

Participatory science and development of innovative tools to improve conservation of threatened bats

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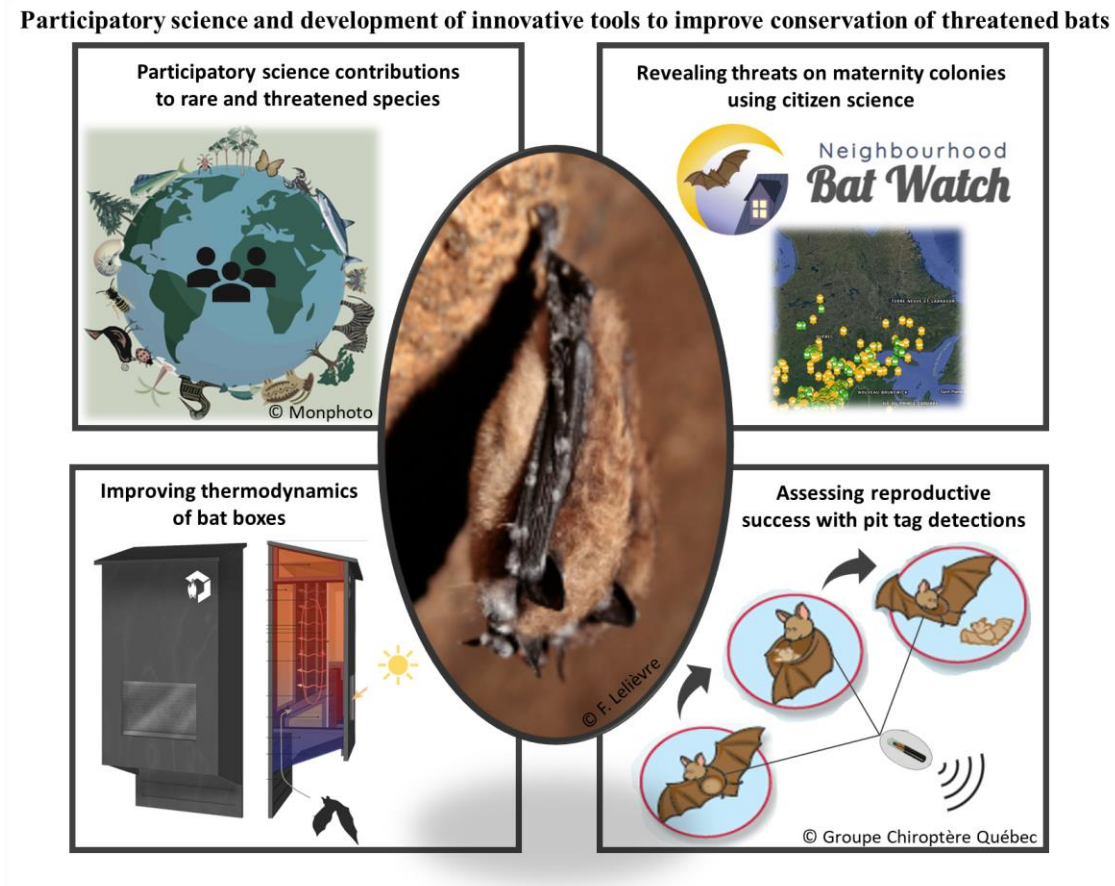
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Abstract



Over 10% of wildlife species are considered threatened by the IUCN, with threats including habitat destruction and degradation (e.g., through urbanization and agricultural activity), overexploitation, invasive species and disease, as well as climate change. Participatory science as well as new technologies are filling important data gaps necessary to ensure effective conservation of rare or threatened species. North American hibernating bats are of particular concern, as White-Nose Syndrome (WNS), a fungal disease, has killed millions of bats since its onset in North America in 2006. Moreover, knowledge about bats in Northeastern Canada is limited. In this thesis, I explore ways to contribute to the conservation of wildlife, more particularly the conservation of reproductive female bats. In chapter 1, I describe threats to wildlife, tools to improve their

conservation, as well as particularities and challenges working with bats. In chapter 2, I explore the wide spectrum of participatory science's contributions to the conservation of rare or threatened species, and factors influencing success of this type of project. Using an online search and project managers' surveys, I demonstrate that participatory science contributes substantially to conservation biology through peer-reviewed scientific publications, grey literature publications, and conservation measures. Contributions increase especially if projects are maintained over the long-term with rigorous data standards and multidisciplinary or transdisciplinary collaborations. Using the participatory science project the Neighbourhood Bat Watch, I reveal in chapter 3 the impact of the WNS and exclusions of bats from buildings on the number of bats at maternity colonies in Quebec. I show the usefulness of participatory science to provide data on *Myotis* species, which declined by 62% - 98% during the first three years after the onset of WNS. I also show that more than one third of the colonies have subsequently been excluded from buildings, with a higher risk of exclusions in the north and in houses. In chapter 4, I select a subsample of five maternity colonies to evaluate if PIT tags detection patterns can be used to infer reproductive status, parturition date and time away from the roost of female *Myotis*. I show that under appropriate conditions, an assessment of reproductive activity is possible for most female bats. Using one colony as a case study, I also demonstrate that early individual arrival date and warm spring mean temperature at night led to early parturition dates while longer nights, warmer temperatures, and heavy rainfall at night increased time away from the roost of gestating females. In chapter 5, I study bat box thermodynamics to create novel bat boxes that better fit reproductive female bat requirements in cold environments. Recording temperatures in bat boxes across a climate gradient at seven sites in Quebec, I show that our new model, based on passive solar architecture mounted on a building with an east orientation, increased the time in the optimal

