularly species in Canada (Chapter 4), which hinders our ability to monitor these species for changes and to test theories of parasite richness and distribution. Targeted ectoparasite collections may be needed for bat species that are not readily caught as part of bat community studies or that are not used as model species for ecology and physiology studies.

Overall, bat ectoparasite communities of *M. lucifugus* and *M. septentrionalis* are influenced by both life history traits and biogeographic factors while more research is needed to better understand the diversity and structuring of bat ectoparasites communities throughout North America. Describing all parasites species may be a near impossible task but having a baseline knowledge of bat ectoparasite communities is important for three reasons. Firstly, we will have a better understanding of the interactions between not only host and ectoparasite, but also other organisms that encounter or eat the ectoparasites as well as a better understanding of the magnitude to which bat ectoparasites negatively affect their hosts. Second, it would allow us to better understand the evolutionary and ecological factors shaping these communities which will inform evolution and ecology theory generally. Third, a better understanding of the intricacies of bat-parasite interactions will allow us to predict changes to these interactions as climate change and habitat loss continue to impact these species into the future. Conservation must consider and include all species, free-living and parasite, in order to maintain balance in our ecosystems.

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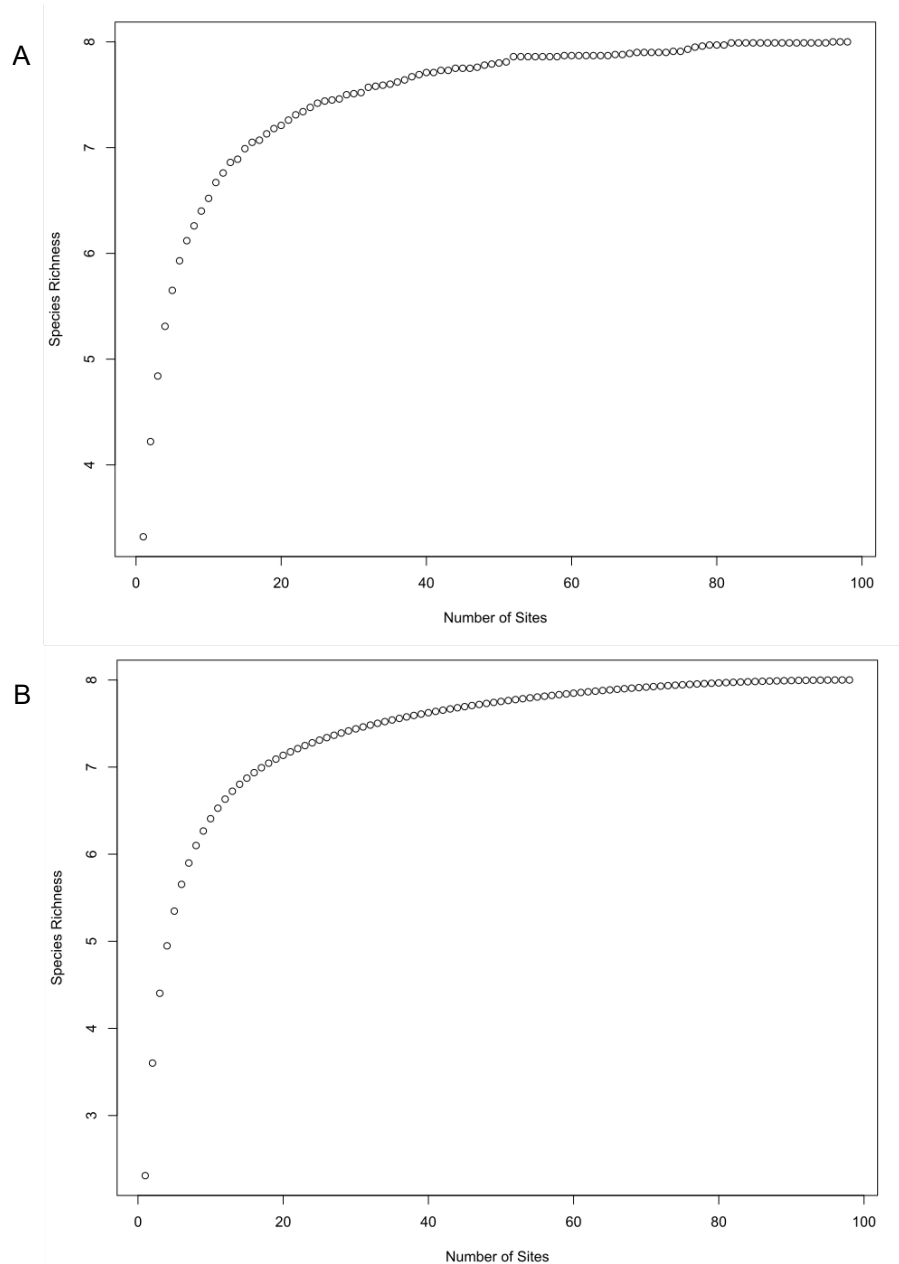
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Appendix A



Supplemental Figure 2.1: Mean species accumulation curve (A) and expected species accumulation curve (B) for ectoparasite species collected at each capture site across Atlantic Canada for both hosts, *Myotis lucifugus* and *Myotis septentrionalis*. Each capture site within a region is included and for locations with multiple sampling years, each year of collection is included as an additional site. Both summer maternity and fall swarming sites are included. Both graphs asymptote at 8 species, suggesting the passive sampling was sufficient to sample the ectoparasite faunas of *Myotis lucifugus* and *M. septentrionalis*.

Supplemental Table 2.1: Collection dates of ectoparasites at each site.

Region	Site	Collection dates
Labrador	Anne Marie Lake	2011-08-02
	Birch Brook, Goose Bay	2011-06-28, 2011-07-28
	Cache River, Labrador	2012-07-12
	Charlottetown Junction	2012-07-26
	English River	2014-07-07
	Esker rd.	2013-07-03
	Grand Lake rd.	2013-07-06, 2013-07-07
	Kaipokok River	2014-07-08
	Mary's Harbour	2012-07-27
	Minipi, Labrador	2012-07-09
	Northwest River	2011-06-23
	Practice Target Area Military Base, south central	2013-06-24, 2013-06-27
	Wabush, Lac Joseph	2011-06-25
New Brunswick	Fundy Nat Park	1999-07-27, 1999-08-17, 1999-08-18, 1999-08-23, 2000-08-09, 2001-08-14, 2001-08-15, 2001-08-16
	Hillsborough	2010-08-30, 2010-09-01
	Rockwood Park, Saint. John	2010-09-02, 2011-08-31
	Turtle Creek	2010-08-29, 2010-08-31
Prince Edward Island	Elmira	2010-07-26
	Head of Hillsborough	2010-07-27
	Hunter River	2005-07-09, 2006-07-22, 2006-07-31
	Morell	2005-07-19
	PEI Nat'l Park	2004-07-27, 2004-07-28
	Wheatley River	2006-06-17, 2006-08-10, 2006-08-11

Supplemental Table 2.1: Collection dates of ectoparasites at each site, continued.

Region	Site	Collection date
Newfoundland	Notre Dame Provincial Park	2011-07-28
	Paddys Pond	2011-08-03
	Pynnsbrook	2011-07-27, 2012-05-13, 2013-08-02, 2015-07-07, 2015-08-04, 2017-07-18
	Salmonier	2011-08-04, 2012-05-15, 2013-07-29, 2014-07-24, 2014-07-26, 2014-07-28, 2014-07-31, 2014-08-02, 2014-08-04, 2014-08-05, 2014-08-07, 2014-08-09, 2014-08-10, 2015-05-19, 2015-05-20, 2015-05-21, 2015-05-29, 2015-06-08, 2015-06-09, 2015-06-18, 2015-06-20, 2015-06-27, 2015-06-28, 2015-06-30, 2015-07-01, 2015-07-05, 2015-07-08, 2015-07-09, 2015-07-11, 2015-07-16, 2015-07-21, 2015-07-23, 2015-07-26, 2015-08-06, 2015-08-07, 2015-08-08, 2015-08-11, 2016-06-02, 2016-06-05, 2016-06-06, 2016-06-09, 2016-06-11, 2016-06-20, 2016-06-24, 2016-06-25, 2016-07-01, 2016-07-08, 2016-07-13, 2016-07-16, 2016-07-17, 2016-07-29, 2016-08-01, 2016-08-02, 2016-08-03, 2016-08-10, 2016-08-13, 2017-05-23, 2017-05-25, 2017-05-30, 2017-06-03, 2017-06-07, 2017-06-08, 2017-06-10, 2017-06-12, 2017-06-17, 2017-06-22, 2017-06-29, 2017-07-11, 2017-07-14, 2017-07-18, 2017-07-24, 2017-07-27, 2017-07-28, 2017-07-31, 2017-08-01, 2017-08-02, 2017-08-04, 2017-08-05

Supplemental Table 2.1: Collection dates of ectoparasites at each site, continued.

