

# **Population trends and behaviours of bats in Maritime Canada**

by

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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**

Sepidar Golestaneh was the sole author of Chapters 1 and 4, which were written under the supervision of Dr. Hugh Broders and were not intended for publication. This thesis consists in part of two manuscripts (Chapters 2 and 3) written for publication. The submission for publication of these manuscripts will acknowledge the contributions of those who made these papers possible with co-authorship.

### Research presented in Chapter 2

Adam D. Grottoli, Dr. Lynne Burns, Caleb C. Ryan, and Dr. Hugh G. Broders, under whom this research was supervised, contributed extensively to data collection in the field and data curation for this work. Dr. Hugh G. Broders assisted in project conceptualization and in funding acquisition.

### Research presented in Chapter 3:

Michela M. C. Contursi, Caleb C. Ryan, and Dr. Hugh G. Broders, under whom this research was supervised, contributed to the conceptualization and study design of this work. Dr. Hugh G. Broders assisted in funding acquisition. Michela M. C. Contursi contributed extensively to data collection in the field for this work.

## **Abstract**

In a rapidly changing world with many drivers of extinction, monitoring wild populations has become of increasing priority to researchers. For many bats (order Chiroptera) in North America, population assessments have become critical in monitoring population trends following disease disturbance, specifically White Nose Syndrome. White Nose Syndrome is a fungal disease that has resulted in mass mortality of many hibernating bat species in eastern North America since its detection in 2006. Given the time elapsed for many areas since White Nose Syndrome introduction, many affected populations have reached an established state where disease-associated mass mortality is not currently observed. As such, the motivation for population assessments has shifted more towards describing patterns of recovery in White Nose-affected populations. However, population assessments for bats, like for other taxa, may be biased and consequently impact the inferences made by researchers. This thesis aims to describe population trends of species affected by White Nose Syndrome in Maritime Canada and assess the impacts of research techniques on study findings. The specific objectives of this thesis were to (1) assess population trends of resident hibernating bats with respect to White Nose Syndrome detection in Maritime Canada, and (2) assess the potential biases of capture surveys on bats, a standard research method used to conduct population assessments and study bat activity.

## Acknowledgements

From my very first bat (adult female *Myotis lucifugus*, 26 May 2023, Grand Bend ON, Canada) to my very last bat (adult female *Myotis lucifugus*, 9 September 2024, Guysborough NS, Canada) and all the bats in between during this degree, thank you for giving me the privilege of seeing your beauty up close. For every bat I have held, seen, and heard in Canada and Belize, you are magnificent. To all the bats and wildlife of the world: I will continue to fight for your existence, persistence, and ensure that everyone else sees you for how incredible you are.

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## List of abbreviations

<u>Abbreviation</u>	<u>Full form</u>
Pd	<i>Pseudogymnoascus destructans</i>
WNS	White Nose Syndrome
CPUE	Capture-per-unit-effort

“The message is simple: love and conserve our wildlife.”

Steve Irwin

# **CHAPTER 1**

## Population trends and behaviours of Maritime Bats: Introduction

## **1.1 Introduction**

Drivers of extinction persist and, as a result, rates of biodiversity loss are accelerating (Brook et al., 2008; Ceballos et al., 2015; Coristine & Kerr, 2011). Invasive pathogens and disease spread (Essl et al., 2020; Hulme, 2009; Scheele et al., 2019), habitat loss (Britnell et al., 2023; Fahrig, 1997), and climate change (Maclean & Wilson, 2011; Song et al., 2021) are among the primary drivers that threaten biodiversity worldwide. These extinction drivers can have population- and species-specific effects depending on these animals' intrinsic traits and ecological niches (Di Marco et al., 2021; Schweiger et al., 2012). Additionally, the synergistic impacts of extinction drivers influence the magnitude of extinction pressure (Brook et al., 2008; Diez et al., 2012; Hof et al., 2011; Jetz et al., 2007). Consequently, when drivers of extinction are present, population- and community-level changes are expected (e.g., Cahill et al., 2013; Pardini et al., 2010; Roemer et al., 2001; Russo & Ancillotto, 2015). In a rapidly changing world, there is an increasing need to conduct population assessments to advance our knowledge on various aspects of animal biology and to examine the impacts of extinction drivers to develop effective conservation strategies (Danielsen et al., 2005; Marsh & Trenham, 2008).

Population assessments can be accomplished in diverse ways, including both direct and indirect methods. Direct methods involve the observation or capture of individuals, often providing estimates of abundance or density of animals in the area. Examples of direct methods include transect surveys and visual counts (Buckland et al., 2008) and capture surveys (Balzer et al., 2021; Schemnitz et al., 2009), sometimes followed by mark-recapture techniques (López-roig & Serracobo, 2014; Powell & Proulx, 2003). Indirect methods typically rely on signs of presence rather than direct observation, such as camera traps (Sytsma et al., 2022) and acoustic monitoring (Cintra

& Naka, 2012; Udell et al., 2024). Researchers often employ a combination of direct and indirect methods to gain greater perspective on their study system and taxa, particularly as studying wild populations offers many challenges (Hughey et al., 2018; Numminen et al., 2023).

Population assessments can be of varying reliability owing to ecological variability and the nature of the study system and focal taxa (Witmer, 2005). Population size and structure naturally fluctuate due to factors such as seasonal or climatic patterns (Ellington et al., 2020; Sendor & Simon, 2003), resource availability (Shepard et al., 2013) and local disturbances (Frid & Dill, 2002; Whiting et al., 2024). Intrinsic factors of the focal taxa, such as social status, size, and sex also influence movement and behaviour (Hewison et al., 2021; Sendor & Simon, 2003) and consequently the likelihood of detection or capture. To obtain greater certainty with the population of interest, and especially to evaluate population trends, there is the need to conduct multiple population assessments over an elapsed period of time (White, 2019). Like any other type of research, population assessments must therefore employ a methodology that is appropriately tailored to the habitat and animal(s) of interest, while also considering researchers' logistical and financial limitations (Witmer, 2005). However, the ease of conducting population assessments differs depending on the species of interest (Numminen et al., 2023), with rarer and more elusive species being more difficult to detect and consequently study.

The small, volant and nocturnal nature of bats has created unique challenges for researchers but some monitoring techniques have become commonplace (Kunz, 2009). Passive monitoring on bats often involves the use of data loggers, acoustic recorders, and infrared or thermal video (Bergmann

et al., 2022; Thomas & Davison, 2022). For direct methods, some of the most common approaches include visual counts at hibernacula (Kilpatrick et al., 2020; Perea et al., 2024). and conducting capture surveys. Capture surveys involve capturing bats with nets, usually mist nets and/or harp traps (Burns & Broders, 2015; Fenton, 1969; Glover & Altringham, 2008). Capture surveys for bats, like for any other animal, can create a stressful situation for captured individuals (Edwards et al., 2022). However, capture surveys allow for the collection of demographic data, morphometric measurements, tissue and other samples, and in some cases greater accuracy in species identification (Kunz, 2009; Powell & Proulx, 2003; Schemnitz et al., 2009).

In North America, population assessments of many bat species have become critical in monitoring the effects of disturbance and in developing conservation strategies. For many hibernating bats in northeastern North America, White Nose Syndrome (WNS), a fungal disease caused by the invasive fungus *Pseudogymnoascus destructans* (Pd), has resulted in severe population declines (Frick et al., 2010, 2015; Gargas et al., 2009). This disease was first detected in North America in 2006 in northeastern United States and in Canada in 2010 (COSEWIC, 2013; Drees et al., 2017). When infected with Pd, hibernating bats that develop WNS experience severe physiological disruptions that can result in death (McGuire et al., 2017; Verant et al., 2014). With mortality rates often >90%, the rapid pace of fungal transmission, and the physiological disturbances infected bats endure, WNS is noted as one of the most severe mammalian diseases observed (Cheng et al., 2021; Frick et al., 2010; Warnecke et al., 2013). In addition to having intrinsic and cultural value (Sieradzki et al., 2022), bats contribute significantly to global biodiversity, ecosystem services, agricultural services, and even human health (Boyles et al., 2011; Frank, 2024; Maine & Boyles, 2015). Consequently, continuing monitoring efforts has been of great priority to many researchers.

For many areas impacted by WNS disturbance, sufficient time has elapsed to have reached an established state wherein mass mortality of bats due to fungal infection is not currently observed (Frank et al., 2019; Langwig et al., 2015). While WNS severely impacted populations of many species, there was interspecific variation in disease response (Cheng et al., 2021; Frick et al., 2015). Consequently, assessing recovery patterns many years after the epidemic stage of WNS can facilitate developing species-specific recovery plans.

For any taxon, the efficacy of surveying techniques can have consequences for our inferences on population status. For bats, the complementary approach of combining indirect and direct methods of monitoring has greatly facilitated research on these animals (Kunz, 2009; O'Farrell & Gannon, 1999; Tanshi & Kingston, 2021; Thomas & Davison, 2022). However, both indirect and direct methods can be biased (Flaquer et al., 2007; Lintott et al., 2014). For example, the equipment used in acoustic surveys, and where and how this equipment is deployed, can greatly influence the species detected and at what frequencies (Adams et al., 2012). For capture surveys, the use of harp traps versus mist nets can yield different findings on population abundance and community composition (Francis, 1989; Larsen et al., 2007). There are also additional factors of interest with capture surveys that may bias capture rates and consequently the inferences made on the studied population(s). The presence of captured bats can increase activity of free-flying individuals (Carter et al., 2015; Fenton et al., 1976; Russ et al., 2004; Ryan et al., 1985). Humans, however, are often perceived as predatory by other animals and consequently avoided (Frid & Dill, 2002; Smith et al., 2017). As avoidant behaviour following increased human activity has previously been observed in bats (Li et al., 2020), bats may also avoid the researchers employing capture surveys. Lastly, the presence of the trap itself may evoke neophobia, being an obstacle in bats' flight path

and a factor that initiates avoidant behaviour (Berry et al., 2004). The presence of captured bats, researchers, and traps may therefore be stimuli that inadvertently bias our studies by altering free-flying bat behaviour.

## **1.2 Research objectives**

In this thesis, I conducted comparative population assessments to comment on the status of endangered bats in Maritime Canada 10+ years after WNS disturbance by assessing population trends with respect to WNS detection. Additionally, I assessed potential factors of bias present during population assessments that may influence our inferences on the studied populations. This thesis is presented as a four-chapter dissertation: this introductory chapter (Chapter 1), the concluding chapter (Chapter 4), and two data chapters (Chapters 2 and 3). In Chapter 2, I conduct a comparative analysis of local and regional populations of resident hibernating bats between pre- and post-WNS periods. I do this by conducting summer, autumn swarming, and overwinter surveys post-WNS at sites that were surveyed pre-WNS. In Chapter 3, I use thermal video to quantify the behavioural response of free-flying bats to potential stimuli that are present during conventional capture surveys. In Chapter 4, I synthesize the overall findings from these data chapters, elucidating the importance of conducting population assessments to monitor wildlife while considering the biases that may be present in these studies.

My two data chapters are formatted as standalone manuscripts to facilitate publication. There is therefore some repetition of background information. Additionally, I use the pronouns “we” and “our” throughout these chapters to acknowledge the contributions of my peers and those that will

be co-authored on publications. However, the writing and data analyses presented in my thesis are of my own work.

### **1.3 Study system and focal taxa**

The Atlantic Maritime Ecozone is primarily made up of the Maritime provinces of New Brunswick, Nova Scotia, and Prince Edward Island, though it also encapsulates part of Quebec's Gaspé Peninsula (Ahmed et al., 2018). Due to its history of European settlement and its small size (2% of Canada's landmass), terrestrial biodiversity of this zone is lower than that of many other ecozones in Canada (Smith et al., 2010). However, this ecozone is heavily forested (Ecological Stratification Working Group, 1996; National Forest Inventory, 2023a, 2023b) and encompasses the transitional zone between deciduous and boreal forests. Consequently, this area of Canada is still of great importance for wildlife as it provides critical habitat for many populations of different taxa. Nova Scotia alone is predicted to have the highest density of disjunct populations of nonflying terrestrial mammals in Canada (Scott & Hebda, 2004). Given the forested landscape of Maritime Canada, one of the primary drivers of extinction on terrestrial species is habitat loss and modification due to extensive forestry (National Forest Inventory, 2023c). This, in addition to other drivers of decline, can further exacerbate extinction pressure on populations in this geographic range. The northeastern range of many bats in North America, including some species impacted by WNS, extends into this Maritime landscape.

There are records for seven bat species in Maritime Canada (Forbes et al., 2010; Segers et al., 2013; Van Zyll de Jong, 1985). In this study, we focus on the resident hibernating species in New

Brunswick and Nova Scotia, the two Maritime provinces where we conducted our research. Our study species include the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*M. septentrionalis*), and the tri-colored bat (*P. subflavus*). The *Myotis* species are more widespread across the Maritimes, whereas the tri-colored bat is more abundant westward in New Brunswick, and in Nova Scotia is restricted to the southwest portion of the province (Broders, 2003; Broders et al., 2001; Farrow & Broders, 2011; Poissant et al., 2010; Vanderwolf et al., 2012). Little brown bats and northern long-eared bats commonly roost in crevices in forested habitat (Broders, 2003; Broders & Forbes, 2004). However, little brown bats also roost in urban areas and anthropogenic structures such as houses, old buildings, and bat boxes (Brittingham & Williams, 2000; Coleman & Barclay, 2011; Randall et al., 2014). Tri-colored bats in Nova Scotia are thought to be a disjunct population partly due to their unique lichen-roosting behaviour (Poissant et al., 2010)

Each of these three species have been classified as endangered at the provincial and federal levels owing to severe WNS disturbance (COSEWIC, 2013; Endangered Species Act, 1998; Species at Risk Act, 2002; Species at Risk Act, 2012; Government of Nova Scotia, 2017).