temperature range (22–40 °C) of *Myotis* species compared to other tested set-ups. Based on bioenergetic models, bats save up to 8% of their daily energy using this set-up compared to the Classic model on a building facing east. Together, this thesis 1) highlights the importance of participatory science to wildlife research and conservation and offers indicators to inform the future development of participatory science activities, 2) provides trends for declining bat species and information on exclusions, thereby guide conservation actions, 3) provides a new method to estimate individual reproductive success, and ultimately to better understand bat ecology and population dynamics, and 4) shows the value of bat box designs integrating passive solar concepts to improve an existing conservation tool. My thesis provides the theoretical and practical foundations to improve the management of threatened female bats and their summer habitat. But its impact goes beyond the conservation of bats, as knowledge and technical innovations I provide can be applied to several other taxa and make a difference in modern conservation efforts in general.

Résumé

La faune fait face à de nombreuses menaces comprenant la dégradation et la destruction d'habitats par l'activité agricole et le développement urbain, la surexploitation, les invasions et les maladies, ainsi que les changements climatiques. La science participative et les nouvelles technologies ont la capacité de combler d'importantes lacunes dans les données nécessaires pour assurer une conservation efficace des espèces rares ou menacées. Parmi les espèces menacées, les chauves-souris cavernicoles d'Amérique du Nord sont particulièrement préoccupantes, car le syndrome du museau blanc (SMB), une maladie fongique, a tué des millions d'individus depuis son apparition en 2006. De plus, les connaissances sur ce taxon sont limitées dans le nord-est du Canada. Dans cette thèse, j'explore certains moyens contribuant à la conservation de la faune sauvage, plus particulièrement la conservation des maternités de chauves-souris. Dans le chapitre 1, je décris les menaces pesant sur la faune, les outils pour améliorer leur conservation, ainsi que les particularités et les défis liés au travail avec les chauves-souris. Dans le chapitre 2, j'explore l'éventail des contributions de la science participative à l'avancement des connaissances et à la conservation des espèces rares ou menacées, ainsi que les facteurs influençant le succès de ce type de projet. À l'aide de recherches en ligne et d'un questionnaire auprès des gestionnaires de projets, je démontre que la science participative contribue de manière substantielle à la conservation de la faune, à travers des publications scientifiques évaluées par des pairs, des publications dans la littérature grise et des mesures de conservation. Les contributions augmentent surtout lorsque les projets sont maintenus à long terme, avec des données qualité et des collaborations multidisciplinaires ou transdisciplinaires. À l'aide du projet de science participative *Chauves-souris aux abris*, je dévoile dans le chapitre 3 l'impact du SMB et des exclusions sur les colonies de maternités du Québec. Bien qu'il y ait une implication importante des professionnels dans le processus de décompte, je

montre l'utilité de la science participative pour fournir des données sur les espèces de *Myotis*, qui ont diminué de 77% à 98% au cours des trois premières années suivant l'apparition du SMB. Je montre également que plus d'un tiers des colonies sont éventuellement exclues des bâtiments dans lesquels elles ont élu domicile, avec des risques d'exclusions plus élevés au nord du Québec et dans les maisons. Dans le chapitre 4, je sélectionne un échantillon de cinq maternités afin d'évaluer si les patrons de détection de Transpondeurs Passifs Intégrés (Passive Integrated Transponders : PIT tags) peuvent être utilisés pour déterminer le statut reproducteur, la date de mise bas et le temps passé à l'extérieur de la maternité de *Myotis* femelles. Je montre qu'avec de bonnes conditions, une estimation du succès reproducteur est possible pour la plupart des femelles. En utilisant la colonie du Domaine Joly comme étude de cas, je démontre également que la date de mise bas estimée est influencée par la date d'arrivée individuelle et la température moyenne printanière, tandis que la durée de la nuit, la température moyenne et les précipitations totales durant la nuit affectent le temps passé à l'extérieur de la maternité des femelles en gestation. Dans le chapitre 5, j'améliore la thermodynamique des dortoirs à chauves-souris afin de mieux répondre aux besoins des femelles reproductrices vivant en milieu tempéré nordique. En enregistrant les températures dans des dortoirs à travers un gradient climatique sur sept sites au Québec, je montre que mon nouveau modèle basé sur l'architecture solaire passive, installé sur un bâtiment avec une orientation est, augmente le temps passé dans l'intervalle de température optimal des *Myotis* (22-40 °C) par rapport aux autres installations testées. Basé sur des modèles bioénergétiques, une chauve-souris économise jusqu'à 8 % de son énergie quotidienne grâce à ce modèle par rapport au modèle Classique, lorsque tous deux installés sur bâtiment orienté à l'est. Ensemble, cette thèse 1) met en évidence l'importance de la science participative pour la recherche et la conservation de la faune et propose des indicateurs pour informer le développement des futures activités de science