Region	Site	Collection date
Nova Scotia	Annapolis Royal	2011-06-16
	Cheverie	2009-08-24, 2010-08-20, 2010-09-07, 2011-08-18
	Coldstream/Gays River Area	2010-08-20
	Dollar Lake Prov Park	2005-06-26, 2006-06-20, 2006-07-29
	Donkin Peninsula, Cape Breton	2012-08-21
	Dutch Settlement	2010-08-15, 2010-09-09, 2011-08-20
	Earltown/ Nuttby	2012-06-11, 2012-06-15, 2012-06-27, 2012-07-12, 2012-07-27, 2012-07-29, 2012-07-30
	Eastern Passage	2012-05-26
	Fortress of Louisbourg	2014-09-01, 2014-09-03, 2014-09-14
	Glenelg	2010-09-06, 2010-09-10, 2011-09-08
	Ingonish, CBH National Park	2009-05-07
	Kejimikujik Nat Park	2001-05-22, 2001-07-12, 2001-09-04, 2001-09-05, 2001-09-06, 2003-06-02, 2003-06-23, 2003-06-24, 2003-07-22, 2003-07-25, 2003-07-26, 2003-07-27, 2003-07-28, 2003-08-19, 2004-06-01, 2007-05-29, 2007-06-03, 2008-06-04, 2008-06-19, 2008-08-05
	Kingston	2010-09-16, 2011-09-26
	Lake Charlotte	2004-10-14, 2010-08-24, 2011-08-16, 2011-08-26
	Londonderry	2004-09-27, 2004-10-13, 2009-08-21, 2010-08-19, 2010-09-02, 2010-09-03, 2010-09-04, 2010-09-10, 2010-09-12, 2010-09-16, 2010-09-18, 2010-09-23
	Martock	2011-05-26
	Millvillage	2011-06-09
	Minasville	2010-08-16, 2010-09-01, 2011-09-15
	Mineville	2011-06-02, 2011-06-13
	Nine Mile River	2010-08-24
	Nuttby	2011-07-12
	Rawdon	2008-05-21, 2010-06-16, 2010-07-02, 2010-07-21, 2010-07-26, 2010-08-09, 2010-08-11, 2010-08-12, 2010-08-13, 2010-08-14, 2010-08-16, 2010-08-18, 2010-08-19, 2010-08-23, 2010-08-27, 2010-08-30, 2010-09-06, 2010-09-12, 2010-09-19, 2010-09-26, 2010-10-03, 2011-06-05, 2011-06-16, 2011-08-24, 2011-08-30

Supplemental Table 2.1: Collection dates of ectoparasites at each site, continued.

Region	Site	Collection date
Nova Scotia	Renfrew	2011-07-28
	River Hebert	2011-08-09
	South Maitland	2003-09-07, 2003-10-05, 2004-08-24, 2004-09-05, 2004-09-25, 2005-05-31, 2006-08-23, 2006-08-24, 2006-08-25, 2006-08-27, 2006-08-28, 2006-08-29, 2006-09-01, 2006-09-09, 2006-09-15, 2006-09-28, 2006-09-30, 2007-10-05, 2010-08-16, 2010-08-26, 2010-09-21, 2010-09-30
	St Croix	2003-09-24, 2010-08-29, 2010-09-19
	Stewiacke	2010-08-21
	Tatamagouche	2010-07-08, 2011-05-30
	Tennycap	2010-08-28
	Vinegar Lake	2004-06-24
	Waverley	2011-07-18
	West Chezzetcook	2011-07-17, 2011-07-29
	Woodville	2010-08-18

Supplemental Table 2.2: Prevalence of ectoparasite infections (%) on *Myotis lucifugus* for each region and demographic. Number of bats sampled per region is included in brackets beside the region name and the number of infected individuals is included in brackets beside the prevalence values. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	SPAM
Labrador	Adult	Female (78)	3.8 (3)	3.8 (3)	9.0 (7)	3.8 (3)	16.7 (13)	76.9 (60)
		Male (0)	NA	NA	NA	NA	NA	NA
		Unknown sex (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (1)
	Juvenile	Female (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (1)	0.0 (0)
		Male (8)	0.0 (0)	0.0 (0)	0.0 (0)	12.5 (1)	62.5 (5)	87.5 (7)
		Unknown sex (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	50.0 (1)	50.0 (1)
	Age class unknown	Female (18)	5.6 (1)	5.6(1)	0.0 (0)	16.7 (3)	77.8 (14)	55.6 (10)
		Male (5)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (5)	20.0 (1)
Newfoundland	Adult	Female (324)	0.3 (0)	1.5 (5)	3.1 (10)	2.5 (8)	35.5 (115)	73.8 (239)
		Male (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (2)	0.0 (0)
	Juvenile	Female (96)	0.0 (0)	0.0 (0)	0.0 (0)	1.0 (1)	7.3 (7)	94.8 (91)
		Male (92)	0.0 (0)	0.0 (0)	0.0 (0)	1.1 (1)	19.6 (18)	85.9 (79)
Nova Scotia	Adult	Female (204)	0.0 (0)	2.9 (6)	2.9 (6)	2.5 (5)	34.3 (70)	70.1 (143)
		Male (67)	0.0 (0)	0.0 (0)	10.5 (7)	3.0 (2)	43.3 (29)	49.3 (33)
	Juvenile	Female (40)	0.0 (0)	2.5 (1)	5.0 (2)	2.5 (1)	42.5 (17)	55.0 (22)
		Male (38)	0.0 (0)	0.0 (0)	7.9 (3)	0.0 (0)	36.8 (14)	60.5 (23)
	Age class unknown	Female (27)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	63.0 (17)	63.0 (17)
		Male (27)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	96.3 (26)	26.0 (7)

Supplemental Table 2.2: Prevalence of ectoparasite infections (%) on *Myotis lucifugus* for each region and demographic, continued. Number of bats sampled per region is included in brackets beside the region name and the number of infected individuals is included in brackets beside the prevalence values. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	SPAM
New Brunswick	Adult	Female (15)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	86.7 (13)	26.7 (4)
		Male (11)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	54.5(6)	45.5 (5)
	Juvenile	Female (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	83.3 (5)	16.7 (1)
		Male (7)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	85.7 (6)	14.3 (1)
	Age class unknown	Female (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	50.0 (2)	50.0 (2)
		Male (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	66.7 (2)	33.3 (1)
Prince Edward Island	Adult	Female (5)	0.0 (0)	0.0 (0)	0.0 (0)	20.0 (1)	20.0 (1)	60.0 (3)
		Male (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	50.0 (1)	50.0 (1)
	Juvenile	Female (3)	33.3 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (3)
		Male (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (2)

Supplemental Table 2.3: Mean intensity of ectoparasite infections on *Myotis lucifugus* for each region and demographic. Number of bats sampled per region is included in brackets beside the region name. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	SPAM
Labrador	Adult	Female (78)	1.0 +/- 0.0	1.0 +/- 0.0	2.0 +/- 1.0	1.0 +/- 0.0	1.0 +/- 0.0	2.2 +/- 0.2
		Male	NA	NA	NA	NA	NA	NA
		Unknown sex (1)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	2.0 +/- 0.0
	Juvenile	Female (1)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	2.0 +/- 0.0	0.0 +/- 0.0
		Male (8)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	2.0 +/- 0.0	3.4 +/- 1.7	1.9 +/- 0.5
		Unknown sex (2)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	2.0 +/- 0.0	1.0 +/- 0.0
	Age class unknown	Female (18)	1.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	5.1 +/- 1.8	1.8 +/- 0.3
		Male (5)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	12.0 +/- 5.0	1.0 +/- 0.0
Newfoundland	Adult	Female (324)	1.0 +/- 0.0	1.4 +/- 0.4	5.3 +/- 2.5	1.3 +/- 0.2	2.4 +/- 0.2	2.2 +/- 0.1
		Male (2)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	29.0 +/- 0.5	0.0 +/- 0.0
	Juvenile	Female (96)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.4 +/- 0.3	2.8 +/- 0.3
		Male (92)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	3.1 +/- 1.5	3.1 +/- 0.3
Nova Scotia	Adult	Female (204)	0.0 +/- 0.0	1.0 +/- 0.0	3.5 +/- 2.5	1.4 +/- 0.4	1.9 +/- 0.2	1.8 +/- 0.1
		Male (66)	0.0 +/- 0.0	0.0 +/- 0.0	1.7 +/- 0.4	1.0 +/- 0.0	1.9 +/- 0.4	1.2 +/- 0.1
	Juvenile	Female (40)	0.0 +/- 0.0	1.0 +/- 0.0	1.5 +/- 0.5	1.0 +/- 0.0	1.6 +/- 0.2	2.4 +/- 0.5
		Male (38)	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.3	1.4 +/- 0.2
	Age class unknown	Female (27)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.8 +/- 0.3	1.7 +/- 0.3
		Male (27)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	4.1 +/- 0.8	1.4 +/- 0.2

Supplemental Table 2.3: Mean intensity of ectoparasite infections on *Myotis lucifugus* for each region and demographic, continued. Number of bats sampled per region is included in brackets beside the region name. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	SPAM
New Brunswick	Adult	Female (15)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.2	1.5 +/- 0.5
		Male (11)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.2 +/- 0.2	1.0 +/- 0.0
	Juvenile	Female (6)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.2 +/- 0.2	3.0 +/- 0.0
		Male (7)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.3 +/- 0.2	2.0 +/- 0.0
	Age class unknown	Female (4)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.5	1.5 +/- 0.5
		Male (3)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.5	1.0 +/- 0.0
Prince Edward Island	Adult	Female (5)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.0 +/- 0.0	2.0 +/- 0.6
		Male (2)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.0 +/- 0.0
	Juvenile	Female (3)	1.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.3 +/- 0.3
		Male (2)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.5

Supplemental Table 2.4: Prevalence of ectoparasite infections (%) on *Myotis septentrionalis* for each region and demographic. Number of bats sampled per region is included in brackets beside the region name and the number of infected individuals is included in brackets beside the prevalence values. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; ORCA = *Orchopeas caedens*, and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	ORCA	SPAM
Labrador	Adult	Female (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (1)
		Male (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (2)
	Juvenile	Female	NA	NA	NA	NA	NA	NA	NA
		Male	NA	NA	NA	NA	NA	NA	NA
Nova Scotia	Adult	Female (50)	0.0 (0)	10.0 (5)	0.0 (0)	10.0 (5)	10.0 (5)	0.0 (0)	78.0 (39)
		Male (35)	0.0 (0)	2.9 (1)	0.0 (0)	0.0 (0)	28.6 (10)	2.9 (1)	68.6 (24)
	Juvenile	Female (29)	0.0 (0)	6.9 (2)	0.0 (0)	10.4 (3)	10.4 (3)	0.0 (0)	89.7 (26)
		Male (41)	0.0 (0)	9.8 (4)	4.9 (2)	7.3 (3)	4.9 (2)	0.0 (0)	87.8 (36)
	Age class unknown	Female (23)	4.4 (1)	0.0 (0)	0.0 (0)	13.0 (3)	8.7 (2)	0.0 (0)	91.3 (21)
		Male (27)	0.0 (0)	7.4 (2)	0.0 (0)	11.1 (3)	18.5 (5)	3.7 (1)	81.5 (22)
New Brunswick	Adult	Female (9)	0.0 (0)	11.1 (1)	0.0 (0)	0.0 (0)	33.3 (3)	0.0 (0)	66.7 (6)
		Male (9)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	22.2 (2)	0.0 (0)	77.8 (7)
	Juvenile	Female (3)	0.0 (0)	33.3 (1)	0.0 (0)	33.3 (1)	33.3 (1)	0.0 (0)	66.7 (2)
		Male (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	16.7 (1)	0.0 (0)	100.0 (6)
	Age class unknown	Female (10)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	10.0 (1)	0.0 (0)	100.0 (10)
		Male (5)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	20.0 (1)	0.0 (0)	100.0 (5)
Prince Edward Island	Adult	Female (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (3)
		Male (4)	0.0 (0)	75.0 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	25.0 (1)
	Juvenile	Female (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (1)
		Male (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (1)

Supplemental Table 2.5: Mean intensity of ectoparasite infections on *Myotis septentrionalis* for each region and demographic. Number of bats sampled per region is included in brackets beside the region name. ANCA = *Androlaelaps casalis*; CIAD = *Cimex adjunctus*; LEMY = *Leptotrombidium myotis*; MACR = *Macronyssus crosbyi*; MYIN = *Myodopsylla insignis*; ORCA = *Orchopeas caedens*, and SPAM = *Spinturnix americanus*.