## **CHAPTER 2**

Mixed scale- and species-specific responses of hibernating bat populations 10 years post-White Nose Syndrome in Maritime Canada

## **2.1 Abstract**

White Nose Syndrome (WNS) is a fungal disease that has caused major population declines for many hibernating bat species across eastern North America, resulting in the little brown bat (*Myotis lucifugus*), northern long-eared bat (*M. septentrionalis*), and tri-colored bat (*Perimyotis subflavus*) being listed as federally endangered in Canada. Our goal was to assess population trends of *M. lucifugus*, *M. septentrionalis*, and *P. subflavus* in Maritime Canada 10 years after WNS arrival by comparing post-WNS capture surveys at summering and autumn swarming sites, and overwinter counts at hibernacula with pre-WNS data from the same survey locations. Pre-WNS, both *Myotis species* were ubiquitous and abundant across Maritime Canada, whereas *P. subflavus* had a restricted distribution and were relatively less abundant. Post-WNS, capture surveys revealed significant declines for each species. From 952 hours of capture survey effort at summering sites, capture rates declined 92.5% ( $\pm 7.5\%$ ) for *M. lucifugus*, 100% for *M. septentrionalis*, and 50% for *P. subflavus* relative pre-WNS rates. From 275 hours of capture survey effort at swarming sites, capture rates of *M. lucifugus* and *M. septentrionalis* declined 84.2% ( $\pm 4.7\%$ ) and 98.6% ( $\pm 0.5\%$ ) respectively compared to pre-WNS rates. However, *P. subflavus* swarming capture rates were comparable between both pre- and post-WNS periods. From overwinter surveys, within 1-4 years of WNS detection, the number of overwintering bats declined 98-100%. From the most recent overwinter surveys (winter 2024-25), we observed signs of population growth but counts of overwintering bats across hibernacula are still 86-100% less than pre-WNS expectations. We highlight species-specific and scale-specific trends to WNS disturbance at a northeastern limit for WNS-affected species.

## **2.2 Introduction**

Drivers of extinction such as climate change, habitat loss, exploitation, and invasive pathogens threaten biodiversity worldwide (Brook et al., 2008; Cahill et al., 2013; Ducatez & Shine, 2017; Fahrig, 1997; Scheele et al., 2019). Significant disturbance can lead to bottleneck events, wherein population abundance is severely reduced, often over a relatively short period of time (Mayr, 1964). Subsequent population recovery from bottleneck events can be difficult owing to reduced genetic variation (Battilani et al., 2025; Briskie & Mackintosh, 2004) and increased difficulty finding mates (Edmands, 2007; Heber & Briskie, 2010). In more social species that communicate and interact with conspecifics about resources, population declines can also lead to increased difficulty in foraging and decision-making in groups (Creel & Creel, 1995; Kerth et al., 2006; Packer et al., 1990). As a result, disturbed populations may have decreased resiliency to additional or existing drivers of decline (Edmands, 2007; Hoelzel et al., 2024; Keller & Waller, 2002).

White Nose Syndrome (WNS) has been a significant driver of decline for many bat populations in northeastern North America since its initial detection in 2006, resulting in extreme population declines of hibernating bats (Blehert, 2012; Blehert et al., 2009; Frick et al., 2010, 2015). Caused by the invasive fungal pathogen *Pseudogymnoascus destructans* (Pd; Warnecke et al., 2012), hibernating bats with WNS can experience severe physiological disruptions during hibernation, resulting in premature depletion of their energy reserves, starvation, and, often, death (McGuire et al., 2017; Meteyer et al., 2009; Verant et al., 2014). Within 1-5 years of initial WNS detection at many known hibernacula, mass mortality was observed with 90-100% population declines for many species (Cheng et al., 2021; Frank et al., 2019; Frick et al., 2010). The rapid spread of the disease, the destructive physiological symptoms, and the consequent extreme population declines

make WNS one of the most severe mammalian diseases observed (Frick et al., 2010; Warnecke et al., 2013).

Bats are particularly vulnerable to disturbance events due to their slow life-history and consequent low reproductive rates (Barclay et al., 2004; Cockrum, 1955; Healy et al., 2014). As such, a recovered state for a WNS-affected bat population does not typically refer to a return to pre-disturbance abundances (Cheng et al., 2024; Westwood et al., 2014) but rather refers to the process of recovery with population stabilization where WNS-associated declines are no longer observed (Dobony & Johnson, 2018; Frick et al., 2017). In an epidemic stage of disease (high prevalence and high mortality), monitoring affected populations will mostly reveal disturbance only (i.e., population declines; Langwig et al., 2015a). In cases where more time has elapsed since invasion, affected populations may show signs of recovery with population stabilization and be in an established stage (Langwig et al., 2015a). With the 10+ years elapsed in many areas since initial WNS detection, many affected bat populations have reached this established stage where stability in population abundance is observed (Frank et al., 2019; Vanderwolf et al., 2025). As such, the need to monitor and re-assess populations affected by WNS prevails to observe whether the persistence and recovery of impacted species are possible (Cheng et al., 2024).

The little brown bat (*Myotis lucifugus*), northern long-eared bat (*M. septentrionalis*), and tricolored bat (*Perimyotis subflavus*) are among the species most impacted by WNS (Cheng et al., 2021; Frick et al., 2015). In Canada, an emergency assessment on these species' population status prompted their designation as federally endangered under the Species at Risk Act in 2014

(COSEWIC, 2013; Environment and Climate Change Canada, 2015; Species at Risk Act, 2002). In the northeastern part of their geographic range in Maritime Canada, these species were also listed as provincially endangered with the associated legislations in each of New Brunswick (Species at Risk Act, 2012) and Nova Scotia (Endangered Species Act, 1998; Government of Nova Scotia, 2017).

In Maritime Canada, WNS was first detected in 2011 (COSEWIC, 2013). Prior to this, *Myotis* species were commonly encountered and broadly distributed, whereas *P. subflavus* were restricted to southwest Nova Scotia and occasionally detected in southern New Brunswick (Broders et al., 2001; Farrow & Broders, 2011; Henderson et al., 2009; Vanderwolf et al., 2012). Like other temperate species, community structure and landscape use for these bats is strongly influenced by seasonal cycles. In the summer, adult females roost in maternity groups, with groups of *M. lucifugus* reaching hundreds of individuals, while groups of the sympatric *M. septentrionalis* typically include up to 25 individuals (Broders & Forbes, 2004). For *P. subflavus*, maternity groups of up to 18 individuals have been documented in Nova Scotia, with bats found preferentially roosting in old man's beard lichens (genus *Usnea*; Poissant et al., 2010). From late summer to early fall, bats congregate at the entrances of potential hibernacula, engaging in autumn swarming (Bradbury, 1977). Through winter, bats will hibernate in underground openings until late April or early May before emerging once again for the summer period. Given the congregative nature of the autumn swarming and winter hibernation periods of bats coming from a larger geographic area (Burns et al., 2014), surveys from these periods allow for inferences on regional populations, whereas surveying across the landscape in the summer period allows for inferences on local populations.

The Maritimes are particularly a region of interest as the bats found here belong to populations at these species' geographic range limits, and the population trends of these populations can have broader implications for the geographic distribution of these species. As it has been more than a decade since Pd was detected in the Maritimes, it is possible that Maritime bat populations are now in the established stage of WNS where the disease is no longer an active threat. A recent study by Vanderwolf et al. (2025) noted historical lows in Pd loads in hibernacula and on hibernating bats in the Maritimes since Pd's initial detection, further prompting the reassessment of these populations to determine the trajectory of species trends in this area. As numerous population surveys of hibernating bats in the Maritimes occurred prior to WNS invasion, we also have a stronger basis upon which we can discuss population trends of these bats with respect to disease disturbance.

Our goal was to assess local and regional population trends of *M. lucifugus*, *M. septentrionalis*, and *P. subflavus* in Maritime Canada, and comment on the current state of these populations 10+ years after WNS arrival. We did this by comparing post-WNS capture surveys at summering and autumn swarming sites, and overwinter counts at hibernacula with historical pre-WNS data from the same survey locations.

### **2.3 Methods**

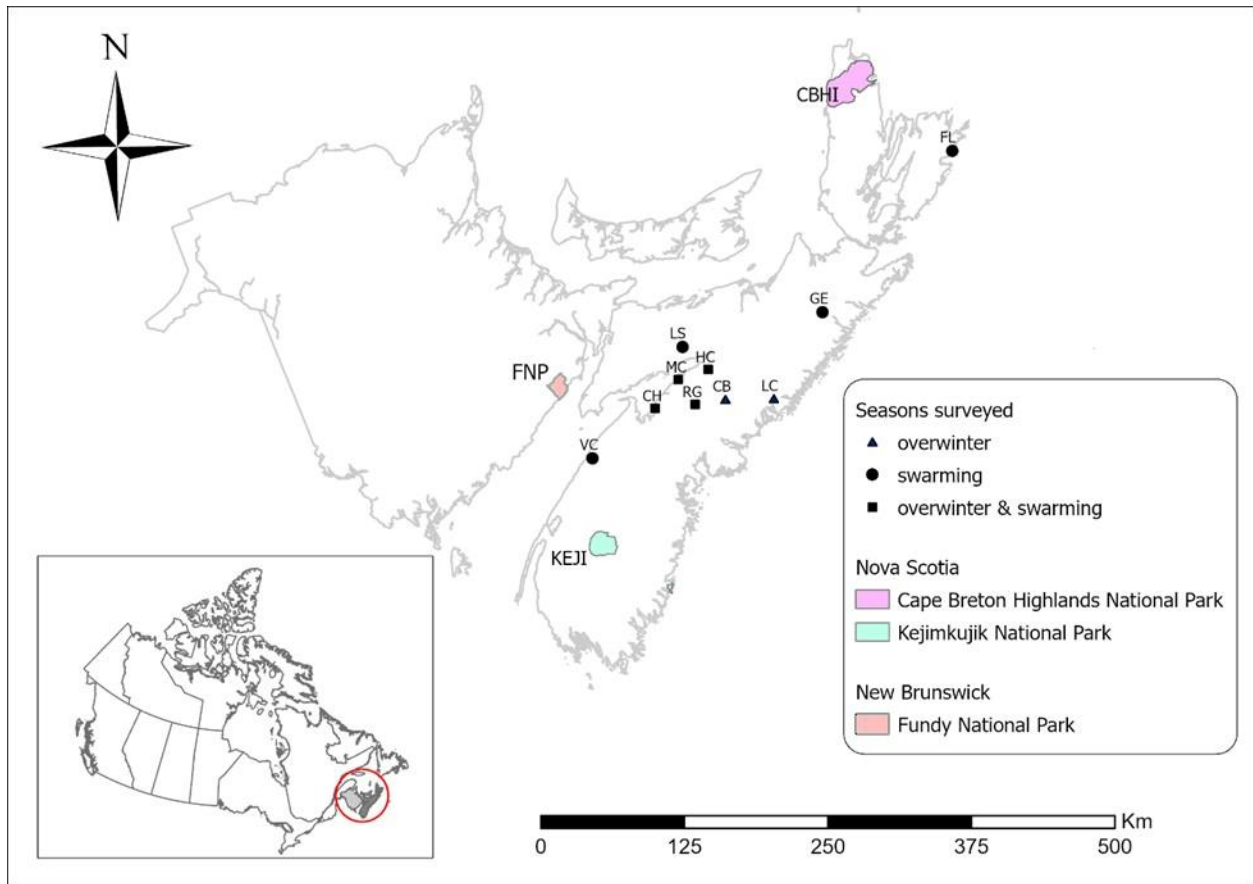
We conducted post-WNS surveys in each of the summer, autumn swarming, and overwinter seasons at sites surveyed pre-WNS to provide comparative population assessments pre- and post-

WNS (Table 2.1, Figure 2.1). For the summer and autumn swarming periods, we conducted capture surveys in Nova Scotia and New Brunswick. For all bats captured, we identified species, sex, and age class (juvenile or adult; Anthony, 1988). For the winter hibernation period, we conducted overwinter counts at hibernacula in Nova Scotia. Evidence of WNS was first detected in the Maritimes in 2011, so for the purpose of this work, we used 2011 as the year that divides pre- and post-WNS periods (COSEWIC, 2013) unless other specified.

**Table 2.1** Sampling effort across seasons at various sites in Nova Scotia and New Brunswick, Canada before and after White Nose Syndrome (WNS) disturbance. For summer and autumn swarming capture surveys without exact known trap effort, number of evenings is provided, though it is standard to survey for 3-5 hours.

Survey locations	Pre-WNS (2004-2011, 2014 <sup>†</sup> )				Post-WNS (2019-2024)			
	Season	Year	Methods	Sampling effort	Season	Year	Methods	Sampling effort
New Brunswick								
<i>Forested roads, trails</i>	Summer	1999-2001	Mist net, Harp trap	>20 evenings/year	Summer	2022	Mist net, Harp trap	206 trap hours
Nova Scotia								
<i>Forested roads, trails, over rivers</i>	Summer	2001, 2003-04, 2007-08	Mist net, Harp trap	128 trap hours	Summer	2019, 2022	Mist net, Harp trap	956 trap hours
<i>Abandoned mines, caves</i>	Swarming	2004-11, 2014 <sup>†</sup>	Mist net, Harp trap	98 evenings	Swarming	2022-24	Mist net, Harp trap	275 trap hours
	Hibernation	1996-97, 2000-01, 2006-07, 2008-12	Overwinter counts	6 sites	Hibernation	2012-15, 2018-19, 2022-24	Overwinter counts	5 sites

<sup>†</sup> WNS had not yet been detected in 2014 at the Fortress of Louisbourg (Site FL), so pre-WNS swarming surveys occurred this year for this survey location



**Figure 2.1.** Survey locations of summer, autumn swarming, and overwinter surveys in New Brunswick (light grey) and Nova Scotia (dark grey), Canada. Summer surveys occurred throughout the landscape in national parks from May to August. Autumn swarming and overwinter surveys occurred at underground openings and abandoned mines. Autumn swarming surveys involved capture surveys at the cave/mine entrances, and overwinter surveys involved counting the number of hibernating bats inside these sites.

While our aim was to present findings on species trends from synthesizing seasonal survey data, we present the approaches for each season surveyed separately. Specifically, we present the methods for summering, swarming, and overwinter surveys given the variable sampling locations and years surveyed for each of these seasons.

### ***2.3.1 Summer***

Summer capture surveys occurred from May to August (1999-2001, 2019-2022) and involved deploying nets and traps at sunset along forested trails, at forest openings, and along the edge of waterways. Historical (pre-WNS) data included summer surveys in Fundy National Park, New Brunswick (1999-2001; Broders, 2003; Broders et al., 2001) and in Kejimikujik National Park, Nova Scotia (2001; Broders et al., 2003). Post-WNS surveys occurred in both Fundy (2022) and Kejimikujik National Park (2019). For an additional point of comparison, post-WNS we also surveyed Cape Breton Highlands National Park, Nova Scotia in July 2022 where we could anticipate similar historical abundances to the other parks surveyed.

A typical night involved 3-4 hours of capture surveys, so we standardized trapping effort using capture-per-unit effort (CPUE) values with one trap hour equivalent to one harp trap set up for 1 hour, or one 12-m mist net set up for 1 hour. For comparison of capture rates from summer surveys, where we have trap effort available, we compare the CPUE values for species at each site separately. Where trap effort is unavailable, we present the raw numbers of captures for each species. As we only have summary data available for each site (cumulative pre-WNS and cumulative post-WNS numbers), we present our findings descriptively.