participative, 2) fournit des tendances sur le déclin des espèces de chauves-souris et des informations sur les exclusions, facilitant ainsi les actions de conservation, 3) donne une nouvelle méthode pour estimer le succès reproducteur individuel afin de mieux comprendre les populations tout en étant moins fastidieux pour les chercheurs et moins stressant pour les chauves-souris que les méthodes actuelles, et 4) montre la valeur théorique des dortoirs à chauves-souris intégrant des concepts solaires passifs, améliorant ainsi un outil de conservation existant. Ma thèse fournit des fondations théoriques et pratiques améliorant la conservation des chauves-souris femelles menacées ainsi que de leur habitat estival. La portée de mon travail va toutefois plus loin, puisque les connaissances et innovations techniques que je fournis peuvent être appliquées à d'autres espèces fauniques et faire une différence dans les efforts de conservation modernes à l'échelle globale.

Acknowledgements

As my Ph.D., this section will be in English and in French. Completing my Ph.D. was a long journey. It has sometimes been challenging and tiring, but mostly gratifying and full of memorable and positive experiences. When I first looked for a Ph.D. project on bats, I quickly realized there was no academic researcher who worked on bats in Quebec. But where there is a will, there is a way! I am really grateful to have found (after a lot of efforts and emails) such a wonderful partnership between my supervisor Kyle Elliott at McGill University and co-supervisor Anouk Simard at the Ministère des Forêts, de la Faune et des Parcs (MFFP).

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Contribution to Original Knowledge

This thesis provides a grounding as well as new ways to better understand and conserve threatened species, particularly bat species in Quebec. This thesis has made several contributions to original knowledge by: (1) assessing global spatiotemporal trends of participatory science projects on rare or threatened species, quantifying different types of scientific contributions, and determining their predictors of success; (2) examining variation in the distribution and abundance of bat populations at maternity colonies in Quebec in relation to white-Nose Syndrome (WNS) progression and maternity colony exclusions from buildings using the participatory science project the Neighbourhood Bat Watch; (3) developing a new approach to assess bat reproductive status and parturition date using pit tag detections; and (4) creating a new bat box design using thermodynamics to improve bat boxes in cold climates.

In chapter 1, I summarize current threats to wildlife and different approaches to monitor and conserve threatened species. I examine in more depth the ecology, energetic and particular threats of WNS-impacted bat species that suffered drastic declines in North America.

In chapter 2, I assess global spatiotemporal trends of participatory science projects on rare or threatened species, quantify different types of scientific contributions, and determine predictors of success. I show that participatory science contributes substantially to rare or threatened species monitoring and conservation in a wide range of ways, from theoretical frameworks in peer-reviewed publications to applied conservation measures. Results gained from this study mixing web searches and a manager survey would have been impossible with a traditional literature-based method. To our knowledge, I provide the first quantitative analysis of multiple types of scientific contributions of participatory science projects focusing on rare or threatened species worldwide (i.e. not just peer-reviewed papers, but also grey literature and conservation measures). I also

provide indicators to inform the future development of participatory science activities and increase scientific contributions. Participatory science should be recognized as a promising approach to help scientists address gaps required to ensure effective conservation of rare or threatened species. This chapter touches on global issues and has practical applications for ecological scientists as well as for policy makers and resource managers.

In chapter 3, I highlight the usefulness of participatory science projects to reveal trends in bat populations. The Neighbourhood Bat Watch program, for which I was the national coordinator during the last five years, has contributed to educating the general public about bats, facilitating the collaboration among provincial and national bat researchers and modifying the official provincial status of bat species. Using a unique dataset partially collected by citizen scientists over 20+ years, I examine variation in the distribution and abundance of bat populations and confirm the importance of WNS and maternity colony exclusions from buildings as threats to Quebec bat species that use buildings. This chapter provides trends for declining bat species in different regions of Quebec and provides information on where colony exclusions happened, thereby facilitating habitat restoration and public awareness efforts.

In chapter 4, I show that, under appropriate conditions, PIT tag recapture methods can provide individual reproductive parameters. This new method provides a way to estimate individual reproductive status and parturition date that is easier for researchers and less stressful for bats than any other current methods, as we do not need to physically recapture the animals. The Domaine Joly colony case study also demonstrates how elucidating the impact of environmental conditions on demographic parameters, such as reproductive success, can help biologists understand how climatic variability may jeopardize bat conservation efforts, particularly in the face of WNS that

is associated with mass mortalities in hibernating bat species of North America, such as the studied species.