Region	Age Class	Sex	ANCA	CIAD	LEMY	MACR	MYIN	ORCA	SPAM
Labrador	Adult	Female (1)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	2.0 +/- 0.0
		Male (2)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	4.5 +/- 2.5
	Juvenile	Female	NA	NA	NA	NA	NA	NA	NA
		Male	NA	NA	NA	NA	NA	NA	NA
Nova Scotia	Adult	Female (50)	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	3.6 +/- 2.4	1.0 +/- 0.0	0.0 +/- 0.0	1.9 +/- 0.2
		Male (35)	0.0 +/- 0.0	2.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.0 +/- 0.0	1.5 +/- 0.3
	Juvenile	Female (29)	0.0 +/- 0.0	1.5 +/- 0.5	0.0 +/- 0.0	1.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.8 +/- 0.2
		Male (41)	0.0 +/- 0.0	1.0 +/- 0.0	2.5 +/- 1.5	2.3 +/- 1.3	1.0 +/- 0.0	0.0 +/- 0.0	1.9 +/- 0.3
	Age class unknown	Female (23)	2.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.3 +/- 0.2	1.0 +/- 0.0	0.0 +/- 0.0	2.3 +/- 0.1
		Male (27)	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.3 +/- 0.2	1.0 +/- 0.0	2.0 +/- 0.3
New Brunswick	Adult	Female (9)	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.3 +/- 0.3
		Male (9)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.4 +/- 0.3
	Juvenile	Female (3)	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	3.0 +/- 1.0
		Male (6)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.8 +/- 0.3
	Age class unknown	Female (10)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	1.5 +/- 0.2
		Male (5)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	2.2 +/- 0.6
Prince Edward Island	Adult	Female (3)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0
		Male (4)	0.0 +/- 0.0	1.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0
	Juvenile	Female (1)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0
		Male (1)	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	0.0 +/- 0.0	1.0 +/- 0.0

Supplemental Table 2.6: Correlation coefficients of prevalence of ectoparasites versus the number of sampled hosts.

Ectoparasite	<i>Myotis lucifugus</i>		<i>Myotis septentrionalis</i>	
	Pearson Correlation Coefficient	<i>p</i> -value	Pearson Correlation Coefficient	<i>p</i> -value
<i>Androlaelaps casalis</i>	-0.61	0.27	0.98	0.02
<i>Cimex adjunctus</i>	0.19	0.76	-0.24	0.76
<i>Leptotrombidium myotis</i>	0.3	0.63	0.98	0.02
<i>Macronyssus crosbyi</i>	-0.46	0.44	0.99	0.01
<i>Myodopsylla insignis</i>	-0.18	0.77	0.44	0.56
<i>Orchopeas caedans</i>	NA	NA	0.98	0.02
<i>Spinturnix americanus</i>	0.36	0.55	-0.13	0.87

Appendix B

Supplemental Table 3.1. The number of *Spinturnix americanus* successfully sequenced from each site across years.

Region	Sites	2010	2011	2012	2013	2014	2015	2016	2017
Labrador	Anne Marie Lake		10						
	Birch Brook		18						
	Cache River			6					
	Charlottetown Junction			10					
	English River					13			
	Grand Lake rd.				7				
	Kaipokok River					11			
	Lac Joseph		4						
	Minipi			4					
	Northwest River		4						
	Wabush		2						
Newfoundland	Notre Dame Provincial Park		10						
	Paddy's Pond		6						
	Pynns Brook		12		1		3		
	Salmonier Nature Park		1			1		2	10
Nova Scotia	Martock		12						
	Millvillage		16						
	Mineville		3						
	Rawdon	3	10						
	Renfrew		8						
	Tatamagouche	5							
	Vault Cave	3							
	Waverley		5						
	West Chezzetcook		8						
Prince Edward Island	Head of Hillsborough	10							

Supplemental Table 3.2. The number of *Myodopsylla insignis* successfully sequenced from each site across years.

Region	Site	2010	2011	2012	2014	2015	2016	2017
Labrador	Anne Marie Lake		23					
	Birch Brook		2					
	Cache River, Labrador			4				
	Charlottetown Junction			7				
	Minipi			2				
Newfoundland	Notre Dame Provincial Park		3					
	Paddys Pond		6					
	Salmonier Nature Park		2		2	5	4	1
Nova Scotia	Annapolis Royal		3					
	Martock		3					
	Rawdon	2	8					
	Renfrew		7					
	Tatamagouche	1	2					

Supplemental Table 3.3. Pairwise F_{ST} values for *Spinturnix americanus* showing the degree of population structuring between pairs of sites in Nova Scotia, Newfoundland, Labrador, and Prince Edward Island between 2010 and 2017. Bold F_{ST} values indicate significant pairs after Bonferroni correction.

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
2	0.00																						
3	0.06	-0.01																					
4	0.26	0.08	0.25																				
5	0.01	-0.08	-0.07	0.18																			
6	0.05	-0.12	-0.03	0.14	-0.10																		
7	0.08	-0.04	-0.04	0.24	-0.09	-0.07																	
8	0.09	-0.05	-0.03	0.19	-0.07	-0.09	-0.06																
9	-0.08	-0.12	-0.17	0.25	-0.25	-0.18	-0.19	-0.14															
10	0.35	0.18	0.32	-0.15	0.27	0.29	0.32	0.28	0.40														
11	-0.02	-0.04	0.01	0.16	-0.02	0.02	0.03	0.04	-0.05	0.21													
12	0.03	-0.01	0.06	0.18	0.02	0.06	0.07	0.08	0.01	0.21	-0.06												
13	0.46	0.30	0.40	0.01	0.39	0.44	0.42	0.38	0.53	-0.09	0.29	0.26											
14	0.25	0.19	0.07	0.63	0.05	0.08	0.04	0.05	-0.08	0.68	0.30	0.33	0.75										
15	0.19	0.10	-0.03	0.76	-0.03	-0.03	-0.04	-0.05	-0.09	0.78	0.22	0.24	0.80	-0.10									
16	0.38	0.32	0.24	0.59	0.22	0.23	0.23	0.18	0.15	0.65	0.41	0.44	0.72	0.12	0.13								
17	0.27	0.17	0.04	0.74	0.02	0.03	0.02	0.01	-0.09	0.77	0.31	0.34	0.80	-0.21	-0.17	0.07							
18	0.25	0.15	0.10	0.44	0.09	0.08	0.08	0.04	0.03	0.49	0.23	0.26	0.57	0.07	-0.04	0.02	0.01						
19	0.33	0.23	0.12	0.60	0.12	0.13	0.11	0.08	0.04	0.65	0.34	0.36	0.71	-0.06	-0.08	0.01	-0.15	-0.01					
20	0.39	0.29	0.14	0.80	0.22	0.25	0.19	0.14	0.32	0.80	0.34	0.32	0.81	0.34	0.09	0.33	0.37	0.07	0.23				
21	0.29	0.23	0.12	0.74	0.17	0.17	0.16	0.10	0.20	0.76	0.29	0.30	0.78	0.27	0.09	0.18	0.29	-0.01	0.15	-0.06			
22	0.13	0.06	0.04	0.35	0.01	-0.02	0.03	-0.02	-0.07	0.46	0.15	0.19	0.59	0.08	-0.06	0.02	0.02	-0.08	0.02	0.05	-0.07		
23	0.39	0.34	0.26	0.63	0.27	0.27	0.28	0.21	0.25	0.68	0.40	0.42	0.74	0.28	0.22	0.00	0.27	0.02	0.15	0.26	0.07	-0.02	
24	0.08	0.08	-0.02	0.52	-0.01	0.05	0.01	0.03	-0.09	0.56	0.10	0.12	0.63	0.09	-0.06	0.28	0.10	0.09	0.14	0.09	0.10	0.05	0.29

Sites in order from 1 to 24: Waverly, Renfrew, Millvillage, Mineville, West Chezzetcook, Tatamagouche, Martock, Rawdon, Vault Cave (Nova Scotia); Paddy's Pond, Notre Dame, Pynnsbrook, Salmonier (Newfoundland); Wabush, Northwest River, Charlottetown Junction, Minipi, BirchBrook, Kaipokok, English River, Grand Lake, Cache River, Anne Marie Lake (Labrador); and Hillsborough (Prince Edward Island).

Supplemental Table 3.4: Pairwise F_{ST} values for *Myodopsylla insignis* showing the degree of population structuring between pairs of sites in Nova Scotia, Newfoundland, and Labrador between 2010 and 2017. Bold F_{ST} values indicate significant pairs after Bonferroni correction.