### ***2.3.2 Swarming***

Autumn capture surveys occurred from August to September (2004-2014, 2022-2024) and involved deploying mist nets and/or harp traps at the entrance of caves and abandoned mines. Historical (pre-WNS) swarming capture data included 93 evenings of surveys from the entrance of 7 hibernacula on mainland Nova Scotia (2004-2011), and 5 evenings of surveys at an abandoned

countermine tunnel at the Fortress of Louisbourg (Site FL) in 2014 as WNS had not yet been detected there (Burns & Broders, 2015). Sites included naturally formed caves (CH, HC, LS, MC, VC) and abandoned mines (FL, GE, RG; Figure 2.1). Post-WNS swarming surveys occurred over 58 evenings between 2022-2024 at the same sites surveyed pre-WNS.

The structured repeatability of nightly pre- and post-WNS autumn swarming data facilitated assessing demographic trends (age and sex structure) and relative bat abundance. Similarly to summer capture surveys, we used CPUE values to compare capture rates of bats from pre- to post-WNS. As we did not have nightly trap effort available for surveys pre-WNS, to facilitate comparison between the pre- and post-WNS periods, we used the average nightly trap effort from post-WNS surveys to calculate all nightly CPUE values for pre- and post-WNS survey data from sites surveyed with harp traps. For surveys at the Fortress of Louisbourg that involved mist nets, we calculated specific survey effort based on the exact trap effort. Specifically, we had the cumulative trap effort available for the pre-WNS period, so we assumed equal sampling effort per night to calculate the CPUE values. For post-WNS surveys at this site, we had exact trap effort available each evening surveyed, and we used those effort values to calculate each night's CPUE value.

We performed statistical analyses for autumn swarming data in RStudio v.4.4.2 (R Core Team, 2024). Our data did not meet assumptions of residual normality or homoscedasticity for parametric analysis, and instead of transforming the data to meet these assumptions, we opted for non-parametric analyses for our study. While these tests can have lower statistical power, in many cases

with data with non-normal distributions, non-parametric tests can be of sufficient or even greater statistical power compared to parametric alternatives (Treister et al., 2015). Additionally, the more conservative nature of these non-parametric approaches means that detected differences are more likely to reflect meaningful biological change, contributing to our goal of making ecologically relevant inferences on these populations, in addition to having more interpretable results by retaining the data in their original scale. We therefore used the non-parametric Mann-Whitney U test for each of our analyses (Blair & Higgins, 1980; Wilcoxon, 1992). We used this non-parametric approach to test for differences in the mean CPUE values at each site surveyed between the pre- and post-WNS period. We did the same for CPUE values of each species (*M. lucifugus*, *M. septentrionalis*, and *P. subflavus*) from each night surveyed to view species-specific patterns and, again, to compare CPUE values between the pre- and post-WNS period.

### ***2.3.3 Overwinter surveys***

Standardized overwinter surveys occurred between 1996 to 2024 at six hibernacula in Nova Scotia (CB, CH, HC, LC, MC and RG; Figure 2.1). Early winter counts were conducted in December, mid-winter counts in January-February, and late winter counts in late March or early April. Since overwinter surveys did not involve bat handling, differentiate between overwintering *M. lucifugus* and *M. septentrionalis* was not possible. For *P. subflavus*, however, they could often be identified due to their smaller and rounder body, and we identified them where possible. For comparison of pre- to post-WNS data, we discuss the trends from the number of overwintering bats counted.

### **2.3.4 Animal care**

For overwinter surveys post-WNS (late-2012 onwards), we followed standard WNS decontamination protocols as outlined in CWHC (2017) to reduce risk of Pd transmission. All surveys were approved and conducted with the appropriate permits including the University of Waterloo's animal care permit (#44138 & #30066), the Nova Scotia Department of Natural Resources Scientific/Species at Risk Permit, and Parks Canada Research and Collection Permit (FNP-2022-42739 & KNP&NHS-2019-32363).

## **2.4 Results**

### **2.4.1 Summer**

Pre-WNS, we captured 230 *M. lucifugus* and 168 *M. septentrionalis* at Fundy National Park from 1999-2001 (Broders, 2003). At Kejimikujik National Park in 2001, we surveyed for 128 trap hours and captured 17 *M. lucifugus*, 26 *M. septentrionalis*, and 3 *P. subflavus*. The CPUE values for each species at Kejimikujik were therefore 0.13 for *M. lucifugus*, 0.20 for *M. septentrionalis*, and 0.02 for *P. subflavus* (Broders et al., 2003).

Post-WNS, we did not capture any of the endangered hibernating bats at Fundy National Park despite 206.63 trap hours in 2022 at the same locations surveyed in 1999-2001. At Kejimikujik, we surveyed for 746 trap hours in 2019 and captured 13 *M. lucifugus* and 6 *P. subflavus*. The post-WNS CPUE values for each species at Kejimikujik post-WNS were therefore 0.02 for *M. lucifugus*, 0.00 for *M. septentrionalis*, and 0.01 for *P. subflavus*. From Kejimikujik only, these CPUE values demonstrate a 78% ( $\pm 20\%$ ) decline in CPUEs across all species compared to pre-WNS CPUE

values at this site, with an 85% decline for *M. lucifugus* capture rates, 100% decline for *M. septentrionalis*, and 50% decline for *P. subflavus*. For both Fundy and Kejimikujik combined, these findings suggest a 92.5% ( $\pm 7.5\%$ ) decline and 100% decline for local populations of *M. lucifugus* and *M. septentrionalis* respectively.

We additionally surveyed for 210 trap hours in Cape Breton Highlands National Park, Nova Scotia in 2022 (a locality not surveyed pre-WNS) but did not have any captures. The only bat documented here was a single male *M. septentrionalis* carcass collected from the road (collected by park staff on 8 June 2022, 46.71150 N, 60.36796 W).

#### **2.4.2 Autumn Swarming**

Across all swarming sites in Nova Scotia pre-WNS, we captured 4662 bats over 98 evenings: 3370 *M. lucifugus*, 1276 *M. septentrionalis* and 16 *P. subflavus*. From these captures, regional population composition pre-WNS was 72.3% *M. lucifugus*, 28.6% *M. septentrionalis*, and 0.003% *P. subflavus*. Pre-WNS populations for each of the three species were adult- and male-biased (Table 2.2). Age class ratios (juvenile:adult) were 1 : 2.9 for *M. lucifugus*, 1 : 1.5 for *M. septentrionalis* and 1 : 1.2 for *P. subflavus*. Sex ratios (female:male) were 1 : 1.3 for *M. lucifugus*, 1 : 1.1 for *M. septentrionalis*, and 1 : 4.3 for *P. subflavus*.

For the post-WNS period at sites surveyed with harp traps, average nightly trap effort ( $\pm$ sd) was 3.45 h ( $\pm 1.5$ h) and this value was used to calculate CPUE values for these sites. For pre-WNS capture rates, the mean CPUE ( $\pm$ SE) values for each site ranged from 1.18 ( $\pm 0.4$ ) at FL to 27.16

( $\pm 4.1$ ) at HC (Figure 2). For species CPUE values across all sites, the mean ( $\pm$ SE) was 10.14 ( $\pm 1.5$ ) for *M. lucifugus*, 3.71 ( $\pm 0.4$ ) for *M. septentrionalis*, and 0.06 ( $\pm 0.01$ ) for *P. subflavus* (Figure 2.3).

Post-WNS, we captured 330 bats over 58 evenings: 315 *M. lucifugus*, 10 *M. septentrionalis* and 5 *P. subflavus*. Post-WNS population composition (rounded to 1 decimal place) was therefore 95.5% *M. lucifugus*, 3.0% *M. septentrionalis*, and 1.6% *P. subflavus*. Post-WNS populations for each species were adult- and male-biased but exhibited changes in demographic ratios, suggesting shifts in demographic structure. Age class ratios (juvenile:adult) remained 1 : 1.3 for *M. lucifugus*, and became equal at 1:1 for *M. septentrionalis* and for *P. subflavus*. Sex ratios (female:male) post-WNS increased to 1 : 1.6 for *M. lucifugus*, 1 : 2.3 for *M. septentrionalis* and 0 : 1 for *P. subflavus* (Table 2.2). For *P. subflavus*, however, the presence of juvenile bats confirms the presence of reproductive adult females in the population despite us not having caught any. We note that for *M. septentrionalis* and *P. subflavus*, these demographic ratios are derived from a much smaller sample size compared to that pre-WNS, representing a handful of individuals.

**Table 2.2** Capture numbers (proportions) of adult, juvenile (juv.), female (♀) and male (♂) bats for each of the endangered, hibernating bat species at swarming sites in Nova Scotia, Canada.

	Pre-WNS (2004-2011, 2014 <sup>†</sup> )		Post-WNS (2022-2024)	
<b><i>M. lucifugus</i></b>	Adult	Juv.	Adult	Juv.
pre: 3370 [3299] <sup>††</sup>	♀ 1041 (0.32)	369 (0.11)	♀ 60 (0.19)	59 (0.19)
post: 315	♂ 1412 (0.43)	477 (0.14)	♂ 115 (0.37)	80 (0.25)
<b><i>M. septentrionalis</i></b>	Adult	Juv.	Adult	Juv.
pre: 1276 [1220] <sup>††</sup>	♀ 340 (0.27)	236 (0.18)	♀ 1 (0.10)	2 (0.20)
post: 10	♂ 394 (0.34)	249 (0.20)	♂ 4 (0.40)	3 (0.30)
<b><i>P. subflavus</i></b>	Adult	Juv.	Adult	Juv.
pre: 16 [15] <sup>††</sup>	♀ 1 (0.07)	2 (0.13)	♀ 0	0
post: 5 [4] <sup>††</sup>	♂ 7 (0.47)	5 (0.33)	♂ 2 (0.5)	2 (0.5)

<sup>†</sup> WNS had not yet been detected in 2014 at the Fortress of Louisbourg (Site FL), so pre-WNS swarming surveys occurred this year for this survey location.

<sup>††</sup> The number of fully identified individuals (individuals identified to both a sex and age class) indicated in square brackets. These values are those from which proportions in the table body are calculated.

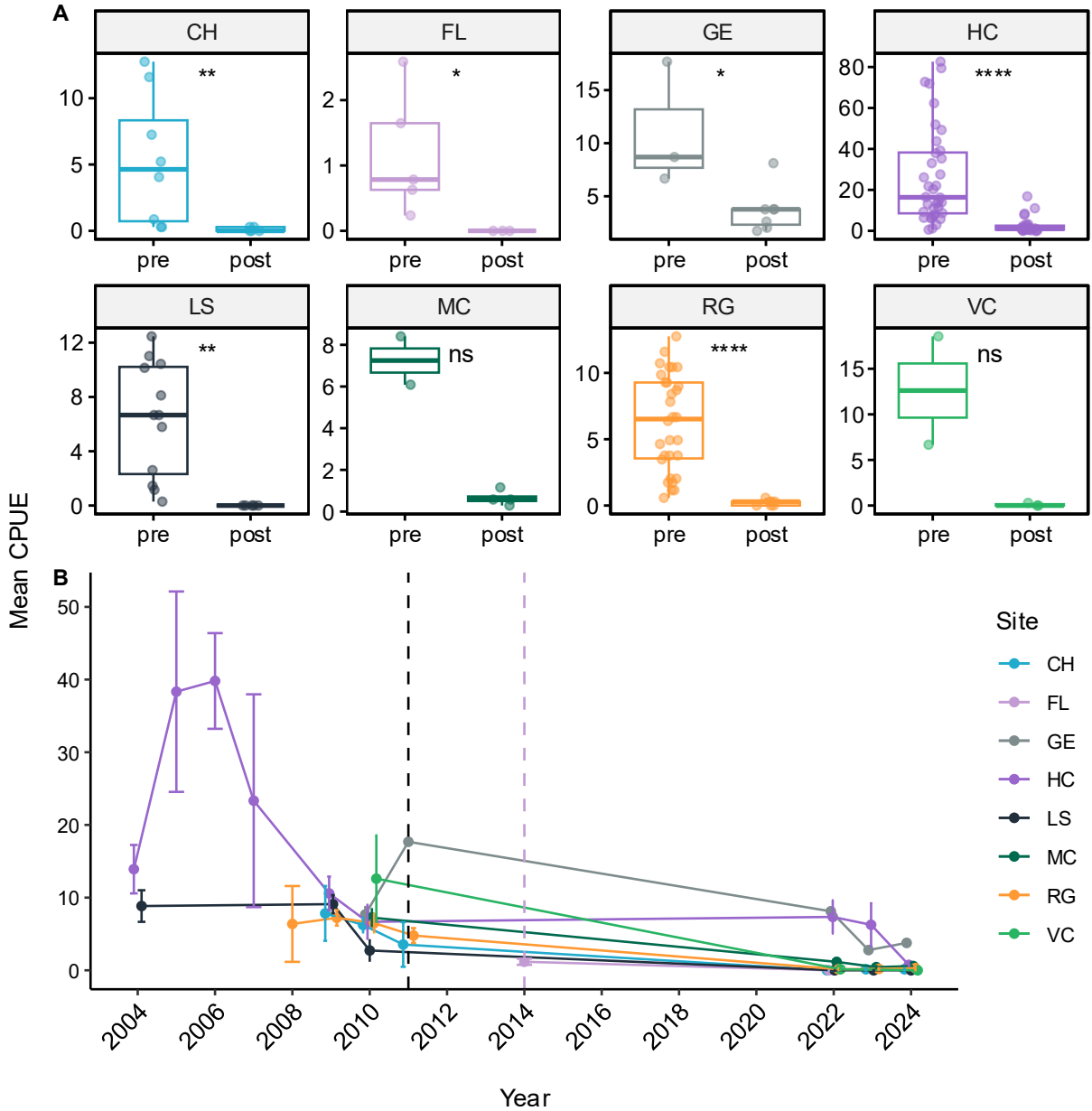
Across all sites, there were significant declines in bat capture rates post-WNS (Wilcoxon signed rank test  $V = 36$ ,  $p = 0.01$ ), with a mean ( $\pm$ SE) 90% ( $\pm 6\%$ ) decline in the regional CPUE value compared to the pre-WNS average. Of our survey sites, 6 of 8 sites exhibited significant declines in CPUE values (Figure 2.2, Table 2.3) The site-specific mean CPUE ( $\pm$ SE) ranged from 0 (FL) to 3.8 ( $\pm 0.83$ ) (GE). There was no significant difference at two sites (VC and MC), however there was limited sampling effort at these locations (2 nights surveyed pre-WNS and <7 nights of sampling across both pre- and post-WNS periods). For species, CPUE values (mean  $\pm$  SE) post-WNS were significantly less than those pre-WNS for both *M. lucifugus* (84.2%  $\pm$  4.6% decline;

W = 932,  $p < 0.0001$ ) and *M. septentrionalis* ( $98.6\% \pm 0.5\%$  decline; W = 474,  $p < 0.0001$ ). *Perimyotis subflavus* CPUEs were comparable between pre- and post-WNS periods ( $36.6\% \pm 40.4\%$  decline; W = 2664,  $p = 0.2$ ) (Figure 2.3, Table 2.3). We also observed evidence of decline pre-WNS (2007-2011) for *M. lucifugus* and *M. septentrionalis* (Figure 2.3B).