In chapter 5, I use thermodynamics to improve bat boxes in temperate cold climates. Bat boxes are a popular measure employed to protect bats and educate citizens, yet they achieve only limited success in cool climates. To address this problem, we tested different orientations and mountings for both traditional and newly designed bat box models, based on passive solar architecture. I worked with a transdisciplinary team, including an engineer and an architect, to optimize bat boxes mounting in temperate cold climates and created an improved bat house design. Using bioenergetics models, I demonstrate that our new design better meets the little brown bat (federally listed as Endangered in Canada due to WNS) requirements than most commonly used bat box models. This is one of the first studies to use architectural energy saving concepts to improve artificial wildlife structures and link their thermodynamics to the animal bioenergetics to show its effectiveness. I think that artificial structure optimization using human architecture concepts shows a great potential to improve conservation tools for other taxa like birds or other hollow-dependent mammals.

Contribution of Authors

The thesis is manuscript-based with each chapter formatted for the journal in which it was published or will be submitted to. All chapters were conceived and written by me and are a result primarily of my research efforts. K. H. Elliott, as my supervisor, provided academic and scientific guidance, ideas, critiques and editorial assistance at all stages of the thesis. A. Simard, as my co-supervisor, also provided foundational ideas for each chapter, as well as, guidance, critiques, and comments on drafts of each chapter. C. K. R. Willis and Q. E. Fletcher, as my supervisory committee members, also provided guidance ideas, and critiques on each chapter.

Chapter 2 is submitted to Conservation Biology. The initial idea stemmed from conversations between A. Simard, C. K. R. Willis, Q. E. Fletcher, K. H. Elliott and myself, which I further developed and transformed into the current project. A. Fontaine conceived the survey idea with feedback from A. Simard, N. D. Brunet, and K. H. Elliott. A. Fontaine, A. Simard, and N. D. Brunet developed the survey. A. Fontaine conducted surveys with the help of A. Morales and J. Guo for the Spanish and Chinese project's search. A. Fontaine analysed the data and is the first author of the manuscript. All authors reviewed the manuscript.

Chapter 3 is written for submission to the Journal of Wildlife Management. A. Fontaine, A. Simard, and G. Larocque conceived the project. A. Fontaine, citizen scientists, and project-affiliated organizations collected the data. A. Fontaine analysed the data and is the first author of the manuscript. All authors reviewed the manuscript.

Chapter 4 is written for submission to the Journal of Mammalogy. A. Fontaine and A. Simard conceived the project. A. Fontaine conducted the main experiments with the help of V. Simard,

and H. G. Broders provided data from Newfoundland. A. Fontaine analysed the data and is the first author of the manuscript. All authors reviewed the manuscript.

Chapter 5 is published in Scientific Reports and as such, does not have the same distinct sections as the other chapters. A. Fontaine and A. Simard conceived the experiments. A. Fontaine, A. Simard, J. Dutel, and B. Dubois elaborated the new bat box designs. A. Fontaine conducted experiments, analysed the data and is the first author of the manuscript. All authors reviewed the manuscript.

Introduction

Threats to wildlife are numerous and include habitat destruction and degradation through urbanization and agricultural activity, overexploitation, invasive species and disease, and climate change (IPBES 2019). Emerging diseases of free-living animals also pose a substantial threat to the conservation of global biodiversity (Daszak et al. 2000). Often, disease outbreaks happen rapidly, so impacts of the disease can be difficult to quantify accurately. In contrast, other threats, such as land use changes or accumulation of several threats, can operate on the scale of one or several lifetimes or on a large scale. Most short-term or local monitoring schemes will therefore be ineffective at detecting a decline, especially for long-lived species (Yoccoz et al. 2001). Fortunately, the increasing use of web-based participatory science monitoring, coupled with expert knowledge and new tools, now slowly fills important data gaps necessary to ensure effective conservation of threatened species.

A recent study showed that 80% of bats assessed needed either conservation or research attention (Frick et al. 2019). Indeed, bats represent one fifth of all mammal species, yet because of their cryptic habits, relatively little is known about the abundance and population dynamics of many species (Burgin et al. 2018; Voigt and Kingston 2016). North American hibernating bats particularly need attention, as White-Nose Syndrome (WNS), a fungal disease, has killed millions of bats since its onset in 2006. Populations have declined by 90% in several regions (Cheng et al. 2021). Conservation and management for WNS-affected bats have long been focused on improving survival during hibernation, but since there is still no effective cure to WNS, the monitoring and management of active-season habitats, such as maternity roosts, may hold the key

for successful reproduction and recovery of the remnant post-WNS populations (Wilcox and Willis 2016; Fuller et al. 2020).