	Newfoundland			Labrador					Nova Scotia			
	Paddy's			Charlottetown			Anne Marie					
Site	Salmonier	Pond	Notre Dame	Cache River	Junction	Minipi	Birch Brook	Lake	Tatamagouche	Martock	Renfrew	Rawdon
Paddy's Pond	0.00											
Notre Dame	-0.02	-0.08										
Cache river	0.07	-0.05	-0.07									
Charlottetown												
Junction	0.13	0.05	0.01	-0.06								
Minipi	0.12	0.03	0.05	0.19	-0.07							
Birch Brook	0.02	-0.11	-0.20	-0.14	-0.13	0.00						
Anne Marie Lake	0.25	0.20	0.17	-0.06	0.06	0.43	-0.03					
Tatamagouche	0.28	0.19	0.25	0.40	0.31	0.38	0.34	0.56				
Martock	0.17	0.06	0.02	0.13	0.16	0.17	0.01	0.39	-0.06			
Renfrew	0.26	0.20	0.22	0.26	0.31	0.42	0.22	0.47	-0.01	-0.03		
Rawdon	0.26	0.21	0.24	0.26	0.32	0.44	0.22	0.44	-0.06	-0.06	-0.03	
Annapolis Royal	0.18	0.09	0.06	0.18	0.17	-0.07	-0.04	0.50	-0.11	-0.05	0.13	0.13

Appendix C

The following tables include the list of bat-ectoparasite associations summarised from the literature that was used for the systematic review in Chapter 4. The references are included in the Bibliography preceding this Appendix. References denoted with a * include data collected from multiple sources.

Supplemental Table 4.1: Bat-ectoparasite associations for bat families Emballonuridae, Molossidae, and Natalidae.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
Emballonuridae				
<i>Balantiopteryx plicata</i>	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Antricola mexicanus</i>	Ixodida	Mexico	Colin-Martínez et al., 2018
	<i>Carios dyeri</i>	Ixodida	Mexico	Colin-Martínez et al., 2018
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
	<i>Expletobia</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Peropteryx macrotis</i>	<i>Carios dyeri</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2016
Molossidae				
<i>Eumops perotis</i>	<i>Hesperoctenes eumops</i>	Hemiptera	USA	Whitaker and Easterla 1975
	<i>Chiroptonyssus haematophagus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Hormopsylla trux</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Rhynchopsyllus pulex</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker and Easterla 1975
<i>Molossus nigricans</i>	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
<i>Nyctinomops femorosaccus</i>	<i>Chiroptonyssus</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Chiroptonyssus haematophagus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Chiroptonyssus venezolanus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
<i>Nyctinomops macrotis</i>	<i>Carios stageri</i>	Ixodida	USA	Whitaker and Easterla 1975
	<i>Chiroptonyssus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Steatonyssus occidentalis</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Hormopsylla trux</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Eudusbabekia</i>	Trombidiformes	USA	Whitaker and Easterla 1975
	<i>Tecomatlana texana</i>	Trombidiformes	USA	Whitaker and Easterla 1975

Supplemental Table 4.1: Bat-ectoparasite associations for bat families Emballonuridae, Natalidae, and Molossidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Tadarida brasiliensis</i>	<i>Trichobius leionotus</i>	Diptera	Mexico	Guzman-Cornejo et al., 2003
	<i>Cimex adjunctus</i>	Hemiptera	USA	Bowles et al., 2013*
	<i>Antricola</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2003
	<i>Carios kelleyi</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2003
	<i>Carios stageri</i>	Ixodida	USA	Ritzi et al., 2001; Whitaker and Easterla 1975
	<i>Carios yumatensis</i>	Ixodida	USA	Dooley et al., 1976
	<i>Androlaelaps casalis</i>	Mesostigmata	USA	Durden et al., 1992
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	Mexico	Guzman-Cornejo et al., 2003
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Foster and Mertins 1996; Durden et al., 1992; McAllister et al., 2006; Ritzi et al., 2001; Whitaker and Easterla 1975; Dooley et al., 1976
	<i>Macronyssus unidens</i>	Mesostigmata	Mexico	Guzman-Cornejo et al., 2003
	<i>Steatonyssus ceratognathus</i>	Mesostigmata	USA	Durden et al., 1992
	<i>Steatonyssus occidentalis</i>	Mesostigmata	USA	Durden et al., 1992; Whitaker and Easterla 1975
	Psocodea	Psocodea	USA	Foster and Mertins 1996
	<i>Dentocarpus macrotrichus</i>	Sarcoptiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Dentocarpus macrotrichus</i>	Sarcoptiformes	USA	Foster and Mertins 1996
	<i>Notoedres (Bakeracarus)</i>	Sarcoptiformes	USA	Foster and Mertins 1996
	<i>Notoedres (Bakeracarus) lasionycteris</i>	Sarcoptiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Notoedres (Notoedres)</i>	Sarcoptiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Nycteriglyphus bifolium</i>	Sarcoptiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Olabidocarpus nyctinomus</i>	Sarcoptiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Sternopsylla distincta</i>	Siphonaptera	Mexico	Guzman-Cornejo et al., 2003
	<i>Sternopsylla distincta</i>	Siphonaptera	USA	Durden et al., 2012; Ritzi et al., 2001; Whitaker and Easterla 1975

Supplemental Table 4.1: Bat-ectoparasite associations for bat families Emballonuridae, Natalidae, and Molossidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Tadarida brasiliensis</i>	Cheyletidae	Trombidiformes	USA	Foster and Mertins 1996
	<i>Ewingana (Doreyana)</i>	Trombidiformes	USA	Foster and Mertins 1996
	<i>Ewingana (Doreyana) inaequalis</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2003; Herrera-Mares et al., 2021*
	<i>Ewingana (Doreyana) inaequalis</i>	Trombidiformes	USA	Foster and Mertins 1996
	<i>Ewingana (Doreyana) longa</i>	Trombidiformes	USA	Durden et al., 1992
	<i>Ewingana (Ewingana) longa</i>	Trombidiformes	USA	Foster and Mertins 1996
	<i>Ewingana (Mormomyobia) longa</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2003; Herrera-Mares et al., 2021*
	<i>Ewingana longa</i>	Trombidiformes	USA	Ritzi et al., 2001
	<i>Leptotrombidium mexicana</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Raphignathus</i>	Trombidiformes	USA	Foster and Mertins 1996
	Trombiculidae	Trombidiformes	USA	Ritzi et al., 2001
	<i>Whartonia</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2003
	<i>Whartonia (Asolentria)</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2003
Natalidae				
<i>Natalus mexicanus</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Trichobius galei</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Natalimyobia handleyi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Natalus stramineus</i>	<i>Trichobius</i>	Diptera	Mexico	Dittmar et al., 2009

Supplemental Table 4.2: Bat-ectoparasite associations for bat family Mormoopidae.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
Mormoopidae				
<i>Mormoops megalophylla</i>	<i>Nycterophilia</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Nycterophilia mormoopsis</i>	Diptera	Mexico	Orta-Pineda et al., 2020; Martínez et al., 2016
	<i>Nycterophilia natali</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Trichobius</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Trichobius galei</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Trichobius hoffmannae</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius leionotus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019; Martínez et al., 2016; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius leionotus</i>	Diptera	USA	Ritzi et al., 2001
	<i>Trichobius sphaeronotus</i>	Diptera	Mexico	Martínez et al., 2016; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius yunkerii</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Antricola</i>	Ixodida	Mexico	Martínez et al., 2016
	<i>Carios mormoops</i>	Ixodida	USA	Whitaker and Easterla 1975
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Eudusbabekia ecuadorensis</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Wagenaaria similis</i>	Trombidiformes	USA	Whitaker and Easterla 1975
<i>Pteronotus davyi</i>	<i>Nycterophilia coxata</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019

Supplemental Table 4.2: Bat-ectoparasite associations for bat family Mormoopidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Pteronotus davyi</i>	<i>Trichobius diphyllae</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius galei</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius hoffmannae</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius johnsonae</i>	Diptera	Mexico	Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019
	<i>Trichobius sphaeronotus</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018
	<i>Trichobius yunkerii</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Antricola coprophilus</i>	Ixodida	Mexico	Salinas-Ramos et al., 2019
	<i>Cameronieta</i>	Mesostigmata	Mexico	Salinas-Ramos et al., 2019
	<i>Lawrenceocarpus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Lawrenceocarpus chilonycteris</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Nycteriglyphus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Beamerella</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Eudusbabekia saguei</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Perates nudosetosus</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Phalcophila</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Phalcophila postica</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
<i>Pteronotus fulvus</i>	<i>Nycterophila parnelli</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius leionotus</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
<i>Pteronotus mesoamericanus</i>	<i>Trichobius caecus</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius johnsonae</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius sparsus</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023

Supplemental Table 4.2: Bat-ectoparasite associations for bat family Mormoopidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Pteronotus parnellii</i>	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Nycterophilia coxata</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018
	<i>Nycterophilia mormoopsis</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019
	<i>Trichobius caecus</i>	Diptera	Mexico	Moskaluk et al., 2018; Orta-Pineda et al., 2020
	<i>Trichobius hoffmannae</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Trichobius johnsonae</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Trichobius longipilis</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Trichobius sparsus</i>	Diptera	Mexico	Martínez et al., 2016; Tlapaya-Romero et al., 2019
	<i>Trichobius sphaeronotus</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Trichobius uniformis</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius yunkeri</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019
	<i>Antricola mexicanus</i>	Ixodida	Mexico	Colin-Martinez et al., 2018
	<i>Carios brodyi</i>	Ixodida	Mexico	Colin-Martinez et al., 2018
	<i>Cameronieta elongatus</i>	Mesostigmata	Mexico	Salinas-Ramos et al., 2019
	Macronyssidae	Mesostigmata	Mexico	Salinas-Ramos et al., 2019
	<i>Periglischrus ojasitii</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Lawrenceocarpus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019