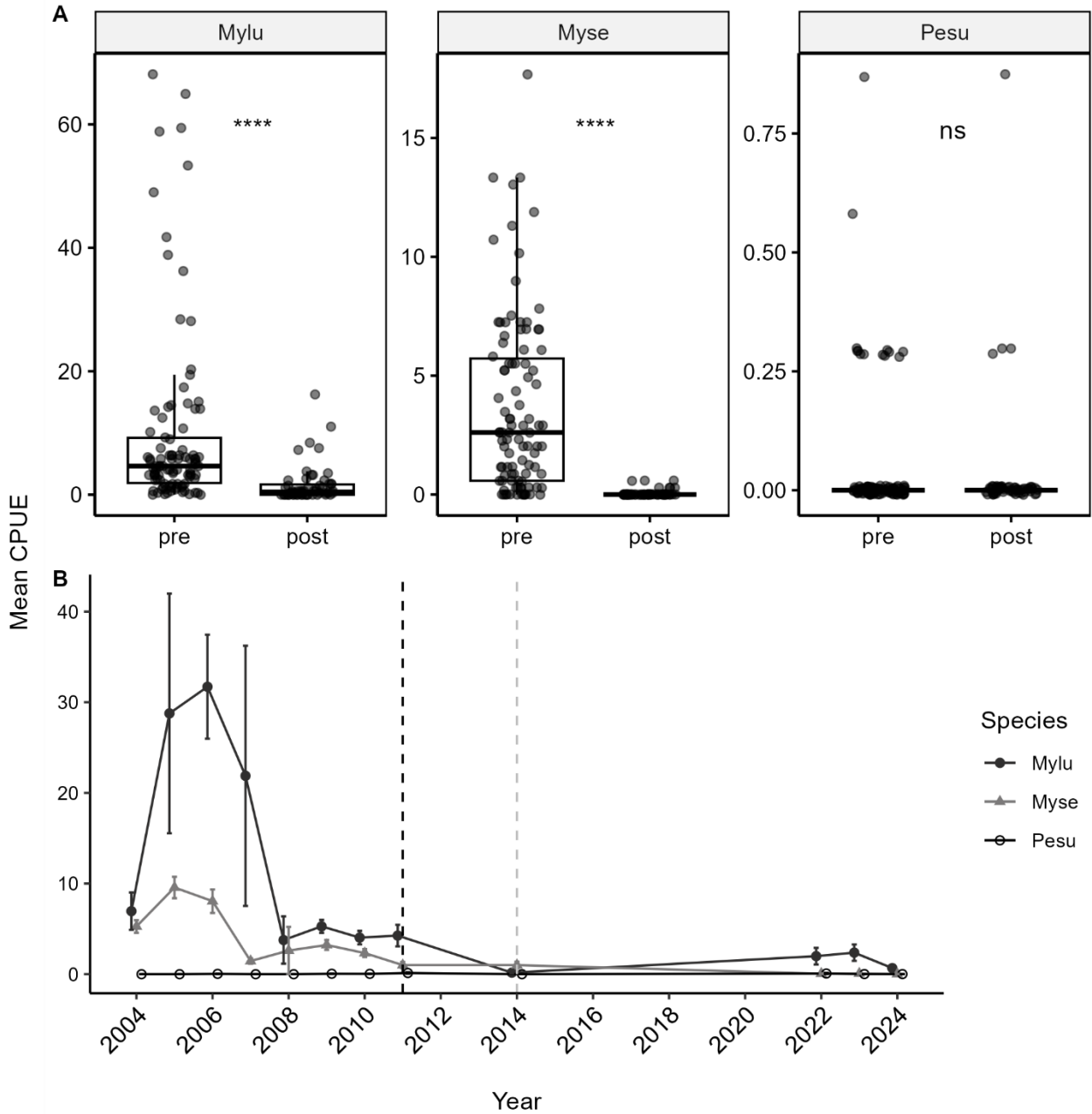
**Table 2.3** Swarming sites sampled pre- (2004-2011, 2014) and post-WNS (2022-2024) and the change in bat activity overall and per species between the two periods. Significant ( $p < 0.05$ ) results are bolded. Standard errors (SE) are rounded to the nearest integer.

Site	Total nights surveyed [pre, post]	% diff. species CPUE ( $\pm$ SE)		
		<i>M. lucifugus</i>	<i>M. septentrionalis</i>	<i>P. subflavus</i>
CH	13 [8,5]	<b>-96.7(<math>\pm</math>2)</b>	-100	-100
FL <sup>†</sup>	8 [5,3]	-100	<b>-100</b>	n/a
GE	10 [3,7]	-60( $\pm$ 18)	<b>-90.1(<math>\pm</math>4)</b>	n/a
HC	60 [36,24]	<b>-87(<math>\pm</math>4)</b>	<b>-99.1(<math>\pm</math>1)</b>	+100( $\pm$ 192)
LS	17 [12,5]	<b>-100</b>	<b>-100</b>	n/a
MC	6 [2,4]	-82( $\pm$ 13)	-100	n/a
RG	37 [30,7]	<b>-94.9(<math>\pm</math>2)</b>	<b>-100</b>	-52.4( $\pm$ 50)
VC	5 [2,3]	-99.2( $\pm$ 1)	-100	n/a

<sup>†</sup> WNS had not yet been detected in 2014 at the Fortress of Louisbourg (FL), so pre-WNS swarming surveys occurred this year for this survey location.



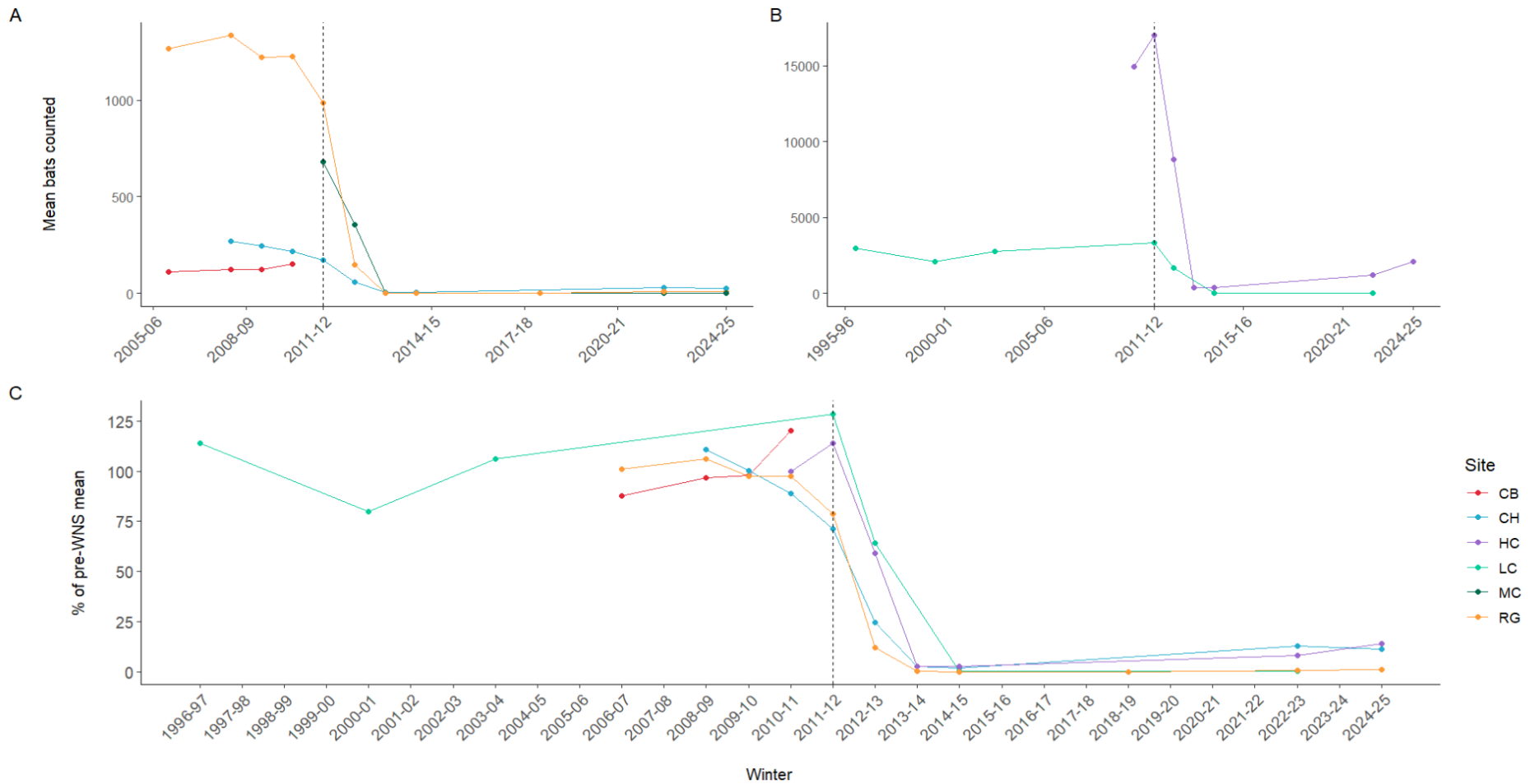
**Figure 2.2** (A) Pre- (2004-11, 2014) and post-WNS (2022-24) capture-per-unit-effort (CPUE) values of bats, and (B) annual trends of CPUE values at swarming sites in Nova Scotia, Canada. For (B), standard error bars are shown, and the black dashed line represents WNS detection in the province, except for Site FL where pre-WNS surveys were conducted in 2014 (light dashed line) as no evidence of WNS nor associated mortality were detected there at that time. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , \*\*\*\* $p \approx 0$ .



**Figure 2.3** (A) Pre- (2004-11, 2014) and post-WNS (2022-24) capture-per-unit-effort (CPUE) values and (B) annual trends of CPUE values for each of the resident hibernating bat species at swarming sites in Nova Scotia, Canada. For (B), standard error bars are shown, and black dashed line represents WNS detection at sites, except for Site FL where pre-WNS surveys were conducted in 2014 (light dashed line) as WNS nor associated mortality were detected there at that time. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , \*\*\*\* $p \approx 0$ .

### **2.4.3 Overwinter surveys**

Pre-WNS, overwinter counts were inter-annually consistent and within-site average counts ranged from 125 to 16300 bats (Table S1, Figure 2.4). We observed the presence of WNS infection in the late winter of 2011-12. The most severe declines (98-100%) of overwintering bats occurred within 1-4 years of WNS detection. Hibernacula with <1500 overwintering bats pre-WNS had zero or near-zero (<30) numbers of overwintering bats post-WNS. At our largest hibernaculum (HC), we observed a slow increase in the number of individuals present in the post-WNS period following 2015. Between late 2013-14 surveys and late 2014-15 surveys at HC, there was an estimated average of 380 bats. During the 2022-23 surveys we estimated 1200 bats, and in our most recent surveys in 2024-25, we estimated 2100 bats, the highest since HC's population collapse following WNS. Most individuals identified at each hibernaculum were *Myotis* spp. Where *P. subflavus* could be identified, in our most recent surveys (2024-25), we counted 30 *P. subflavus* at HC (30/2100 bats), 3/10 bats at RG, and at MC all 27 overwintering bats counted were *P. subflavus*. Across all sites, the number of overwintering bats is 0-14% of the average number of overwintering bats observed pre-WNS (Figure 2.4)



**Figure 2.4.** Number of overwintering bats counted at (A) smaller (<1500 bats) and (B) larger hibernacula, and (C) the proportion of overwintering bats each year relative to the pre-WNS average number of bats counted at that site. Black dashed line represents detection of WNS at hibernacula.

## **2.5 Discussion**

From summer surveys of local populations and swarming and overwinter surveys of regional populations, we find that each of the three endangered hibernating bat species in Maritime Canada experienced disturbance and population declines. Summer surveys suggest local populations of bats have been functionally, if not completely, extirpated from regions where they were once abundant, with 50-100% declines across species. Similarly, surveys from autumn swarming sites reveal significantly lower capture-per-unit-effort (CPUE) values compared to historical data for both sites (6/8 sites) and species (2/3 species), along with changes in community structure. Overwinter hibernation surveys reveal most hibernacula have experienced near-complete disappearance of overwintering bats, with abundances from all sites combined being 84% less of what they were pre-WNS. Our findings align with those of many other studies across the geographic range for *Myotis lucifugus*, *M. septentrionalis*, and *P. subflavus*: WNS had considerable impacts on each of these species' populations, and disturbance was observed in multiple areas of these species' life history (Cheng et al., 2021; Hooton et al., 2023). More than a decade after initial WNS detection, local populations historically surveyed show no evidence of recovery. For *M. septentrionalis*, regional populations continue to decline and do not currently indicate a trajectory towards recovery. Regional populations of *M. lucifugus* and *P. subflavus*, on the other hand, show evidence of population growth and potential recovery underway.

### ***2.5.1 Species-specific responses***

The most widespread hibernating bat in Maritime Canada, *M. lucifugus*, experienced dramatic declines as a result of WNS with an estimated 92.5% ( $\pm 7.5\%$ ) population decline observed during

summer surveys, 84.2% ( $\pm 4.6\%$ ) decline during autumn swarming surveys, and near 100% decline at all but one hibernaculum from overwinter surveys. From each of these seasons' surveys, we observed that 10+ years after WNS disturbance, the remaining local and regional populations still have substantially lower abundances compared to pre-WNS averages. However, from recent overwinter surveys at HC, our largest hibernaculum, we observed increases in the number of *Myotis* bats following 2015. This aligns with earlier findings from Langwig et al. (2012) that in a WNS-affected population, stabilization and subsequent increases in the number of overwintering *M. lucifugus* are observed 4 years after WNS detection, the predicted period where disease establishment may begin. Though we did not differentiate between overwintering *Myotis* species, evidence from autumn swarming and summer occupancy data (Balzer et al., 2021) demonstrate that *M. lucifugus* are far more common in the system than *M. septentrionalis*.