My thesis objective is to develop tools and advance knowledge to better conserve threatened species, more specifically North American bats. In chapter 2, I begin with an assessment of the scientific contributions of participatory science projects to the conservation of rare or threatened species, and factors influencing the success of this type of project. The goal is to quantify participatory science success in terms of the number of scientific contributions and provide indicators guiding the future development of participatory science activities. In chapter 3, I use data from a participatory science project, the Neighbourhood Bat Watch, to provide trends for declining bat species occurring in maternity colonies, as well as information on colony exclusions from buildings, thereby facilitating targeted conservation actions. In chapter 4, using a subsample of five maternity colonies, I evaluate if PIT tag detection patterns can be used to estimate reproductive status, parturition date and time away from the roost of female *Myotis*. The goal is to facilitate our understanding of reproductive outputs using a method that is simpler for both bats and researchers. Finally, in chapter 5, I improve bat box thermodynamics to better fit reproductive female bat requirements and use bioenergetic models to show the efficacy of our new bat box design that integrates passive solar architecture.

In chapter 1, I briefly review published literature describing current threats to wildlife and the different approaches to monitor and conserve threatened species with a focus on participatory science. I then explore in depth the ecology, energetic, and particular threats of North American bats, on which this thesis is focused.

Chapter 1 – Literature Review

1.1 Conservation of threatened species

Long-term and large-scale monitoring of wildlife populations is fundamental to answer questions relevant to conservation, such as species range shifts, phenology, changes in community composition and ecology of infectious disease (Dickinson et al. 2010). Knowledge of population size is often a vital prerequisite to identify declining trends and manage wildlife populations effectively. Animal numbers can be estimated by total counts, sampled counts, mark–recapture, or various indirect methods, but ultimately the methodology depends on the facility to see, trap, or detect an animal (Sinclair et al. 2006). Age structure, mortality and reproductive rates are also crucial to population dynamics, determining whether the population increases, remains constant, or decreases.

When a population declines, conservation actions must frequently be taken to reverse the decline and avoid extinction. To implement efficient conservation actions, one must first find the factors driving the decline (Maxwell et al. 2016). Sometimes identifying the causes of the decline is difficult, for instance, when there is a cumulative effect of several threats, such as with the monarch butterfly, facing different threats on the wintering grounds from the summer breeding grounds (Thogmartin et al. 2017). In other cases, the cause is obvious, such as for an emerging disease, but removing or alleviate the disease prior to extinction or population crashes may be difficult or even impossible. For example, the devil facial tumour disease still has no efficient cure

and has caused mass die-offs in Tasmanian devils over the past 25 years (McCallum 2008). In such cases, managers must find other ways to limit the decline and help the remnant populations.

Many species are threatened by more than one factor, and many factors themselves overlap. Among the most important is habitat destruction and degradation (IPBES 2019). Indeed, urban and agricultural areas are rapidly expanding, causing extensive habitat modifications that have significant consequences for the environment and wildlife, and increase human-wildlife conflicts (Barth 2012). Climate change also poses strong pressures upon wildlife and can affect impacts of other threats. For example, climate change can influence access to food, timing of migration, hibernation, and reproduction of several species of birds and bats (Carey 2009; Sherwin and al 2013).

Emerging diseases of free-living animals, whether originating from domestic animals, other anthropogenic causes, or natural events, pose a substantial threat to the conservation of wildlife (Daszak et al. 2000). Increased human-wildlife interactions can increase the probability that humans transfer diseases among wildlife populations. Amphibian chytridiomycosis (Fisher et al. 2009), avian malaria (LaPointe et al. 2012), and WNS (Cheng et al. 2021) are all examples of diseases that dramatically impacted their respective host populations. As public awareness about the conservation of wildlife has recently been facilitated by new technologies and social media (Wu et al. 2018), an array of monitoring schemes is now available to better understand threats to wildlife and their impacts on populations.

1.2 Participatory science to monitor wildlife

To conserve threatened species, efficient monitoring of their populations is often required. Wildlife monitoring schemes can take many forms depending on the scale and species sampled. Among them, participatory science has become a popular and valuable tool to obtain additional data and for monitoring trends in wildlife across larger scales (Whitelaw et al. 2003; Devictor et al. 2010). Participatory science, or citizen science, is defined as the collection and analysis of data relating to the natural world by members of the general public, typically as part of a collaborative project with professional scientists (OED 2020).

Pocock et al. (2017) list three drivers for the growth of ecological and environmental participatory science: the rise of technologies, a change in the societal and cultural acceptability of different types of projects, and advances in statistical approaches. Participatory science projects generate large datasets, often with wide monitoring coverage at low cost, that allow scientists and members of the public alike to answer ecological questions otherwise impossible to address. However, obtaining reliable scientific results from participatory science data may require new analytical tools to handle big datasets and issues related to data fragmentation or inaccuracy, monitoring biases, lack of experimental design, or insufficient quality control (Conrad and Hilchey 2011).

Several studies highlight the educational and social values of participatory science (Bell et al. 2009; Bonney et al. 2009; Dickinson et al. 2012; Pocock et al. 2017). In addition, increasing evidence shows that participatory science can also produce quality data beyond its educational potential (Kosmala et al. 2016; McKinley et al. 2017) and act as a productive scientific tool (Dickinson et al. 2010; Conrad and Hilchey 2011; Pocock et al. 2017). As traditional sampling

approaches have limited value for rare and threatened species (Green and Young 1993; Rushton et al. 2004), participatory science approaches have been found to be particularly valuable for such species. Indeed, because data are usually sparse and collection requires more effort than for common species, participatory science can facilitate data collection, the monitoring of trends, and the understanding of drivers of decline for rare or threatened species.