Supplemental Table 4.2: Bat-ectoparasite associations for bat family Mormoopidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Pteronotus parnellii</i>	<i>Lawrenceocarpus chilonycteris</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Nycteriglyphus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Eudusbabekia jimenezi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	Myobiidae	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Phalcophila postica</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
<i>Pteronotus personatus</i>	<i>Nycterophilia coxata</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Salinas-Ramos et al., 2018; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Trichobius johnsonae</i>	Diptera	Mexico	Martínez et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius sphaeronotus</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Trichobius yunkerii</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Cameronieta</i>	Mesostigmata	Mexico	Salinas-Ramos et al., 2019
	<i>Lawrenceocarpus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Lawrenceocarpus chilonycteris</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Nycteriglyphus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Perates nudosetosus</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2018
	<i>Phalcophila postica</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2018
	<i>Whartonia glenni</i>	Trombidiformes	Mexico	Salinas-Ramos et al., 2019

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Anoura geoffroyi</i>	<i>Anastrebla modestini</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Aspidoptera delatorrei</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Exastinion clovisi</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; Trujillo-Pahua and Ibáñez-Bernal 2019; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Nycterophilia coxata</i>	Diptera	Mexico	Hernández-Arciga et al., 2016
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; Morales-Malacara and Lopez-Ortega 2023*
<i>Artibeus hirsutus</i>	<i>Megistopoda</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Paratrichobius</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Trichobius intermedius</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
<i>Artibeus jamaicensis</i>	<i>Anastrebla mattadeni</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Aspidoptera delatorrei</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Aspidoptera phyllostomatis</i>	Diptera	Mexico	Martínez et al., 2016; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Megistopoda aranea</i>	Diptera	Mexico	Martínez et al., 2016; Bolivar-Cime et al., 2018; Moskaluk et al., 2018; Tlapaya-Romero et al., 2015; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Megistopoda proxima</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019; Orta-Pineda et al., 2020
	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Martínez et al., 2016; Bolivar-Cime et al., 2018; Tlapaya-Romero et al., 2015; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020
	<i>Nycterophilia coxata</i>	Diptera	Mexico	Martínez et al., 2016; Orta-Pineda et al., 2020
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Artibeus jamaicensis</i>	<i>Strebla hertigi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius assimilis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius brennani</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius intermedius</i>	Diptera	Mexico	Bolivar-Cime et al., 2018; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Trichobius tuttlei</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Carios yumatensis</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2017
	<i>Periglischrus herreraei</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Spelaeorhynchus praecursor</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Artibeus lituratus</i>	<i>Aspidoptera falcata</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Megistopoda aranea</i>	Diptera	Mexico	Martínez et al., 2016; Orta-Pineda et al., 2020
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Martínez et al., 2016; Moskaluk et al., 2018; Tlapaya-Romero et al., 2019; Trujillo-Pahua and Ibáñez-Bernal 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Paratrichobius lowei</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius assimilis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius brennani</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius intermedius</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Carios brodyi</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2017
	<i>Periglischrus herreraei</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Carollia perspicillata</i>	<i>Anastrebla mattadeni</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Speiseria ambigua</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Strebla harderi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius joblingi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Spelaeorhynchus praecursor</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia carolliae</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Carollia sowelli</i>	<i>Speiseria ambigua</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Strebla hertigi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius joblingi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Carios brodyi</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2017
	<i>Eudusbabekia carolliae</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Carollia subrufa</i>	<i>Strebla guajiro</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
<i>Centurio senex</i>	<i>Eudusbabekia centurio</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Chiroderma salvini</i>	<i>Eudusbabekia vampyrops</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Choeroniscus godmani</i>	<i>Exastinion clovisi</i>	Diptera	Mexico	Martínez et al., 2016
<i>Choeronycteris mexicana</i>	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016
	<i>Trichobius</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Trichobius dugesii</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016
	<i>Periglischrus leptosternus</i>	Mesostigmata	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; (Morales-Malacara and Lopez-Ortega, 2001)
	<i>Eudusbabekia choeronycteris</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Eudusbabekia choeronycteris</i>	Trombidiformes	Mexico	Guzman-Cornejo et al., 2004
	<i>Eudusbabekia choeronycteris</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Dermanura azteca</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Parichoronyssus lopezi</i>	Mesostigmata	Mexico	(Morales-Malacara, 1996)
<i>Dermanura phaeotis</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
<i>Dermanura tolteca</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Paratrichobius dunni</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius intermedius</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Martínez et al., 2016; Orta-Pineda et al., 2020
	<i>Eudusbabekia macrophyllum</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Dermanura watsoni</i>	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
<i>Desmodus rotundus</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Strebla wiedemanni</i>	Diptera	Mexico	Abundes-Gallegos et al., 2017; Bolivar-Cime et al., 2018; Moskaluk et al., 2018; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Trichobius parasiticus</i>	Diptera	Mexico	Martínez et al., 2016; Abundes-Gallegos et al., 2017; Bolivar-Cime et al., 2018; Moskaluk et al., 2018; Tlapaya-Romero et al., 2019; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Carios brodyi</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2017
	<i>Carios yumatensis</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2017
	<i>Periglischrus herreraei</i>	Mesostigmata	Mexico	Morales-Malacara et al., 2018

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Desmodus rotundus</i>	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
	<i>Eudusbabekia arganoi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Diphylla ecaudata</i>	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
<i>Enchisthenes hartii</i>	<i>Eudusbabekia paralepidoseta</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Glossophaga commissarisi</i>	<i>Megistopoda proxima</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius handleyi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius keenani</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus caligus</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia glossophaga</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Glossophaga morenoi</i>	<i>Eudusbabekia glossophaga</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Glossophaga mutica</i>	<i>Paraeuctenodes longipes</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius diphyllae</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius dugesii</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius uniformis</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
<i>Glossophaga soricina</i>	<i>Anastrebla mattadeni</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Megistopoda aranea</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Nycterophilia mormoopsis</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Paraeuctenodes longipes</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Strebla guajiro</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius diphyllae</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius dugesii</i>	Diptera	Mexico	Martínez et al., 2016; Najera-Cortazar et al., 2023

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Glossophaga soricina</i>	<i>Trichobius handleyi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius joblingi</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015; Martínez et al., 2016
	<i>Trichobius keenani</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius parasiticus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2019
	<i>Trichobius uniformis</i>	Diptera	Mexico	Martínez et al., 2016; Tlapaya-Romero et al., 2019
	<i>Androlaelaps fahrenheitzi</i>	Mesostigmata	Mexico	Martínez et al., 2016
	<i>Periglischrus caligus</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia glossophaga</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Hylonycteris underwoodi</i>	<i>Steptolaelaps liomydis</i>	Mesostigmata	Mexico	Martínez et al., 2016
<i>Leptonycteris nivalis</i>	<i>Basilica corynorhini</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Trichobius sphaeronotus</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Periglischrus calcariflexus</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023
	<i>Periglischrus paracaligus</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
	<i>Periglischrus vargasi</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Morales-Malacara and Lopez-Ortega 2023*
	<i>Nycteriglyphus</i>	Sarcoptiformes	USA	Whitaker and Easterla 1975
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Sternopsylla distincta</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Eudusbabekia provirilia</i>	Trombidiformes	Mexico	Morales-Malacara et al., 2002; Herrera-Mares et al., 2021*
	<i>Ioanella leptonycteris</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Leptonycteris yerbabuenae</i>	<i>Anastrebla modestini</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016
	<i>Exastinion clovisi</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Leptonycteris yerbabuenae</i>	<i>Nycterophilia coxata</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; Salinas-Ramos et al., 2018; Orta-Pineda et al., 2020; Zamora-Mejias et al., 2020b; Najera-Cortazar et al., 2023; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Nycterophilia parnelli</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019
	<i>Trichobius johnsonae</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Trichobius sphaeronotus</i>	Diptera	Mexico	Hernandez-Arciga et al., 2016; Martínez et al., 2016; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019; Orta-Pineda et al., 2020; Najera-Cortazar et al., 2023; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Trichobius yunkerii</i>	Diptera	Mexico	Salinas-Ramos et al., 2018
	<i>Carios</i>	Ixodida	Mexico	Salinas-Ramos et al., 2019
	<i>Carios dyeri</i>	Ixodida	Mexico	Zamora-Mejias et al., 2020
	<i>Periglischrus paracaligus</i>	Mesostigmata	Mexico	Hernandez-Arciga et al., 2016; Salinas-Ramos et al., 2019; Zamora-Mejias et al., 2020b; Morales-Malacara and Lopez-Ortega 2023*; Zamora-Mejias et al., 2022
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Martínez et al., 2016; Morales-Malacara and Lopez-Ortega 2023*
	<i>Nycteriglyphus</i>	Sarcoptiformes	Mexico	Salinas-Ramos et al., 2019
	<i>Eudusbabekia provirilia</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Ioanella leptonycteris</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	Myobiidae	Trombidiformes	Mexico	Salinas-Ramos et al., 2019
<i>Macrotus californicus</i>	Hippoboscidae	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Nycterophilia coxata</i>	Diptera	Mexico	Herrera M. et al., 2016; Najera-Cortazar et al., 2023
	<i>Cimex adjunctus</i>	Hemiptera	USA	Bowles et al., 2013*
	<i>Antricola</i>	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Carios dyeri</i>	Ixodida	Mexico	Zamora-Mejias et al., 2020