The current status for *M. septentrionalis* is of significant concern as this species experienced the most severe declines in capture rates in our study area, with a 100% decline observed from summer capture surveys and a 98.6% ( $\pm 0.5\%$ ) decline from autumn swarming surveys. Across their geographic range, *M. septentrionalis* have consistently shown greater magnitudes of decline associated with WNS compared to sympatric species (Cheng et al., 2021; Frick et al., 2015; Langwig et al., 2015b). The primary factor predicted to contribute to these disproportionate declines of *M. septentrionalis* is the substantially higher fungal loads of Pd when these bats become infected with Pd (Cheng et al., 2024; Langwig et al., 2016). While pre-WNS colony size has shown to be an important factor for WNS-susceptible species, declines of *M. septentrionalis* are density-independent (Frick et al., 2015, 2017).

*Perimyotis subflavus* present an interesting case where our interpretations of recovery differ depending on season surveyed. Summer surveys post-WNS at Kejimikujik National Park suggest substantial decline for this species. Prior to WNS, the CPUE estimates of *P. subflavus* in Kejimikujik were consistent (Broders et al., 2003; Poissant et al., 2010), whereas our post-WNS CPUE estimates suggest half of the pre-WNS average. In the first State of the Bats report, summer abundances of *P. subflavus* were also noted to have declined by half across North America (NABCA, 2023). Autumn swarming data, however, suggest capture rates of *P. subflavus* are comparable between pre- and post-WNS periods. Additionally, post-WNS overwinter counts reveal successful overwintering *P. subflavus*, with one small hibernaculum being used exclusively by this species. Despite *P. subflavus* being a species most impacted by WNS (Cheng et al., 2021), leading to federal endangerment status for this species in both the United States and Canada (Environment and Climate Change Canada, 2015; USFWS, 2022), our results highlight that *P. subflavus* decline may not be as severe relative to *M. lucifugus* and *M. septentrionalis*. This aligns with more recent research suggesting that *P. subflavus* respond differently to WNS compared to other majorly affected species (Ingersoll et al., 2016), perhaps as a result of lower fungal loads (Frick et al., 2017; Langwig et al., 2016). With regional trends for this species in our area, we also acknowledge the possibility of geographic refugia for local populations where WNS decline may be absent or of lesser impact (e.g., Ford et al., 2011; Perea et al., 2022). We do, however, err on the side of caution with interpreting our findings from swarming and overwinter surveys as pre-WNS capture rates, and consequently power to detect population changes, of *P. subflavus* in the Maritimes were low (Broders et al., 2003). Consequently, any level of decline, even if of lesser magnitude than those of sympatric *M. lucifugus* and *M. septentrionalis* in Maritime Canada, can be detrimental to the stability and persistence of this disjunct population.

### ***2.5.2 Scale-specific trends***

The inferences made on population recovery for bats can differ depending on survey season as seasons provide information on population trends at different scales. Summer surveys in our study provide information on local populations along the landscape, whereas swarming and overwinter surveys that sample congregations of bats provide information on regional trends (Burns et al., 2014). For our study, we observed the greatest levels of decline across species in summer surveys, showing that local populations we studied pre-WNS declined significantly, if not entirely. Regional trends may lag behind local trends (O'Regan et al., 2015), however given the time elapsed since WNS detection in our area, our findings from swarming and overwintering sites suggest that these bats are still found across the province (i.e., regionally), albeit for *M. lucifugus* and *M. septentrionalis* at much lesser abundances. For *P. subflavus*, regional trends may mask declines experienced by certain populations (Costley et al., 2024), such as what we observed for this species. Generally, our regional findings align with those of many others across the WNS-affected range of these species, where declines for *M. lucifugus* are 80-100%, declines for *M. septentrionalis* are >90%, and for *P. subflavus*, while often variable, an average of 50% population decline (Cheng et al., 2021; Frick et al., 2015; NABCA, 2023).

### ***2.5.3 Change in community structure***

Species-specific levels of decline can exacerbate to larger-scale changes (Frick et al., 2015), such as changes in community structure, which is what we observed with the resident hibernating bats in Maritime Canada. Prior to WNS, regional population composition as inferred from swarming surveys showed 72.3% of bats were *M. lucifugus*, 27.5% *M. septentrionalis*, and 0.003%

*P. subflavus*. In the post-WNS period, however, population composition became 95.5% *M. lucifugus*, 3.0% *M. septentrionalis*, and 1.6% *P. subflavus*. Since fewer numbers of bats post-WNS results in a smaller denominator from which population composition is determined, the higher population occupancy of *P. subflavus* may simply be due to differences in community sample size pre- and post-WNS. Alternatively, this finding for *P. subflavus* may reiterate that there are other local populations that belong to this Maritime community. Ultimately, what we find is that species-specific responses scale up to community-level changes: regional species richness for this hibernating bat community has not yet changed, but the species evenness, an important consideration for measuring diversity (Hill, 1973), has declined in Maritime Canada.

#### ***2.5.4 Demographic shifts post-WNS***

Additional inferences on the potential for population and species recovery may be made by assessing demographic information (Maslo et al., 2015; Reed et al., 2003; Selwood et al., 2015). Our small sample sizes post-WNS for *M. septentrionalis* and *P. subflavus* do limit our ability to make concrete statements, but we present points of consideration with our findings assuming they reflect true population structure. From our autumn swarming surveys, there is indication of demographic shifts with sex and age classes post-WNS. Populations of each species pre-WNS were adult- and male-biased, consistent with earlier findings on these species (e.g., Davis, 1959; Glover & Altringham, 2008; Lacki et al., 2015). Post-WNS, population age structure for became more even, with an increased proportion of juveniles for all species. This may reflect decreased adult survival (Hopkins et al., 2021; Meierhofer et al., 2018), or more encouragingly, greater juvenile recruitment (Dobony & Johnson, 2018).

For sex ratios, post-WNS ratios may suggest a shift towards more male-bias, particularly for *M. septentrionalis* and *P. subflavus*. However, given our sample size for these two species, the male captures post-WNS may simply be the artifact of an already male-biased population. We note, however, that females often exhibit lower survival rates post-WNS infection and that this sex difference in disease response is more pronounced in *M. septentrionalis* and *P. subflavus* than in *M. lucifugus* (*sensu* Kailing et al., 2023). A smaller proportion of females in the populations can limit the rate at which population growth occurs and consequently hinder population recovery (Angulo et al., 2018; Kailing et al., 2023; Kramer et al., 2009).

### ***2.5.5 Additional considerations for recovery***

While WNS was a clearly observed driver of population decline for WNS-affected species across their range, we also acknowledge evidence of regional declines in the Maritimes prior to WNS arrival. From our swarming surveys, we observed declines preceding WNS detection for *M. lucifugus* and *M. septentrionalis*. There are a few considerations that may explain this observation. First, while we were interested in documenting population trends for these Maritime bat hibernators with respect to WNS, we cannot isolate the impacts of WNS as other drivers of decline are present. For this area, timing-specific events that may have contributed to these pre-WNS declines may include hurricanes associated with these years (Public Safety Canada, 2018), which could have contributed to direct mortality and/or habitat loss (Gannon & Willig, 1994; Jones et al., 2001). Additional drivers of decline to consider also include, but are not limited to, increased insecticide use and climate change, both of which significantly contribute to lesser prey abundance, wind turbine mortality, and habitat modification (Davy et al., 2022; Frick et al., 2020; O’Shea et al., 2016; Put et al., 2018). The declines we observed pre-WNS could have also exacerbated the

impact of WNS on these populations in Maritime Canada (Frick et al. 2015). Why these declines were not reflected in the overwinter period, however, may relate to our understanding of autumn swarming behaviour. Autumn swarming is recognized as a critical transition period of mating and information transfer that occurs near the entrance of potential hibernacula (Bradbury, 1977; McGuire & Fraser, 2023), but we are unaware where else along the landscape social congregations prior to winter hibernation may occur. In any case, to facilitate the persistence and recovery of WNS-affected populations in our area and elsewhere, reducing drivers of decline is critical (Cheng et al., 2024; Frick et al., 2020; Maslo et al., 2015).

## **2.6 Conclusion**

We documented significant reductions in the numbers of bats following WNS that suggest major population declines for each of *Myotis lucifugus*, *M. septentrionalis*, and *P. subflavus* in Maritime Canada. This decline was most evident at summering sites, while autumn swarming and overwinter hibernation surveys point to stable populations for *P. subflavus* and stabilizing populations for *M. lucifugus*. The situation for *M. septentrionalis* is dire as they experienced the most severe declines across seasons surveyed and among species. Despite this, captures of *M. septentrionalis* at autumn swarming sites post-WNS confirm that this species remains present, reinforcing the need to continue conservation efforts to protect these bats.

Across eastern North America, WNS was detrimental to many hibernating bat species, but the persistence of many populations years after WNS impact provides hope for recovery. Optimistically, fungal loads of Pd in our study area are at historical lows since the introduction of

WNS (Vanderwolf et al., 2025), and our data suggest that disease disturbance from WNS may no longer be an active threat. However, a secondary fungal species was recently identified in European bats that has the potential to cause WNS (Fischer et al., 2025). While many bats in North America display advantageous physiological or behavioural adaptations that allowed for survival following the WNS epidemic (Auteri & Knowles, 2020; Fuller et al., 2020; Lacki et al., 2015; Langwig et al., 2016; Lilley et al., 2016), these adaptations may not protect bats from a different fungal agent. As such, it is of utmost priority that we continue to monitor and protect these remaining WNS-affected populations to allow for population and, ultimately, species persistence.

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## 2.9 Supplementary materials

**Table S1.** Hibernaculum counts of over-wintering bats in Nova Scotia. Early winter surveys were conducted in December and late winter surveys occurred in late March or April. Counts were taken by averaging 2 or 3 independently-derived or best estimate of systematic counts of the site.

Winter	Survey period	Site					
		CB <sup>†</sup>	CH	HC	LC <sup>††</sup>	MIC	RGM
Pre-WNS							
1996-97	late				2973 <sup>‡</sup>		
2000-01	late				2079 <sup>‡</sup>		
2003-04	late				2761 <sup>‡</sup>		
2006-07	early	110					1267
2008-09	early	154	270				1335
	late	89					
2009-10	early	123					1224
	late		244				
2010-11	early						1213
	late	151	217	14923			1240
2011-12	early		147	17268		769	1114
	late		200*	16736*	3351*	591*	860*
Post-WNS							
2012-13	early		97	16148	3347	899	386
	mid					131	56
	late		22	1511	4	31	3
2013-14	late		6	360		0	1
2014-15	early		4	506	2	1	0
	late			272			
2018-19	early						0
2022-23	early		32	1259	2	1	8
	late		30	1112		0	7
2024-25	early		27	2100		1	10

<sup>†</sup> A rock fell at the entrance of this site between winter 2010-2011 and before fall 2011. The site was deemed too hazardous for entry for surveys in 2011-12 and later.

<sup>††</sup> In 2004, the entrance of this mine was gated and access into the site was not possible until winter 2011-2012 at which time the gate was damaged, permitting entry.

<sup>‡</sup> Data provided by the Nova Scotia Department of Natural Resources, the means by which these values were derived is unknown.

\* First record of fungus on bats at these sites that was consistent with Pd (classified as *Geomyces destructans* at the time.

## **CHAPTER 3**

Behavioural responses of free-flying bats towards humans, traps, and other captured bats during autumn swarming

### **3.1 Abstract**

Studies on animal activity and behaviour strive to have measurable and unbiased metrics to be able to make inferences. One of the most common approaches to studying bats in the field involves capturing free-flying individuals, a method by which we can obtain information such as habitat use, and population and demographic trends. However, previous research suggests that free-flying bat activity and behaviour may be influenced by the presence of other captured individuals in the area, humans, and traps, each of which are factors present during conventional capture surveys. Our goal was to investigate the effect of these factors on bat behaviour by quantifying the incidence and behaviour of little brown bats (*Myotis lucifugus*) in response to these factors at a swarming site in eastern Canada. Traps and humans may be perceived by bats as risky, whereas captured bats may be beneficial to investigate, as highlighted by previous research. We therefore predicted that when humans and traps are present, there would be fewer incidences of bats present in the area and that bats present would be more distant from the stimulus. With a captured bat, we predicted greater incidences of bats present and that bats would fly more proximal to the stimulus. We did not find evidence that humans, traps, or captured bats impacted the incidence of free-flying bats, but we did observe changes in spatial distribution relative to the stimuli. Specifically, free-flying bats flew higher in our study area when humans and traps were present. These data may suggest more avoidant behaviour when stimuli associated with greater risk are present. Future work involving trapping should consider the implications of this elicited behaviour, particularly with respect to demographic or heterospecific responses and how that can bias our interpretations on demographic structure and species abundance in a population. We highlight the importance of considering the inherent biases that may arise when employing certain methodologies and how they influence our observations and study results.

### **3.2 Introduction**

Intrinsic and extrinsic factors influence how animals interact with their environment (Ferrari et al., 2022; Istvanko et al., 2016; Lewis et al., 2015). Intrinsic factors such as sex, age, and reproductive status of individuals can influence the time spent foraging (Oakes et al., 1992), dispersal patterns (Hewison et al., 2021), and habitat selection (Rensel et al., 2022). Extrinsic factors, including changes in the environment and presence of certain stimuli, may elicit behavioural responses that alter an individual's movement (Elvidge et al., 2016; Greenberg & Mettke-hofmann, 2001). For example, the addition of a novel stimulus to an animal's environment can trigger neophobia (i.e., fear of novelty) and result in avoidance of the area where the stimulus was present (Crane & Ferrari, 2017; Szabo & Ringler, 2023). Alternatively, animals may exhibit neophilia (i.e., attraction to novel stimulus; Russ et al., 1998; Souganidis et al., 2024). How animals respond to stimuli ultimately depends on how stimuli are perceived (Belguermi et al., 2011; Goumas et al., 2022). Perception of stimuli may depend on previous exposure and experiences, but this perception and the consequent behavioural response are linked to the fitness costs and benefits associated with the stimuli (Ha, 2010).

Generally, quantifying animal behaviour can be difficult (Hughey et al., 2018; Stevens, 2010), particularly with inter- and intra-individual variability (Farrar et al., 2021). We therefore rely on making inferences from measurable metrics to understand behaviour. Like for other studies, methodological approaches for field studies are tailored to the focal taxa (Marion et al., 2020; Schemnitz et al., 2009). As such, there is a diversity of field methods used to answer a diversity of questions. One commonplace approach in field studies is conducting capture surveys wherein individuals are captured using traps (Schemnitz et al., 2009). While there are less invasive

approaches to study behaviour (Hughey et al., 2018), capture surveys allow for the collection of demographic data, morphometric measurements, and tissue collection (Powell & Proulx, 2003; Schemnitz et al., 2009).