Because of their cryptic habits, relatively little is known about the abundance and population dynamics for many bat species, which make them good candidates for participatory science projects. Participatory scientists might be especially valuable for documenting threats and assessing conservation of North American hibernating bats, as several species can be found in urban and semi-urban areas and populations suffered great losses from the fungus disease named White-Nose Syndrome (WNS).

1.3 Diversity, life cycle and energetic of North American hibernating bats

Bats are an ecologically and taxonomically diverse group representing approximately a fifth of all mammals. North American bats belong to four different families: Mormoopidae, Phyllostomidae, Vespertilionidae, and Molossidae. The most diverse family of North American bats, in terms of species, is the Vespertilionidae, which includes all Canadian species (Harvey et al. 2011). Most species of North American bats are insectivorous, have only one young per year in early summer. Several species migrate, but most of them hibernate during the winter (Barbour and Davis 1969) and have a similar life cycle.

In the fall, hibernating bats can be seen flying in large numbers (Fig. 1.1). This event, called swarming, generally happens near the entrances of hibernacula, and is usually where mating

occurs. Between fall and early spring (October or November to March or April), bats hibernate in caves, abandoned mines, or crevasses (Fenton 1969; Fig. 1.1). During hibernation, bats decrease their heart rate and body temperature. Bats can survive in the absence of food during the winter because of these physiological adaptations and fat reserves. Bats will come out of prolonged torpor bouts about once a month likely to feed, drink, urinate, copulate, or switch roost (Boyles and al. 2006). Arousing from torpor requires a large amount of energy since they must warm their body temperature from just above freezing to 36°C in a very short amount of time. A single arousal can consume fat reserves that represent the energy required for 30–60 days of hibernation (Thomas et al. 1990).

Although insemination occurs during the fall, sperm is kept viable in the female's uterus during the whole winter. After bats come out of hibernation in April, females ovulate, and fertilization occurs (Harvey et al. 2011). At this same time, bats are on the hunt for food, having exhausted almost all of their fat reserves. Climatic conditions in the spring are therefore crucial, as they dictate the emergence of insects, which bats need as an immediate source of food. This is even more important for pregnant females who need more energy than males and non-reproductive females to give birth to young (Grinevitch et al. 1995; Dzal and Brigham 2013; Linton and Macdonald 2018).

Torpor, a state of decreased physiological activity including low body temperature and metabolic rate, is one strategy used by insectivorous bats to cope with the costs of maintaining a high body temperature (Ransome 1989; O'Shea et al. 2010). Bats frequently use daily torpor to deal with the wide range of temperature occurring daily in temperate zones during the spring and the summer. For instance, in Quebec, Canada, while the average summer high temperature ranges

from 25 to 30 °C, night temperatures at higher latitude are sometimes under 0 °C. Although entering torpor during spring and summer allow bats to save energy on cool days when insects are not available (Speakman et al. 2003), it may also delay female reproduction by slowing fetal development and reducing milk production (Racey 1973; Racey and Swift 1981; Wilde et al. 1999). By delaying development, torpor use can then have negative consequences on the probability of survival throughout hibernation for both mother and offspring (Beer and Richards 1956; Pagels 1975; Ransome 1989; O'Shea et al. 2010).