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Macrotus californicus</i>	<i>Carios rossi</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	Mexico	Herrera M. et al., 2016
	<i>Macronyssoides kochi</i>	Mesostigmata	Mexico	Herrera M. et al., 2016
	<i>Periglischrus delfinadoae</i>	Mesostigmata	Mexico	Herrera M. et al., 2016
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
	<i>Colicus</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Hoffmanniella</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Hoffmanniella beltrani</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Microtrombicula carmenae</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Tecomatlana watkinsi</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Whartonia glenni</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
<i>Macrotus waterhousii</i>	<i>Nycterophilia coxata</i>	Diptera	Mexico	Herrera M. et al., 2016
	<i>Trichobius</i>	Diptera	Mexico	Herrera M. et al., 2016
	<i>Antricola coprophilus</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Carios azteci</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Carios mormoops</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Carios rossi</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Carios yumatensis</i>	Ixodida	Mexico	Herrera M. et al., 2016
	<i>Periglischrus delfinadoae</i>	Mesostigmata	Mexico	Herrera M. et al., 2016
	<i>Paralabidocarpus</i>	Sarcoptiformes	Mexico	Herrera M. et al., 2016
	<i>Colicus</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Eudusbabekia samsinaki</i>	Trombidiformes	Mexico	Herrera M. et al., 2016; Herrera-Mares et al., 2021*
	<i>Hoffmanniella beltrani</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Microtrombicula boneti</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Microtrombicula carmenae</i>	Trombidiformes	Mexico	Herrera M. et al., 2016

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
Macrotus waterhousii	Phyllostomyobia	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Speleocola</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Tecomatlana sandovali</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Whartonia glenni</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
	<i>Whartonia similis</i>	Trombidiformes	Mexico	Herrera M. et al., 2016
Micronycteris microtis	<i>Eudusbabekia micronycteridis</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
Mimon cozumelae	<i>Carios dyeri</i>	Ixodida	Mexico	Guzman-Cornejo et al., 2016
	<i>Eudusbabekia mimon</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2017; Herrera-Mares et al., 2021*
	<i>Ioanella mimon</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2017; Herrera-Mares et al., 2021*
Phyllostomus discolor	<i>Aspidoptera phyllostomatis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Megistopoda aranea</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Strebla hertigi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobioides perspicillatus</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius costalimai</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius tuttlei</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus torrealbai</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia phyllostomi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
Platyrrhinus helleri	<i>Aspidoptera phyllostomatis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Megistopoda aranea</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Paratrichobius salvini</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Paratrichobius sanchezi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Sturnira hondurensis</i>	<i>Aedes quadrivittatus</i>	Diptera	Mexico	Abella-Medrano et al., 2018
	<i>Aspidoptera delatorrei</i>	Diptera	Mexico	Martínez et al., 2016; Tlapaya-Romero et al., 2019; Trujillo-Pahua and Ibáñez-Bernal 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Aspidoptera falcata</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Aspidoptera phyllostomatis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Culex restuans</i>	Diptera	Mexico	Abella-Medrano et al., 2018
	<i>Megistopoda</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Megistopoda aranea</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Megistopoda proxima</i>	Diptera	Mexico	Martínez et al., 2016; Tlapaya-Romero et al., 2019; Trujillo-Pahua and Ibáñez-Bernal 2019; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
	<i>Paratrichobius longicrus</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius assimilis</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Trichobius brennani</i>	Diptera	Mexico	Trujillo-Pahua and Ibáñez-Bernal 2019
	<i>Periglischrus ojastii</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Eudusbabekia lepidoseta</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Sturnira lilium</i>	<i>Megistopoda aranea</i>	Diptera	Mexico	Moskaluk et al., 2018
	<i>Metelasmus pseudopterus</i>	Diptera	Mexico	Tlapaya-Romero et al., 2015
<i>Sturnira ludovici</i>	<i>Megistopoda aranea</i>	Diptera	Mexico	Moskaluk et al., 2018

Supplemental Table 4.3: Bat-ectoparasite associations for bat family Phyllostomidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Sturnira parvidens</i>	<i>Aspidoptera delatorrei</i>	Diptera	Mexico	Martínez et al., 2016; Bolivar-Cime et al., 2018; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Aspidoptera falcata</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Aspidoptera phyllostomatis</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Megistopoda</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Megistopoda aranea</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Megistopoda proxima</i>	Diptera	Mexico	Martínez et al., 2016; Bolivar-Cime et al., 2018; Orta-Pineda et al., 2020; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Nycterophilia fairchildi</i>	Diptera	Mexico	Martínez et al., 2016
	<i>Trichobius brennani</i>	Diptera	Mexico	Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Periglischrus herrerae</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus ojastii</i>	Mesostigmata	Mexico	Martínez et al., 2016; Orta-Pineda et al., 2020
	<i>Periglischrus vargasi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-Ortega 2023*
	<i>Steptolaelaps liomydis</i>	Mesostigmata	Mexico	Martínez et al., 2016
	<i>Eudusbabekia lepidoseta</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Eudusbabekia viguerasi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Uroderma bilobatum</i>	<i>Paratrichobius sanchezi</i>	Diptera	Mexico	Orta-Pineda et al., 2020
	<i>Periglischrus iheringi</i>	Mesostigmata	Mexico	Orta-Pineda et al., 2020

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Antrozous pallidus</i>	<i>Basilia</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Basilia antrozoi</i>	Diptera	USA	Whitaker and Easterla 1975; Lewis 1996; Chilton et al., 2000; Ritzi et al., 2001
	<i>Basilia rondanii</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Trichobius corynorhini</i>	Diptera	USA	Ritzi et al., 2001
	<i>Cimex</i>	Hemiptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex pilosellus</i>	Hemiptera	USA	(Dooley et al., 1976
	<i>Argasidae</i>	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Carios</i>	Ixodida	USA	Lewis 1996
	<i>Carios kelleyi</i>	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Carios kelleyi</i>	Ixodida	USA	Whitaker and Easterla 1975; Ritzi et al., 2001; Steinlein et al., 2001; Bowles et al., 2013*
	<i>Carios rossi</i>	Ixodida	USA	Whitaker and Easterla 1975; Steinlein et al., 2001
	<i>Carios yumatensis</i>	Ixodida	USA	Dooley et al., 1976
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Spinturnix orri</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Lewis 1996; Ritzi et al., 2001
	<i>Steatonyssus antrozoi</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Dooley et al., 1976; Lewis 1996; Ritzi et al., 2001
	<i>Myodopsylla collinsi</i>	Siphonaptera	USA	Ritzi et al., 2001
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Albeckia senase</i>	Trombidiformes	USA	Ritzi et al., 2001
	<i>Erythraeus</i>	Trombidiformes	USA	Ritzi et al., 2001
	<i>Whartonia capenteri</i>	Trombidiformes	USA	Dooley et al., 1976
	<i>Whartonia perplexa</i>	Trombidiformes	USA	Whitaker and Easterla 1975
	<i>Whartonia whartoni</i>	Trombidiformes	USA	Lewis 1996
	<i>Acanthophthirius</i> (Myotimyobia) <i>baueris</i>	<i>Trombidiformes</i>	Mexico	Herrera-Mares et al., 2021*

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Bauerus dubiaquercus</i>	<i>Acanthopthirius</i> (<i>Myotimyobia</i>) <i>baueris</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Corynorhinus mexicanus</i>	<i>Trichobius corynorhini</i>	Diptera	Mexico	Villegas-Guzman et al., 2005; Ramirez-Martinez and Tlapaya-Romero 2023
	<i>Carios yumatensis</i>	Ixodida	Mexico	Villegas-Guzman et al., 2005
	<i>Macronyssus cyclaspis</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Ornithonyssus pipistrelli</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Spinturnix americanus</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Spinturnix traubi</i>	Mesostigmata	Mexico	Morales-Malacara and Lopez-W 1998
	<i>Acanthopthirius</i> (<i>Acanthopthirius</i>) <i>lopezi</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Microtrombicula carmenae</i>	Trombidiformes	Mexico	Villegas-Guzman et al., 2005
	<i>Pteracarus elegans</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Corynorhinus rafinesquii</i>	<i>Nycteridopsylla chapini</i>	Siphonaptera	USA	Eckerlin 2016
	<i>Hoffmanniella solickiana</i>	Trombidiformes	USA	Crossley and Clement 2015
<i>Corynorhinus townsendii</i>	<i>Basilica corynorhini</i>	Diptera	Mexico	Villegas-Guzman et al., 2005
	<i>Basilica corynorhini</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Trichobius corynorhini</i>	Diptera	Mexico	Villegas-Guzman et al., 2005
	<i>Trichobius corynorhini</i>	Diptera	USA	Whitaker and Easterla 1975; Reisen et al., 1976; Ritzi et al., 2001
	<i>Carios</i>	Ixodida	USA	Reisen et al., 1976
	<i>Carios kelleyi</i>	Ixodida	USA	Steinlein et al., 2001
	<i>Carios rossi</i>	Ixodida	USA	Whitaker and Easterla 1975
	<i>Carios yumatensis</i>	Ixodida	Mexico	Villegas-Guzman et al., 2005
	<i>Cryptonyssus</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Ichoronyssus</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Macronyssus</i>	Mesostigmata	USA	Ritzi et al., 2001

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Corynorhinus townsendii</i>	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Macronyssus cyclaspis</i>	Mesostigmata	Mexico	Villegas-Guzman et al., 2005
	<i>Macronyssus longisetosus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Macronyssus unidens</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Acanthophthirius plecotius</i>	Trombidiformes	Mexico	Villegas-Guzman et al., 2005
	<i>Albeckia senase</i>	Trombidiformes	USA	Reisen et al., 1976
	<i>Microtrombicula carmenae</i>	Trombidiformes	Mexico	Villegas-Guzman et al., 2005
<i>Eptesicus fuscus</i>	<i>Basilica forcipata</i>	Diptera	USA	Whitaker and Easterla 1975; Pearce and O'Shea 2007
	<i>Cimex adjunctus</i>	Hemiptera	Canada	Talbot et al., 2016
	<i>Cimex adjunctus</i>	Hemiptera	USA	Whitaker 1973; Bowles et al., 2013*; Talbot et al., 2016; McKee et al., 2018
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	<i>Cimex pilosellus</i>	Hemiptera	USA	Philips 1966; Pearce and O'Shea 2007; Pearce et al., 2007
	Argasidae	Ixodida	Mexico	Najera-Cortazar et al., 2023
	Argasidae	Ixodida	USA	Philips 1966
	<i>Carios kelleyi</i>	Ixodida	USA	Whitaker and Mumford 1971; Whitaker 1973; Steinlein et al., 2001; Dick et al., 2003; Pearce and O'Shea 2007; Bowles et al., 2013*; Nadolny et al., 2021; Occi et al., 2021; Sullivan et al., 2022
	<i>Carios rossi</i>	Ixodida	USA	Whitaker and Easterla 1975; Steinlein et al., 2001
	<i>Carios yumatensis</i>	Ixodida	USA	Dooley et al., 1976
	<i>Ixodes scapularis</i>	Ixodida	USA	Occi et al., 2022
	<i>Androlaelaps glasgowi</i>	Mesostigmata	USA	Philips 1966
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Durden et al., 1992
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Philips 1966