The small, volant, and nocturnal nature of bats (order Chiroptera) has long created challenges for behavioural studies (Kunz, 2009). However, capture surveys, particularly when combined with other surveying methods, have greatly facilitated research on these animals (Kunz, 2009; O'Farrell & Gannon, 1999; Tanshi & Kingston, 2021; Thomas & Davison, 2022). Bat capture surveys typically involve capturing free-flying bats with mist nets and/or harp traps (Burns & Broders, 2015a; Fenton, 1969; Glover & Altringham, 2008). The type of trap used and its placement, as well as extrinsic and intrinsic factors, sway the likelihood of capturing certain species and individuals of certain demographic traits (Culina et al., 2017; Francis, 1989), potentially introducing bias.

With bat capture surveys, there are additional extrinsic factors that may act as stimuli that influence bat behaviour. First is the presence of captive bats which can induce mob-like behaviour wherein free-flying individuals gather and dive around the captive (Carter et al., 2015; Fenton et al., 1976; Russ et al., 2004; Ryan et al., 1985). Additionally, distress calls in animals are often emitted by individuals in stressful situations, such as being constrained (Conover, 1994). While individuals may use distress calls to warn conspecifics of a dangerous situation (e.g., predator presence; Conover, 1987; Manser et al., 2001), distress calls can also prompt inspection (Allwin Mages Raj et al., 2018; Carter et al., 2015; Fenton et al., 1976). Another extrinsic factor of interest with capture

surveys is the presence of the trap, which is a novel object introduced to the study environment. Trap detection and consequent avoidance is common in bats (Berry et al., 2004), particularly as bats learn with repeated exposure where and when the trap is deployed (Marques et al., 2013). Lastly, the researchers themselves may be a considerable factor. People are perceived as threatening by many taxa, often evoking a response similar to that of predator encounters (Frid & Dill, 2002; Smith et al., 2017), and bats have previously been observed to reduce their activity following increases in human activity (Li et al., 2020). Additionally, bat researchers typically wear headlamps for visibility, and studies on bat response have shown avoidant behaviour of bats to bright lights (Spoelstra et al., 2017; Stone et al., 2012). Repeated trap exposure and human presence may therefore be perceived as risky cues by bats, whereas the presence of captured individuals may be an attractant. Combining this information with the factors that are present at research sites prompt the question of what key factor(s) alter bat behaviour. Specifically, whether our approach to understanding bat behaviour inadvertently alters it.

Temperate bats are strongly influenced by seasonal cycles (Bradbury, 1977), so the particular setup for bat capture surveys depends on time of year. From late summer to early fall, hibernating bats engage in autumn swarming where individuals will congregate at the entrances of potential hibernacula (Bradbury, 1977). Current hypotheses to explain motivations for swarming include mating (Burns & Broders, 2015b; Furmankiewicz & Altringham, 2007; Rivers et al., 2006), and information transfer between conspecifics (Burns & Broders, 2015a; Stumpf et al., 2017), including mothers guiding young-of-year to potential hibernacula (Stumpf et al., 2017). Studying bats during autumn swarming, given the congregative nature of this period, is often completed by

setting traps at hibernaculum entrances (e.g., Burns & Broders, 2015a; Glover & Altringham, 2008; van Schaik et al., 2015).

The goal of our study was to quantify the effect of a common research method on bat behaviour during the autumn swarming period. We hypothesized that each of human presence, traps, and captured bats are stimuli that influence bat behaviour. We predicted that: (1) human and trap presence would deter free-flying bats and (2) a captured bat that is being held would increase the incidence of free-flying bats in the immediate vicinity. Additionally, to gain insight into spatial distribution, we assessed where in our study area individuals were flying. We predicted that (1) with human and trap presence, bats that were present would be further from the stimuli whereas for (2) with captured bats, free-flying bats would be flying closer to the stimulus.

### **3.3 Methods**

#### ***3.3.1 Study site & species***

We conducted this study at the entrance of a gypsum cave in Hants County, Nova Scotia, Canada that is an active autumn swarming and winter hibernation site. It is currently the largest hibernaculum known in Nova Scotia, with an estimated main chamber length of 365 metres and historically used by >15,000 bats during the winter hibernation period (Moseley, 1996, 2007). This cave is in a mixed forest landscape, primarily composed of coniferous trees such as spruce, and the ground-level cave entrance around which the bats swarm is at the base of a 20-metre cliff face.

This site has been subjected to significant declines in bat abundance following White Nose Syndrome disturbance, a fungal disease that has impacted hibernating bats across northeastern North America (Cheng et al., 2021; Frick et al., 2015). The hibernating bat species engaging in autumn swarming that can be found at this cave include the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*M. septentrionalis*) and the tri-colored bat (*Perimyotis subflavus*). However, following White Nose disturbance, the little brown bat is the dominant species observed and comprises >90% of the over-wintering population (Balzer et al., 2021).

### **3.3.2 Data collection**

We deployed a tripod-mounted thermal camera (Pulsar Axion 2 XG35 thermal monoscope, Lithuania) 33 metres from and facing the cliff above the cave entrance, recording the same field of view (7.2 metres by 5.4 metres at the cliff face) each night. We conducted 2-3 hours of standard capture surveys each sampling night using a harp trap deployed in the centre of the thermal camera's field of view. These capture surveys involved checking the trap at least every 15 minutes and placing any captured bats in individually numbered bags for processing. Processing, which included species identification and morphometric sampling, occurred within 5 metres of the harp trap and within the camera's field of view. Following capture surveys, we randomly selected 1-2 captured *M. lucifugus* to be used in our experiment, and all other captures were released. After this, we conducted 2 hours of behavioural trials.

The experimental period each night implemented a complete randomized block design to measure the impact of four stimulus scenarios on the presence and distribution of free-flying bats. The four

scenarios were: (A) control (no stimulus); (B) human (people talking at a standard conversational volume with their headlamps on); (C) trap (harp trap deployed without capture bag to ensure no further capture of animals); and (D) bat (an experimental bat in a bat bag hanging 1 metre above the ground on a tripod). For the 'bat' scenario, one experimental bat was randomly selected to be used as the stimulus. When not being used as a stimulus, the experimental bats were held in an 18 L soundproof insulated box. Each scenario was run twice each sampling night (Figure S1) and designed to both control for variability across time blocks (e.g., differences in environmental conditions, time of night) and permit comparison of stimuli on bat behaviour. Within each block, each of the four scenarios was run for 12-minutes and followed by a three-minute transition/buffer period, resulting in two 60-minute blocks each night that started 2-3 hours after sunset. Each night, the order of each scenario within a block was determined by a random number generator. Our control scenario (A) acted as a negative control and allowed us to understand baseline activity, especially since swarming activity can fluctuate within and across nights (Bell, 2022). Our human (B) and trap (C) scenarios correspond to prediction (1), and our bat (D) scenario to prediction (2).

Study design and animal handling were approved and conducted with the appropriate permits, including the University of Waterloo's animal care permit (#44138), and the Nova Scotia Department of Natural Resources Scientific/Species at Risk Permit.

### ***3.3.3 Data analysis***

We used VLC media player (v.3.0) to view thermal videos and manually quantify bat presence in the study environment at a baseline data resolution of discrete 10-second intervals. At each interval, we paused the video and counted the number of bats within the study environment, creating 72 samples per 12-minute scenario. To measure fine-scale spatial distribution, a horizontal line was overlaid in the centre of the video and, with manual inspection, we noted whether bats observed were in the upper or lower half of the frame at each time interval. Summarising the findings to later analyse, our final data output included: night sampled, the scenario employed, block (early or late), the number of instances of bats, and the proportion of instances of bats in the upper and lower halves of the camera frame.

For statistical analyses, we used RStudio v.4.4.2 (R Core Team, 2024). To select the appropriate time interval for assessing the effects of each novel stimulus, we created a linear mixed model for response variables at 10s, 20s, 30s, 40s, and 50s observation intervals. To ensure comparability of the models, any transformation that was applied to one was applied to all so that models were operating on the same scale. To meet the assumptions of residual normality we square-root transformed our observation count data (instances of bats observed). Additionally, to account for heteroscedasticity, we used a weighted variance structure in the model that allowed residual variances to vary across scenarios. We made our models using the `lme` function in the ‘nlme’ package, and used the `varIdent` weighting structure in this package for heteroscedasticity (Pineiro et al., 2025). Our final models for each of the candidate observation intervals therefore included the square-root number of instances of bats as our dependent variable, and scenario as our independent variable (fixed effect). We also included night and block as random effects as bat

swarming activity can vary within and across nights (Bell, 2022; Parsons et al., 2003). To select the optimal interval time from our candidate choices, we considered both the Akaike Information Criterion (AIC) values and the marginal  $R^2$  values from the models.

After determining our optimal observation interval, we used the associated data for the remainder of our analyses. We performed a Type III Analysis of Variance (ANOVA) to assess whether the scenario implemented was a significant factor in determining the number of instances of free-flying bats observed. For assessing differences in spatial distribution across scenarios, since we were interested in looking at differences in proportions of where free-flying bats were when counted (% upper : % lower), we used a generalised linear mixed model (GLMM) with logit link function and binomial distribution (Martínez-Flórez et al., 2021). Similar to activity (instances of bats), we had sampling night and block as random effects in our model. To view pairwise comparisons of spatial distribution across scenarios, we conducted Tukey's post-hoc test using the emmeans function in the 'emmeans' package (Lenth et al., 2024).

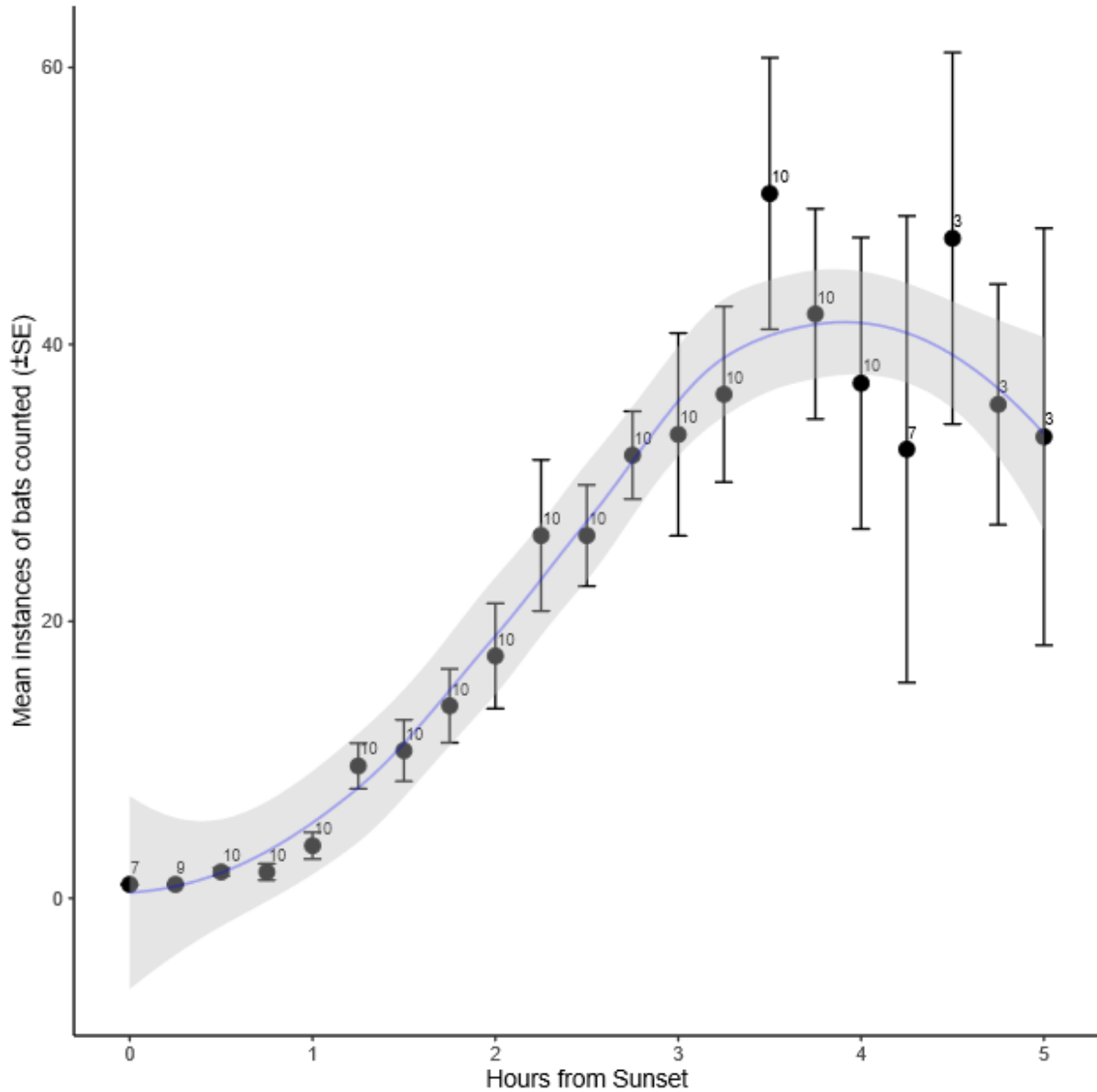
### **3.4 Results**

Observing instances and distribution of bats at 40s intervals was most suitable for our data as the model from this time approach the lowest AIC and highest marginal  $R^2$  compared to other candidate interval times (Table 3.1). We therefore continued our statistical analyses using observations of bats obtained at these discrete 40s intervals, having 18 samples per 12-minute scenario.

**Table 3.1** Comparison of linear mixed models (LMM) on instances of bats observed (square-root transformed) based on 10s, 20s, 30s, 40s, and 50s discrete interval observation times.  $R^2_m$  = marginal  $R^2$ , the variation explained by fixed effects (here, the scenario employed).  $R^2_c$  = conditional  $R^2$ , the variation explained by full model (fixed and random effects). Model selected for statistical analyses of data is bolded.

Observation interval time for LMM	df	AIC	$R^2_m$	$R^2_c$
10s	10	408.50	0.019	0.48
20s	10	353.47	0.026	0.57
30s	10	337.24	0.029	0.49
<b>40s</b>	<b>10</b>	<b>312.30</b>	<b>0.036</b>	<b>0.50</b>
50s	10	2705.23	0.01	0.25

Swarming activity peaked 3.5-3.75 hours after sunset (Figure 3.1). We recorded 2482 instances of bats over the 40s observation intervals during the experimental period for each of 10 survey nights. Instances of bats during this experimental portion ranged from 74 to 427 observations per night (mean  $\pm$  SD = 248.2  $\pm$  113.81 observations).