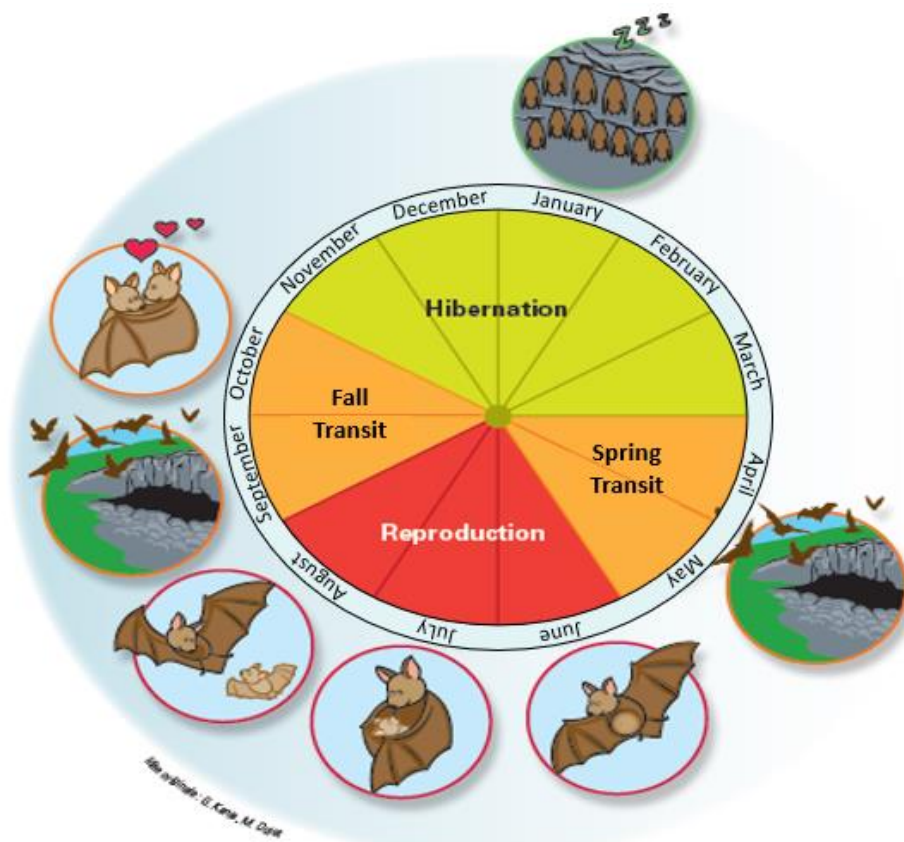
From late spring to late summer, females of most temperate bat species aggregate in roosting groups called maternity colonies, ranging from a few, to several hundred individuals (Fig. 1.1). Within these groups, offspring are gestated and nursed until weaned (Kunz et al. 2003). To reduce torpor use and optimize their fitness, reproductive females from several species, such as the little brown bats (*Myotis lucifugus*), inhabit warm roosts close to feeding sites (home range within 20–30 ha; Henry 2001). This strategy reduces energy expenditure, increases time spent in normothermia and facilitates short and shallow torpor bouts (Barclay 1982; Dzal and Brigham 2013).

The thermoneutral zone of little brown bats is 32–37 °C (Studier et al. 1976), meaning that an individual can maintain internal temperatures with minimal heat production within this range. For bats, it is also meaningful to determine at which temperature, although outside of that ideal range, females can manage to maintain adequate temperatures without entering torpor or suffering from detrimental effects (e.g., slowing gestation by using torpor when too cold, or dehydration or death when too hot). Although not functionally equivalent to the thermoneutral zone, a temperature range of 22–40 °C is likely suitable for breeding females while resting to remain homeothermic

without altering their behavior (i.e., moving to find a cooler location), therefore minimizing energy expenditure and maximizing reproductive success (Zahn 1999; Henry 2001; Ruczyński 2006; Flaquer et al 2014; Wilcox and Willis 2016).

Bats have long life expectancy and reproduce slowly (Barclay et al. 2003). Most Canadian species give birth after a gestation of about 60 days (Harvey et al. 2011). Females mostly give birth in June or July to one or two young depending on the species. Nursing lasts 4–5 weeks. After the nursing period, the young are weaned and learn to fly. Young stay with the adults until the end of the summer, learning where to find food and locate the best roosts. Females usually return to the same roosts every year (Lewis 1995).

Since most bat species are strictly insectivores, the role of bats in Canada's ecosystems is particularly important because they are the main predator of nocturnal insects. As such, the ecological services provided by bats reduce harvest damages by insect pests (Boyles et al. 2011). Yet these ecological and economical services are becoming scarcer, as more than half of North American insectivorous bat species are declining due to anthropogenic pressures, exacerbated more recently by exposure to WNS (Mickleburgh et al. 2002; Boyles et al. 2011).



Translated by Amélie Fontaine from Groupe Chiroptères du Québec 2016

Figure 1.1 Life cycle of Quebec hibernating bats.

1.4 White-nose syndrome and other threats to North American bats

In 2006, *Pseudogymnoascus destructans* (Pd; Ascomycota) was introduced from Europe to North America, leading to the appearance of WNS. This fungus, which thrives in cold and humid environments, grows on hibernating bats, which initiates a cascade of physiologic disturbances that has complex impacts on its host. Moreover, depleted fat reserves and wings lesions or necrosis caused by the fungus on survivors can have lasting consequences for survival and reproductive success during the active season (Reichard and Kunz 2009).

WNS is transmitted through contact among individuals and has spread rapidly across the continent (Froschauer and Coleman 2012). This disease induces high mortality in cave-dwelling bats during hibernation, with a decline of more than 90% for several severely impacted species (Cheng et al. 2021). The species most affected are members of the genus *Myotis*, including the little brown bat and Northern long-eared bat (*Myotis septentrionalis*). Big brown bats (*Eptesicus fuscus*) share hibernacula with *Myotis* spp. and have also been diagnosed with WNS (Blehert et al. 2009), but exhibit evidence of resistance with only mild WNS symptoms (Frank et al. 2014; Moore et al. 2018).