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Eptesicus fuscus</i>	<i>Spinturnix bakeri</i>	Mesostigmata	USA	Whitaker 1973; Whitaker and Easterla 1975; Pearce and O'Shea 2007; Pearce et al., 2007
	<i>Steatonyssus ceratognathus</i>	Mesostigmata	USA	Durden et al., 1992
	<i>Steatonyssus occidentalis</i>	Mesostigmata	USA	Philips 1966; Whitaker and Mumford 1971; Whitaker 1973; Whitaker and Easterla 1975; Dooley et al., 1976; Durden et al., 1992; Pearce and O'Shea 2007; Pearce et al., 2007; Storm and Ritzi, 2008
	<i>Alabidocarpus</i>	Sarcoptiformes	USA	Whitaker 1973
	<i>Alabidocarpus eptesicus</i>	Sarcoptiformes	USA	Pearce and O'Shea 2007
	<i>Mydopholeus</i>	Sarcoptiformes	USA	Durden et al., 1992
	<i>Nycteriglyphites pennsylvanicus</i>	Sarcoptiformes	USA	Durden et al., 1992
	<i>Myodopsylla borealis</i>	Siphonaptera	Canada	Chilton et al., 2000
	<i>Myodopsylla borealis</i>	Siphonaptera	USA	Pearce and O'Shea 2007
	<i>Myodopsylla insignis</i>	Siphonaptera	USA	Philips 1966; Dick et al., 2003
	<i>Myodopsylla insignis</i>	Siphonaptera	USA	Philips 1966
	<i>Acanthopthirius</i>	Trombidiformes	USA	Whitaker and Mumford 1971; Whitaker 1973
	<i>Acanthopthirius caudata</i>	Trombidiformes	USA	Whitaker and Easterla 1975; Pearce and O'Shea 2007
	<i>Cheletonella vespertilionis</i>	Trombidiformes	USA	Whitaker 1973
	Cheyletidae	Trombidiformes	USA	Whitaker and Mumford 1971
	<i>Euschoengastia hamiltoni</i>	Trombidiformes	USA	Whitaker 1973
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Whitaker and Mumford 1971; Whitaker 1973
	<i>Leptotrombidium myotis</i>	Trombidiformes	USA	Whitaker 1973; Pearce and O'Shea 2007
	<i>Myobia</i>	Trombidiformes	USA	Philips 1966
	<i>Neotrombicula microti</i>	Trombidiformes	USA	Whitaker 1973
	<i>Pteracarus aculeus</i>	Trombidiformes	USA	Pearce and O'Shea 2007
	<i>Whartonia perplexa</i>	Trombidiformes	USA	Whitaker and Easterla 1975; Ritzi et al., 2001

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Euderma maculatum</i>	<i>Basilia rondanii</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Cryptonyssus</i>	Mesostigmata	USA	Whitaker and Easterla 1975
<i>Idionycteris phyllotis</i>	<i>Carios kelleyi</i>	Ixodida	USA	Steinlein et al., 2001
	<i>Carios rossi</i>	Ixodida	USA	Steinlein et al., 2001
<i>Lasionycteris noctivagans</i>	<i>Cimex adjunctus</i>	Hemiptera	USA	Whitaker 1973; Bowles et al., 2013*
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker 1973
<i>Lasiurus borealis</i>	<i>Steatonyssus furmani</i>	Mesostigmata	USA	Whitaker 1973
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker 1973
<i>Lasiurus cinereus</i>	<i>Basilia antrozoi</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Steatonyssus furmani</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	<i>Acanthophthirius (Myotimyobia) lasiurus</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Pteracarus chalinobus</i>	Trombidiformes	USA	Whitaker 1973
<i>Myotis keenii</i>	<i>Cimex adjunctus</i>	Hemiptera	USA	Whitaker 1973
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Whitaker 1973
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Whitaker 1973
	<i>Olabidocarpus whitakeri</i>	Sarcoptiformes	USA	Whitaker 1973
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker 1973
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Whitaker 1973
<i>Myotis austroriparius</i>	<i>Cimex adjunctus</i>	Hemiptera	USA	Bowles et al., 2013*
	<i>Chirodiscidae</i>	Sarcoptiformes	USA	Whitaker and Mumford 1971
	<i>Olabidocarpus whitakeri</i>	Sarcoptiformes	USA	Whitaker 1973
	<i>Ctenocephalides felis</i>	Siphonaptera	USA	Durden et al., 2012
	<i>Leptopsylla segnis</i>	Siphonaptera	USA	Durden et al., 2012

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis austroriparius</i>	<i>Xenopsylla cheopis</i>	Siphonaptera	USA	Durden et al., 2012
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Whitaker and Mumford 1971; Whitaker 1973
<i>Myotis californicus</i>	<i>Basilica forcipata</i>	Diptera	Canada	Chilton et al., 2000
	<i>Hippoboscidae</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex</i>	Hemiptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	<i>Carios kelleyi</i>	Ixodida	USA	Bowles et al., 2013*
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Dooley et al., 1976
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Macy, 1947
<i>Myotis evotis</i>	<i>Basilica forcipata</i>	Diptera	Canada	Chilton et al., 2000
	<i>Carios rossi</i>	Ixodida	USA	Steinlein et al., 2001
<i>Myotis grisescens</i>	<i>Trichobius major</i>	Diptera	USA	Ubelaker 1966
	<i>Ichoronyssus</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Paraspinturnix globosus</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Spinturnix banksi</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Myodopsylla collinsi</i>	Siphonaptera	USA	Ubelaker 1966
<i>Myotis leibii</i>	<i>Carios kelleyi</i>	Ixodida	USA	Gikas et al., 2011; Bowles et al., 2013*
	<i>Androlaelaps casalis</i>	Mesostigmata	USA	Gikas et al., 2011
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Gikas et al., 2011*
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Gikas et al., 2011*
	<i>Euschoengastia hamiltoni</i>	Trombidiformes	USA	Gikas et al., 2011*
	<i>Leptotrombidium myotis</i>	Trombidiformes	Canada	Gikas et al., 2011*
	<i>Leptotrombidium myotis</i>	Trombidiformes	USA	Gikas et al., 2011*

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis lucifugus</i>	<i>Basilia forcipata</i>	Diptera	Canada	Chilton et al., 2000
	<i>Cimex</i>	Hemiptera	Canada	Weber et al., 2015
	<i>Cimex adjunctus</i>	Hemiptera	Canada	Talbot et al., 2016; Sauk and Broders (in prep, Chapter 3)
	<i>Cimex adjunctus</i>	Hemiptera	USA	Bernth and Kunz 1981; Dick et al., 2003; Bowles et al., 2013*; Talbot et al., 2016
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	<i>Carios kelleyi</i>	Ixodida	USA	Whitaker and Mumford 1971; Whitaker 1973; Dick et al., 2003; Bowles et al., 2013*
	<i>Androlaelaps casalis</i>	Mesostigmata	Canada	Sauk and Broders (in prep, Chapter 3)
	<i>Macronyssus crosbyi</i>	Mesostigmata	Canada	Czenze and Broders 2011; Weber et al., 2015; Sauk and Broders (in prep, Chapter 3)
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Whitaker 1973
	<i>Mesostigmata</i>	Mesostigmata	Canada	Sauk and Broders (in prep, Chapter 3)
	<i>Spinturnix americanus</i>	Mesostigmata	Canada	Poissant and Broders 2008; Czenze and Broders 2011; Weber et al., 2015; Sauk and Broders (in prep, Chapter 3)
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Dick et al., 2003
	<i>Myodopsylla gentilis</i>	Siphonaptera	Canada	Chilton et al., 2000
	<i>Myodopsylla insignis</i>	Siphonaptera	Canada	Chilton et al., 2000; Poissant and Broders 2008; Czenze and Broders 2011; Weber et al., 2015; Banerjee et al., 2020; Sauk and Broders (in prep, Chapter 3)
	<i>Myodopsylla insignis</i>	Siphonaptera	USA	Whitaker and Mumford 1971; Whitaker 1973; Bernth and Kunz 1981; Dick et al., 2003; Eckerlin 2016; Eckerlin and Gardner 2021
	<i>Siphonaptera</i>	Siphonaptera	Canada	Sauk and Broders (in prep, Chapter 3)
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker 1973
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Whitaker and Mumford 1971; Whitaker 1973
	<i>Leptotrombidium myotis</i>	Trombidiformes	Canada	Poissant and Broders 2008; Weber et al., 2015; Sauk and Broders (in prep, Chapter 3)