**Figure 3.1** Within-night activity of bats after sunset at a swarming site in Nova Scotia, Canada. Mean instances of free-flying bats ( $\pm$ SE) over the course of a night as observed by counting the number of bats at discrete 40s-time intervals from thermal footage. Each point represents the average number of instances for a 15-minute time period, and the sample size (number of nights for which we had footage at each time point) are indicated beside the point. Blue line with gray ribbon represents loess-smoothed trendline and its standard error.

On average ( $\pm$ SE), we observed 28.50 ( $\pm$ 4.53) instances of bats for scenario A (control), 25.85 ( $\pm$ 3.22) for scenario B (human), 30.80 ( $\pm$ 4.73) for scenario C (trap), and 38.95 ( $\pm$ 6.41) for scenario D (bat) per night (Figure 3.2a). There was not a significant difference in the number of free-flying bats depending on scenario (Table 3.2; ANOVA  $F = 1.86$ ,  $p = 0.15$ ).

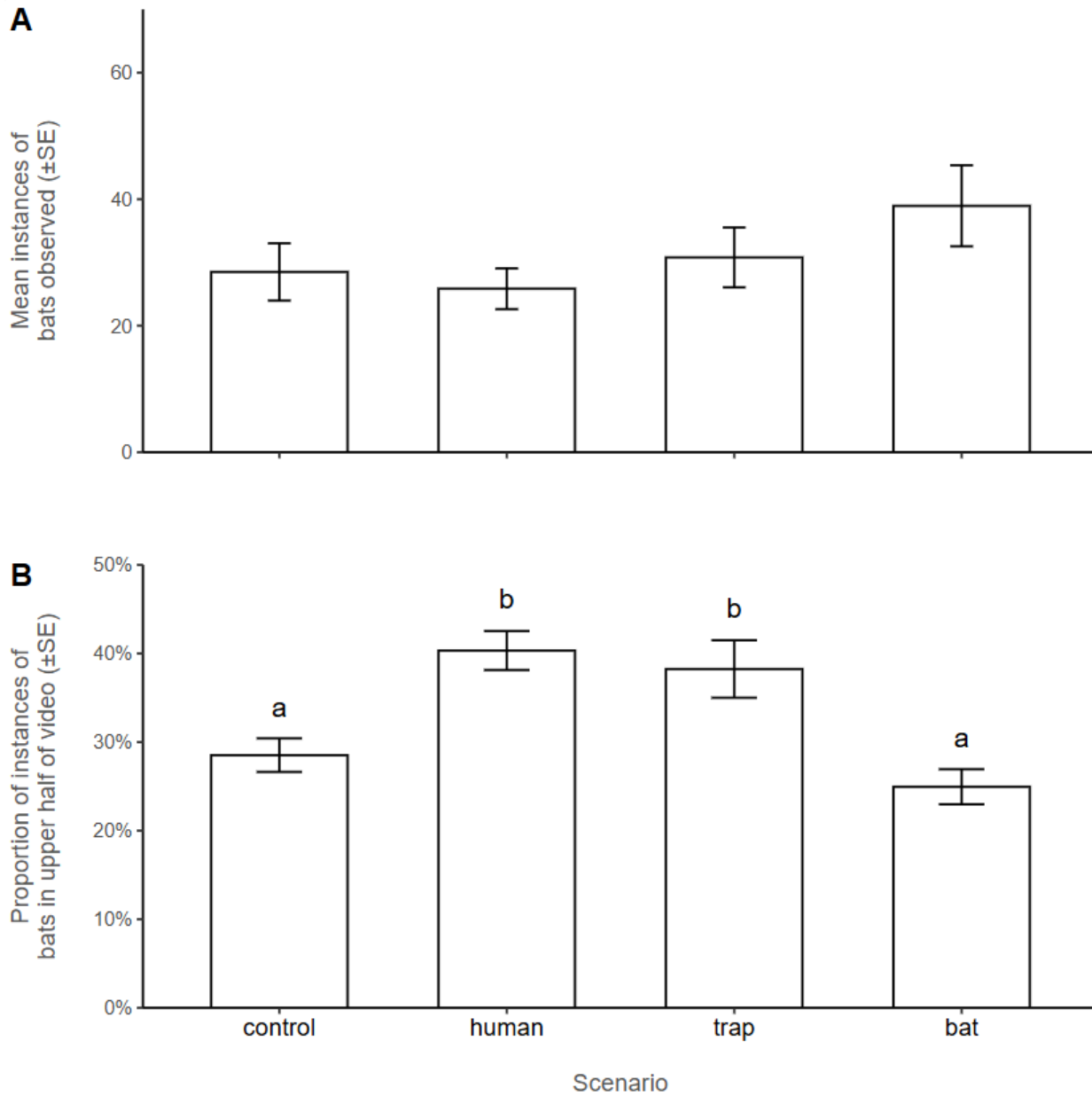
**Table 3.2** Linear mixed model (LMM) of average instances of free-flying bats observed (square-root transformed) during different experimental scenarios at a swarming site in Nova Scotia, Canada. Significant ( $p < 0.05$ ) values are denoted with an asterisk (\*).

	Value	SE	df	T	p
Intercept (control)	5.03	0.48	57	10.55	0.00*
Scenario - human	-0.17	0.37	57	-0.46	0.64
Scenario - trap	0.20	0.40	57	0.49	0.63
Scenario - bat	0.84	0.42	57	1.97	0.05

For spatial distribution of free-flying bats observed, there were significantly higher proportions of bats in the upper half of the video frame in our human (mean  $\pm$  SE =  $0.43 \pm 0.03$ ) and trap ( $0.40 \pm 0.04$ ) scenarios compared to our control ( $0.29 \pm 0.03$ ) and bat ( $0.26 \pm 0.03$ ) scenarios (Figure 3.2b, Table 3.3). There was no difference in spatial distribution between our control and our captive bat scenarios.

**Table 3.3** Tukey’s post-hoc summary of a generalised linear mixed model (GLMM) of proportions of free-flying bats in the upper and lower halves of recorded thermal footage across different scenarios. GLMM employed used a logit link function with binomial distribution. Significant values ( $p < 0.05$ ) are denoted with an asterisk (\*).

Contrast (Scenarios)	Odds ratio	SE	z ratio	p value
Control – Human	0.45	0.06	-5.96	<0.0001*
Control – Trap	0.52	0.07	-5.06	<0.0001*
Control – Bat	0.96	0.12	-0.30	0.99
Human – Trap	1.15	0.14	1.16	0.65
Human – Bat	2.12	0.26	6.15	<0.0001*
Trap – Bat	1.84	0.23	5.18	<0.0001*



**Figure 3.2** Mean (A) instances of bats observed and (B) proportions of these instances in the upper half of the video frame across different experimental scenarios from 10 experimental survey nights. Standard error bars are shown. Significant differences ( $p < 0.05$ ) in (B) are denoted by different letters. There was no significant difference in activity across scenarios for (A).

### **3.5 Discussion**

As stimuli, there was no evidence that either humans, traps, or captured bats impacted the number of free-flying bats observed. However, these stimuli did influence the spatial distribution of free-flying bats. We found greater proportions of bats in the upper half of our videos' field of view in scenarios where humans and traps were present compared to the control scenario and scenarios where captive bats were present.

We had predicted that both human and trap presence would be perceived as risky cues that would deter other individuals, resulting in fewer instances of free-flying bats in the area. We did not observe this, and this lack of predicted response may be attributed to a few factors. For the human stimulus, habituation and tolerance have been documented in urban habitats and in nature parks where animals frequently encounter humans (Samia et al., 2015; Wheat & Wilmers, 2016), and our study site is regularly visited by people for recreational activities. Since 2004, we have also conducted many swarming surveys at this site for many independent research projects which may have habituated these animals to the annual presence of researchers. Additionally, *M. lucifugus* are more associated with people and urban environments than other bats (Coleman et al., 2012), and may consequently exhibit greater tolerance towards humans. For bat response to traps, detection and avoidance are quite common (Larsen et al., 2007). Depending on the study area and how traps are placed, harp trap capture rates of bats flying by range from as little as <3% to as much as 80% (Berry et al., 2004; Kunz & Anthony, 1977; Larsen et al., 2007). The capture rate and consequent number of captured bats being processed by humans may influence risk-perception and subsequent response of free-flying bats in that area. At our study site, we deployed a single harp trap adjacent to the cave entrance, but the with entirely open space across the cave cliff face, the trap could

easily be avoided. As such, the trap may not have been perceived as a significant threat given the open flyways available.

Our observation of a greater proportion of bats in the upper field of view in our human and trap scenarios may reflect avoidant behaviour in response to the stimuli, whereby instead of leaving the area entirely, bats alter their flight paths and fly further from these stimuli. Trap avoidance in this manner has been well documented across many bat species (Dobson et al., 2001). In both Larsen et al. (2007) and Dobson et al. (2001), >90% of bat encounters with harp traps resulted in bats simply turning around or navigating around the trap. Learning behaviour has also been observed, where bats that have previously encountered traps will alter their flight path to avoid the trap in subsequent encounters, even if coming from the same flight corridor (Larsen et al., 2007). Similar findings were observed in Natterer's bats (*Myotis nattereri*) and in lesser horseshoe bats (*Rhinolophus hipposideros*) where bats would stay in the study's field of view but alter their flight path slightly to avoid the trap (Berry et al., 2004). Bats use both visual and acoustic cues to achieve obstacle avoidance (Jones & Moss, 2021), and in our study, human presence with lights, and use of speech, could have been these cues that facilitated avoidance. Flying higher in our study area may therefore allow bats to avoid perceived risks with humans and traps while still being able to investigate these stimuli and engage in autumn swarming.

Regarding free-flying response to captured bats, our findings of no perceived response surprised us given the high documentation of heightened activity as a response to live and acoustic lures. Many studies that use acoustic lures often use distress calls (Allwin Mages Raj et al., 2018; Russ

et al., 1998, 2004; Ryan et al., 1985), but we found no statistical evidence that a temporarily captive bat attracted other bats, nor can we confirm whether our captive bat was vocalising. For some species, heightened response towards captive bats only occurs in certain scenarios, such as a certain social context (Eckenweber & Knörnschild, 2016) or within a certain acoustic range of the captive (Loeb & Britzke, 2010). For example, Russo et al. (2009) observed a decline in heterospecific activity upon presenting a vocal stimulus. In our study area, *Myotis lucifugus* represent approximately 90% of bats observed at this site (Balzer et al., 2021), however *M. septentrionalis* and *Perimyotis subflavus* are also species that may be present.

Interestingly, our motivation for documenting spatial distribution in our study stemmed from seemingly investigative behaviour of free-flying bats with a captive bat, wherein from preliminary video analysis, we observed free-flying bats interacting directly with the captive (e.g., making contact with the bat bag, circling directly around the captured bat). Similar to other stimuli like humans and traps, individual variation in personality can influence an animal's response to novel subjects (Goumas et al., 2020; Kuo et al., 2023), and behavioural response may depend more so on the individual and what they perceive of the stimulus rather than the presence of the stimulus itself (Allan et al., 2020). Additionally, with typical swarming behaviour of bats congregating at potential hibernaculum entrances (Bradbury, 1977), we may not be able to differentiate inspection of the captive bat from regular swarming behaviour as all stimuli were presented at the focal swarming area by the cave entrance.

Our findings of consistent activity in numbers of bats but changes in spatial distribution between scenarios may reflect a few factors. First is the evolutionary advantage of engaging in autumn swarming. Autumn swarming is an important seasonal behaviour that serves many functions (Burns & Broders, 2015b; Rivers et al., 2006; Stumpf et al., 2017). The swarming period is energetically demanding, and it occurs prior to an even more physiologically demanding hibernation period (Bradbury, 1977; Fraser & McGuire, 2023). One cost is the energy required to travel the distance to swarming sites: the distance between roosts and swarming sites may be reasonable for these bats, being within a few kilometers range (Gallant & Broders, 2015), but bats exhibit high fidelity to swarming sites and often travel long distances (in rare cases, >500km) to reach swarming areas from summer roosts (Glover & Altringham, 2008; Norquay et al., 2013). Due to the high energetic cost of swarming itself, bats typically engage in swarming behaviour over a short period of time to maximize foraging opportunities throughout the night in preparation for hibernation (McGuire et al., 2009; Suba et al., 2010). Some species (e.g., *Pipistrellus pipistrellus*) have been noted to engage in swarming for as little as 15 minutes in a night (Sendor & Simon, 2003 as cited in Simon et al., 2004). With human and trap stimuli, the benefits of complete avoidance and leaving the swarming site may not offset the costs of disengagement from autumn swarming. Bats are successful at navigating around people and traps (Dobson et al., 2001; Larsen et al., 2007; pers. obs.), and when obstacles such as these are successfully detected by bats, bats will navigate around them during swarming as opposed to completely avoiding the swarming site. Similarly, for captive bats, perhaps investigation by free-flying bats need not occur closer to this stimulus. That is, altering flight path to fly closer to the captive may not be necessary and may just infer an additional cost without benefit.

Another consideration is social and demographic differences in behavioural responses. (Krivek et al., 2022; Loeb & Britzke, 2010; Thomas et al., 1979). Heterospecific response, for example, is an important demographic factor of interest; while our study represents primarily one species (*M. lucifugus*; Balzer et al. 2021), certain species may respond differently to stimuli depending on factors such as these species' ecological flexibility and tolerance to disturbance (Suraci et al., 2019, 2021; Voigt-Heucke et al., 2010). The demographic traits such as age and sex, and in turn the social status of the bats, are also important to recognize. Given the drastic declines in bat populations owing to White Nose Syndrome (WNS) disturbance, we had to be opportunistic with bats we captured and select experimental bats randomly. However, free-flying bat behaviour may stem more from social and demographic statuses of surrounding bats: for example, in a recent study on camera flash on the behaviour of free-flying bats, the behaviour of free-flying bats was more so influenced on social factors and which bats were present in the frame compared to the researcher-introduced stimulus, elucidating the influence of social and demographic factors, not only of free-flying bats to a stimulus but also to other free-flying individuals in the vicinity (Krivek et al., 2022). If bats of particular species and/or demographic traits are responding with more avoidant behaviour and flying higher than traps, for example, this may be reflected in capture success too and consequently impact the inferences made on certain populations with regards to species composition and demographic structure.

Ultimately, an animal's perception of risk is a spectrum where the costs and benefits of behavioural response are considered (Ha, 2010). Our predictions for free-flying bat response to our scenarios were motivated from a Pavlovian perspective (Domjan, 2005), wherein there is a stimulus/cue,

association with risk/reward, and predictable response. However, the same stimulus may evoke different behavioural responses depending on the extent of inter- and intraindividual risk perception (Kuo et al., 2023) and context (Allan et al., 2020). For example, human disturbance outside of bat maternity roosts in the reproductive (summer) period can change roosting behaviour (Ancillotto et al., 2019), such as evoking a roost switch or permanent emigration from the disturbed roost (López-Roig & Serra-Cobo, 2014). The associated fitness costs with remaining at the disturbed roost likely outweigh the benefits, prompting this avoidant behavioural response during this period. This is but one example that highlights that cost-benefit ratios, and consequently the persistence of a certain behaviour, vary depending on ecological and individual context (Ha, 2010).

While we considered specific behaviours, the goals of our study were to address bias in behavioural research. From our model on bat activity, scenario explained very little (<5%) of the activity observed. We did adopt a reductionist approach, assessing major components of capture surveys individually, but swarming activity may also depend more on environmental factors than introduced stimuli (Parsons et al., 2003). We also acknowledge that while our predictions for free-flying bat response were relative to our control scenario, we researchers were still present at the swarming site (albeit out of the field of view). This may have influenced the response to non-human scenarios. Lastly, our study occurred at the focal point of autumn swarming at this cave which was the cave entrance, but our inferences into bat activity and spatial distribution are limited to this focal swarming point and our current understanding of the autumn swarming period.

### **3.6 Conclusion**

We found that major components of capture surveys influence bat behaviour. Though the instances of bats observed were not influenced by major components of a standard capture technique, individual bats flew higher when both humans and traps were present in recordings. While capture surveys may not always bias inferences made on general bat activity, they can influence how bats navigate the study area and consequently the inferences made on specific species or bats of certain demographic traits. As capture surveys are often a necessary approach to obtain demographic and morphometric data, we suggest repeating this experiment more holistically, with combinations of scenarios more closely emulating true capture surveys to understand the extent of potential research biases. Ultimately, there are many reasons why certain methodological approaches continue to be implemented, and we simply remind ourselves that as researchers, it is our duty to reflect on the nature of our approaches and what biases may arise when studying a phenomenon of interest.

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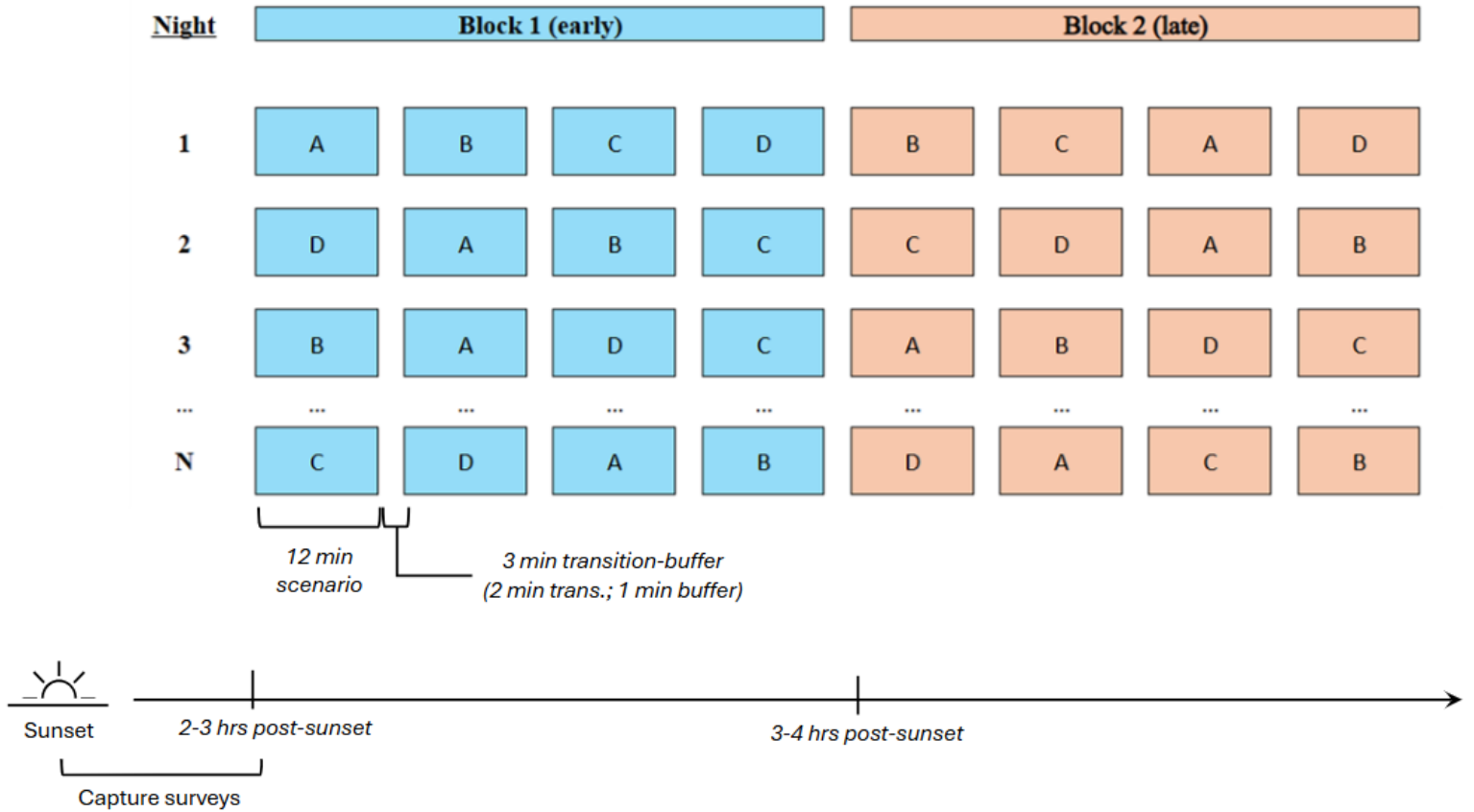
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### 3.8 Supplemental materials

**Figure S1.** Example of randomized block design with scenarios (A-D) each sampling night. Scenario order within blocks was pre-determined with a random number generator, where scenarios A-D were assigned to a number 1-4 respectively. Note that time arrow is not to scale.



## **CHAPTER 4**

### **Population trends and behaviours of bats in Maritime Canada: Synthesis**

The overarching goal of this thesis was to conduct population assessments on species affected by a significant driver of decline while also considering the biases that may arise when conducting these assessments. Specifically, I conducted comparative population assessments for disease-affected hibernating bats in Maritime Canada and quantified the behavioural response of free-flying bats to capture surveys, a common approach to assess bat abundance.

In Chapter 2, from long-term datasets involving summer, autumn swarming, and overwinter surveys of hibernating bats in New Brunswick and Nova Scotia, I observed species- and season-specific patterns on recovery 10+ years following White Nose Syndrome (WNS) disturbance. These findings align with those of many others that each of the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*M. septentrionalis*) and the tri-colored bat (*Perimyotis subflavus*) experienced WNS-associated declines (Cheng et al., 2021; Frick et al., 2015). However, by incorporating survey data from each seasonal period with which these bats engage, I observed differences in local versus regional trends. Summer capture surveys represent patterns of local populations, whereas the congregative nature of autumn swarming and hibernation allow for inferences on regional trends and may mask declines experienced by local populations. The magnitude of decline detected was greatest in the summer period, demonstrating that the local populations of hibernating bats studied pre-WNS have declined significantly, however the presence of bats at swarming and overwintering sites suggests that these bats are still found across the landscape, albeit at much lesser abundances.

Species-specificity also proved to be an important consideration when conducting these population assessments. Across seasons, *M. septentrionalis* experienced the greatest magnitude of decline in Maritime Canada, aligning with a recent population assessment of this species in this area (Balzer et al., 2021), and with findings from across the northeastern range of this species (Cheng et al., 2021; Frick et al., 2015). For *M. lucifugus* and *P. subflavus*, they did experience WNS-associated decline, though data indicate at least some signs of recovery. Namely, *P. subflavus* capture rates from swarming surveys were comparable between pre- and post-WNS periods. From swarming surveys, I observed significant decline in *M. lucifugus* populations, however overwinter counts at the largest hibernaculum surveyed show a gradual increase in the number of overwintering bats since 2015, and the most recent overwinter survey (winter of 2024-25) reveal the greatest number of overwintering bats since WNS population collapse. While we did not differentiate between *Myotis* species for overwinter surveys, swarming activity is reflective of hibernaculum occupancy (van Schaik et al., 2015), and combining these findings with those of others of disproportionate *M. septentrionalis* decline (Balzer et al., 2021; Cheng et al., 2021), it seems reasonable to presume that most of the overwintering bats at this hibernaculum are *M. lucifugus*. Additionally, I acknowledge that bats previously overwintering at smaller hibernacula may have abandoned these hibernacula to maintain social connectivity following WNS-associated mortality of conspecifics, but the increased proportion of juveniles detected from swarming surveys is a positive sign and suggests reproduction and juvenile recruitment.

Despite the severity of WNS alongside other drivers of extinction (Frick et al., 2020), the species I studied have persisted 10+ years following WNS introduction in Maritime Canada. While I acknowledge how detrimental WNS was for these resident hibernating bats, I more importantly

want to emphasize that these bats are still present and that monitoring them to better understand and facilitate recovery is crucial. Many have vouched for the efficacy of overwinter surveys to study WNS disturbance as WNS infection on overwintering bats is visible during this period, and these overwinter surveys allow for regional-level inferences on populations (CWHC, 2022; Janicki et al., 2015; Verant et al., 2018). However, I remind of the importance of summer and autumn swarming capture surveys to obtain information on local and regional population trends respectively where species and demographic traits can more reliably be identified (Flaquer et al., 2007; Kunz, 2009). Understanding trends at local scales facilitates the implementation of protection strategies for these local populations and ultimately contributes to more regional and global conservation efforts (Rodríguez-Caro et al., 2024).

The findings of Chapter 2 highlight the many considerations to be had when conducting population assessments. In Chapter 3, I considered the nature of the surveys themselves, specifically assessing the factors present during capture surveys and their potential bias on the bats we wished to study. From 10 nights of capture surveys and thermal video recording at the largest swarming site known in Nova Scotia, I found that major components of capture surveys did not influence the overall instances of free-flying bats (activity) observed, but these factors did result in significant differences in fine-scale distribution (behaviour) of free-flying bats. Specifically, free-flying bats displayed signs of more avoidant behaviour, flying further from human and trap stimuli compared to my control and captive bat stimulus. As *M. lucifugus* are the most common bat in my study system, increasingly so after WNS, they were my focal species upon which I made inferences. However, as I cannot confirm species nor demographic traits from thermal video, the elicited behaviours from my implemented scenarios may have species-, age- and/or sex-specific responses.

As such, if bats of certain social or demographic traits exhibit more avoidant responses and are less likely to be captured, our inferences on community composition and demographic structure can be biased.

With humans and traps, flying in the upper half of the video further away from these introduced stimuli may be reflective of more risk-avoidant behaviour. As we were present and conducting capture surveys earlier in the night, free-flying individuals may further associate humans and traps with risky cues. Trap avoidance has been well documented in bats (Berry et al., 2004; Marques et al., 2013), and many other taxa respond similarly to humans as they do to other predators, fleeing or altering movement patterns to reduce chances of encounter (Ciuti et al., 2012; Li et al., 2020; Smith et al., 2017). However, as I did not observe a change in free-flying bat activity, this behavioural shift may reflect the cost and benefit considerations of swarming behaviour. Autumn swarming is a pivotal period in these temperate bats' seasonal cycles. As such, the costs of completely avoiding the focal point of autumn swarming may thus not outweigh the benefits. Given bats' abilities to navigate efficiently around obstacles (Berry et al., 2004; Larsen et al., 2007), such as humans and traps in my case, the costs of finely altering flight paths may be far less than the costs of avoiding a social hub that serves various functions for these bats.

For free-flying bat behaviour in response to a captive bat stimulus, I found no detectable differences compared to my control. This finding was surprising, particularly as captive bats and acoustic lures have been documented to increase free-flying activity, with acoustic lures also being employed to increase efficacy of capture surveys (Hill et al., 2014; Hill & Greenaway, 2005;

Thomas et al., 1979). However, I cannot confirm whether our captive bat was vocalizing. Additionally, by again considering life history and the context of autumn swarming, since free-flying bats are congregating at the cave entrance anyway, I may not be able to disentangle typical autumn swarming behaviour from congregations at this site to investigate a captive bat.

As my second chapter was centered around assessing bias, it is important to acknowledge my own. First, I acknowledge that my inferences made depend on our current definition of autumn swarming, and that I cannot comment on changes in activity or behaviour that may have occurred beyond the scope of our camera's field of view (away from the hibernaculum entrance). Additionally, I adopted a reductionist approach but a holistic approach wherein all factors (humans, traps, captive bats) are present simultaneously may yield different findings with respect to free-flying bat activity and behaviour.

Reviewing the work of this thesis collectively, I demonstrate the importance of considering methodological design, geographic specificity, seasonal trends, and species ecology and life history when conducting population assessments. This work reiterates that documenting species trends and behaviours can be difficult, particularly with how much these things vary with ecological and intrinsic factors (Hughey et al., 2018; Shepard et al., 2013; Suraci et al., 2021) and how researchers may accidentally introduce bias (Burghardt et al., 2012; Tuytens et al., 2014). However, the accelerating biodiversity crisis makes population assessments increasingly critical to effectively monitor and develop conservation strategies for species. Population assessments, particularly those of more direct methods involving animal capture and handling, require

significant researcher involvement and may be stressful to focal taxa (de Moura et al., 2023; Moussy et al., 2022; Witmer, 2005). However, the costs of these population assessments can be outweighed by the benefits of gained knowledge that can be used to protect focal taxa (Danielsen et al., 2005; Kilpatrick et al., 2020).

From my research, I can reiterate and recommend some strategies to conduct necessary population assessments while obtaining more accurate data. To effectively study local populations, researchers should be detailed in tailoring surveys to species ecology as drivers of decline can result in species-specific responses (Reusch et al., 2019; Schweiger et al., 2012). Additionally, for population assessments via capture surveys, more precise estimates of abundance and diversity can often be obtained by moving traps daily to prevent taxa from learning of trap location and consequently avoiding traps (Marques et al., 2013). Researchers should also conduct research in a manner that minimizes risk of human or equipment disturbance on the focal taxa (Frid & Dill, 2002; Hughey et al., 2018). Lastly, much research focused on animal conservation has highlighted the importance of large-scale population assessments to provide a more global understanding of the taxa of interest (e.g., Hingee et al., 2022; Lindenmayer et al., 2022; Torres et al., 2016). However, understanding local patterns provides important details on populations that may facilitate the development and implementation of effective surveying techniques and conservation strategies (O'Regan et al., 2015; Ratajc et al., 2023; Rodríguez-Caro et al., 2024).

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