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis occultus</i>	<i>Basilia forcipata</i>	Diptera	USA	Valdez et al., 2009
	<i>Cimex pilosellus</i>	Hemiptera	USA	Valdez et al., 2009
	<i>Carios</i>	Ixodida	USA	Valdez et al., 2009
	<i>Chiroptonyssus robustipes</i>	Mesostigmata	USA	Valdez et al., 2009
	<i>Cryptonyssus</i>	Mesostigmata	USA	Valdez et al., 2009
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Valdez et al., 2009
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Valdez et al., 2009
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Valdez et al., 2009
	<i>Alabidocarpus</i>	Sarcoptiformes	USA	Valdez et al., 2009
	<i>Alabidocarpus calcaratus</i>	Sarcoptiformes	USA	Valdez et al., 2009
	<i>Glycyphagus hypudaei</i>	Sarcoptiformes	USA	Valdez et al., 2009
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Valdez et al., 2009
	<i>Acanthophthirius lucifugus</i>	Trombidiformes	USA	Valdez et al., 2009
	<i>Leptotrombidium myotis</i>	Trombidiformes	USA	Valdez et al., 2009
	<i>Pteracarus</i>	Trombidiformes	USA	Valdez et al., 2009
	Trombiculidae	Trombidiformes	USA	Valdez et al., 2009
<i>Myotis peninsularis</i>	Argasidae	Ixodida	Mexico	Najera-Cortazar et al., 2023
<i>Myotis septentrionalis</i>	<i>Cimex adjunctus</i>	Hemiptera	Canada	Czenze and Broders 2011; Talbot et al., 2016; Sauk and Broders (in prep, Chapter 3)
	<i>Cimex adjunctus</i>	Hemiptera	USA	Ritzi and Whitaker, 2003; Gikas et al., 2011*
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	<i>Carios kelleyi</i>	Ixodida	USA	Dick et al., 2003; Bowles et al., 2013*
	<i>Androlaelaps casalis</i>	Mesostigmata	Canada	Czenze and Broders 2011; Sauk and Broders (in prep, Chapter 3)
	<i>Macronyssus crosbyi</i>	Mesostigmata	Canada	Czenze and Broders 2011; Sauk and Broders (in prep, Chapter 3)
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Ritzi and Whitaker, 2003; Gikas et al., 2011*
	Mesostigmata	Mesostigmata	Canada	Sauk and Broders (in prep, Chapter 3)

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis septentrionalis</i>	<i>Spinturnix americanus</i>	Mesostigmata	Canada	Poissant and Broders 2008; Czenze and Broders 2011; Sauk and Broders (in prep, Chapter 3)
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Dick et al., 2003; Gikas et al., 2011*
	<i>Steatonyssus ceratognathus</i>	Mesostigmata	USA	Gikas et al., 2011*
	<i>Olabidocarpus whitakeri</i>	Sarcoptiformes	USA	Gikas et al., 2011*
	<i>Myodopsylla insignis</i>	Siphonaptera	Canada	Chilton et al., 2000; Poissant and Broders 2008; Czenze and Broders 2011; Sauk and Broders (in prep, Chapter 3)
	<i>Myodopsylla insignis</i>	Siphonaptera	USA	Dick et al., 2003; Gikas et al., 2011*; Eckerlin 2016
	<i>Orchopeas caedens</i>	Siphonaptera	Canada	Sauk and Broders (in prep, Chapter 3)
	<i>Siphonaptera</i>	Siphonaptera	Canada	Sauk and Broders (in prep, Chapter 3)
	<i>Acanthophthirius</i>	Trombidiformes	Canada	Czenze and Broders 2011
	<i>Acanthophthirius gracilis</i>	Trombidiformes	USA	Ritzi and Whitaker, 2003; Gikas et al., 2011*
	<i>Demodex</i>	Trombidiformes	USA	Gikas et al., 2011*
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Gikas et al., 2011*
	<i>Eutrombicula alfreddugesi</i>	Trombidiformes	USA	Gikas et al., 2011*
	<i>Leptotrombidium myotis</i>	Trombidiformes	Canada	Poissant and Broders 2008; Gikas et al., 2011*; Sauk and Broders (in prep, Chapter 3)
	<i>Leptotrombidium myotis</i>	Trombidiformes	USA	Gikas et al., 2011*
	Trombidiformes	Trombidiformes	Canada	Sauk and Broders (in prep, Chapter 3)
<i>Myotis sodalis</i>	<i>Cimex adjunctus</i>	Hemiptera	USA	Whitaker et al., 2000; Bowles et al., 2013*
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Whitaker 1973; Whitaker et al., 2000
	<i>Paraspinturnix globosus</i>	Mesostigmata	USA	Whitaker 1973; Whitaker et al., 2000
	<i>Steatonyssus occidentalis</i>	Mesostigmata	USA	Whitaker and Mumford, 1971
	<i>Acanthophthirius</i>	Trombidiformes	USA	Whitaker 1973

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis thysanodes</i>	<i>Basilia forcipata</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Cimex adjunctus</i>	Hemiptera	USA	Bowles et al., 2013*
	<i>Carios kelleyi</i>	Ixodida	USA	Steinlein et al., 2001
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	<i>Pteracarus elegans</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Myotis velifer</i>	<i>Basilia forcipata</i>	Diptera	USA	Ritzi et al., 2001
	<i>Hippoboscidae</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Trichobius major</i>	Diptera	USA	Whitaker and Easterla 1975; Reisen et al., 1976; Ritzi et al., 2001; Lack et al., 2011
	<i>Cimex pilosellus</i>	Hemiptera	USA	Ritzi et al., 2001
	<i>Oeciacus vicarius</i>	Hemiptera	USA	Ritzi et al., 2001
	<i>Carios</i>	Ixodida	USA	Reisen et al., 1976
	<i>Carios kelleyi</i>	Ixodida	USA	Steinlein et al., 2001
	<i>Chirotonyssus robustipes</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Ichoronyssus</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Macrocheles</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Reisen et al., 1976; Ritzi et al., 2001
	<i>Macronyssus unidens</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Paraspinturnix globosus</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Ubelaker 1966; Whitaker and Easterla 1975; Reisen et al., 1976; Ritzi et al., 2001
	<i>Spinturnix banksi</i>	Mesostigmata	USA	Ubelaker 1966
	<i>Steatonyssus occidentalis</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Nycteriglyphus</i>	Sarcoptiformes	USA	Reisen et al., 1976; Whitaker and Easterla 1975
	<i>Olabidocarpus</i>	Sarcoptiformes	USA	Reisen et al., 1976

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis velifer</i>	<i>Myodopsylla collinsi</i>	Siphonaptera	USA	Ubelaker 1966; Whitaker and Easterla 1975; Reisen et al., 1976; Ritzi et al., 2001
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975
	<i>Acanthophthirius caudata</i>	Trombidiformes	USA	Ritzi et al., 2001
	<i>Albeckia senase</i>	Trombidiformes	USA	Reisen et al., 1976
	<i>Cheyletus</i>	Trombidiformes	USA	Reisen et al., 1976
	<i>Whartonia perplexa</i>	Trombidiformes	USA	Ritzi et al., 2001
<i>Myotis vivesi</i>	<i>Basilica</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Antricola</i>	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Acanthophthirius (Myotimyobia) pizonixeos</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
	<i>Pteracarus pizonychos</i>	Trombidiformes	Mexico	Herrera-Mares et al., 2021*
<i>Myotis volans</i>	<i>Basilica forcipata</i>	Diptera	USA	Whitaker and Easterla 1975; Chilton et al., 2000
	<i>Basilica rondanii</i>	Diptera	USA	Whitaker and Easterla 1975
	Hippoboscidae	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Trichobius corynorhini</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Spinturnix americanus</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Myodopsylla gentilis</i>	Siphonaptera	Canada	Chilton et al., 2000
	<i>Myodopsylla insignis</i>	Siphonaptera	Canada	Chilton et al., 2000
<i>Myotis yumanensis</i>	<i>Basilica</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Basilica rondanii</i>	Diptera	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	Hippoboscidae	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex</i>	Hemiptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex pilosellus</i>	Hemiptera	Canada	Chilton et al., 2000
	Argasidae	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Carios kelleyi</i>	Ixodida	USA	Ritzi et al., 2001; Bowles et al., 2013*
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Ritzi et al., 2001

Supplemental Table 4.4: Bat-ectoparasite associations for bat family Vespertilionidae, continued.

Bat Species	Ectoparasite Lowest Taxon	Ectoparasite Order	Country	References
<i>Myotis yumanensis</i>	<i>Spinturnix americanus</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	<i>Steatonyssus antrozoi</i>	Mesostigmata	USA	Whitaker and Easterla 1975
	<i>Notoedres myotis</i>	Sarcoptiformes	USA	Whitaker and Easterla 1975
	<i>Nycteriglyphus</i>	Sarcoptiformes	USA	Whitaker and Easterla 1975
	<i>Myodopsylla collinsi</i>	Siphonaptera	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	<i>Myodopsylla gentilis</i>	Siphonaptera	Canada	Chilton et al., 2000
	<i>Myodopsylla gentilis</i>	Siphonaptera	USA	Whitaker and Easterla 1975; Ritzi et al., 2001
	Trombiculidae	Trombidiformes	USA	Ritzi et al., 2001
<i>Parastrellus hesperus</i>	<i>Basilis rondanii</i>	Diptera	USA	Whitaker and Easterla 1975
	<i>Hippoboscidae</i>	Diptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex</i>	Hemiptera	Mexico	Najera-Cortazar et al., 2023
	<i>Cimex pilosellus</i>	Hemiptera	USA	Whitaker and Easterla 1975; Dooley et al., 1976
	Argasidae	Ixodida	Mexico	Najera-Cortazar et al., 2023
	<i>Carios kelleyi</i>	Ixodida	USA	Steinlein et al., 2001; Bowles et al., 2013*
	<i>Carios rossi</i>	Ixodida	USA	Whitaker and Easterla 1975
	<i>Carios yumatensis</i>	Ixodida	USA	Dooley et al., 1976
	<i>Chiroptonyssus venezolanus</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Cryptonyssus desultorius</i>	Mesostigmata	USA	Ritzi et al., 2001
	<i>Steatonyssus emarginatus</i>	Mesostigmata	USA	Whitaker and Easterla 1975; Dooley et al., 1976
	<i>Albeckia senase</i>	Trombidiformes	USA	Ritzi et al., 2001
	<i>Loomisia</i>	Trombidiformes	USA	Dooley et al., 1976
	<i>Whartonia capenteri</i>	Trombidiformes	USA	Dooley et al., 1976
<i>Perimyotis subflavus</i>	<i>Carios kelleyi</i>	Ixodida	USA	Bowles et al., 2013*
	<i>Macronyssus crosbyi</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Macronyssus unidens</i>	Mesostigmata	USA	Reisen et al., 1976
	<i>Euschoengastia pipistrelli</i>	Trombidiformes	USA	Whitaker and Mumford 1971; Whitaker 1973