Although WNS is currently the greatest threat to cave-hibernating bats in North America, they are also subject to other stressors resulting from anthropogenic activities, including wind turbines, pesticides, and disturbances in hibernacula. Habitat modification, caused by urban development, decreases the abundance of natural roosts such as cavities in old and large snags traditionally used by females to raise their young during the summer (Fabianek et al. 2015). Nonetheless, some species adapt to urban areas and use buildings as maternity roosts, which offer large and warm permanent structures (Lewis 1995). In big brown bats, fidelity to buildings is higher than to tree cavities, likely because buildings offer a warmer and more stable microclimate (Brigham 1991), leading to greater long-term reproductive success for building-roosting bats (Lausen and Barclay 2006). While natural roosts become scarcer, and modern materials make houses wildlife proof, roost loss through building renovation or bat control operations may be an additional threat to those cavity-dwelling bats using buildings as maternity roosts.

Since bats are usually cryptic species, those using buildings are particularly suitable to test new tools and for participatory science schemes. However, to be valuable tools to the conservation

of threatened wildlife such as bats, participatory science and new technologies must provide concrete contributions. Few studies have assessed the impacts of participatory science on ecological research, and those studies have been largely limited in scope to peer-reviewed publications (Conrad & Hilchey, 2011; Dickinson et al. 2012; Chandler et al. 2017). A diversity of contributions is critical for the conservation of rare or threatened species. Thus, in the next chapter, I assess participatory science project's contributions to the conservation of rare or threatened animals, and factors influencing their success in a larger spectrum, including peer-reviewed publications, grey literature publications, as well as conservation measures.

Chapter 2 – The scientific contributions of participatory science applied to rare or threatened animals

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Abstract

Participatory science is filling important data gaps necessary to ensure effective conservation of rare or threatened animals, as well as empowering non-academic actors to engage in knowledge creation and evidence-based policy. Explore and quantify the large spectrum of participatory science's contributions to the conservation of rare or threatened animals, and factors predicting the success of those projects in terms of the number of scientific contributions, is valuable for conservationists, project managers and participants. To address those objectives, we found 332 projects online, and surveyed 119 project managers to assess global spatiotemporal trends, quantify different types of scientific contributions and determine predictors of success. The number of projects increased rapidly since 2010. Almost half of the surveyed projects produced at least one peer-reviewed scientific publication and 64% produced at least one grey literature publication or conservation measure. Longevity, data quality and collaboration type best explained quantities of all types of scientific contributions. We conclude that participatory science contributes substantially to knowledge advancement and conservation biology, especially if programs are maintained over the long-term with rigorous data standards and multidisciplinary or transdisciplinary collaborations.

Introduction

Long-term and large-scale monitoring of wildlife populations is fundamental to answer questions relevant to conservation, such as species range shifts, phenology, changes in community composition and ecology of infectious disease (Krebs et al. 1997; Macdonald and Newman 2002; Sinclair et al. 2006; Nielsen et al. 2009; Dickinson et al. 2010; Magurran et al. 2010). Such

monitoring has been deemed as crucial for understanding drivers of decline for rare or threatened species and for incorporating population trends into policy frameworks for legislative protection (Robinson et al. 2018). However, monitoring is difficult for those species because data are usually sparse and require more effort than for common species. Traditional sampling approaches have limited value for rare and threatened species because a very low proportion of randomly chosen sampling sites, even in the appropriate habitat, are likely to be inhabited by those species (Green & Young 1993; Rushton et al. 2004). Alternative sampling plans exist for rare or elusive species, but methodology for abundance estimation continues to be challenging (Thompson 2013; Specht et al. 2017).

Participatory science or citizen science, here defined as the collection and analysis of data relating to the natural world by members of the general public, typically as part of a collaborative project with professional scientists (OED 2020), can contribute to a diversity of outcomes. Participatory science has been found to be particularly valuable to collect data or monitoring trends in rare or threatened species. Participatory science project can focus on a particular area where the rare or threatened species is located, mostly through systematic monitoring and elaborate approaches, or occurred across a large scale, mostly through mass participation and simple approaches (Pocock et al. 2017). Examples include monitoring of monarch butterfly (*Danaus plexippus*) migration (monarchjointventure.org), the arrival of white-nose syndrome in bats in Canada (batwatch.ca), or tracking movements of humpback whales (*Megaptera novaeangliae*) in the Caribbean Sea (caribbtails.org).

Several studies highlight the educational value of participatory science (Bell et al. 2009; Bonney et al. 2009; Dickinson 2012; Follet and Strezov 2015; Pocock et al. 2018; Feldman et al. 2021). Indeed, participatory science can be valuable for democratizing science, building social capital, incorporating the general public in planning and management of local ecosystems, and providing opportunities for participants to gain scientific knowledge, reconnect with nature and develop positive attitudes toward science (Miller 2005; Pollock & Whitelaw 2005; Schwartz 2006; Bonney et al. 2009). Despite past scepticism mainly related to data reliability (Cohn 2008; Dickinson et al. 2010), participatory science is also rising in popularity worldwide to address a variety of ecological and environmental questions (Conrad & Hilchey 2011; Pocock et al. 2017), providing increasing evidence that participatory science can also produce quality data beyond its educational potential (Kosmala et al. 2016; McKinley et al. 2017).

Participatory science projects have the capacity to generate large datasets, often with wide monitoring coverage at low cost, that allow scientists and members of the public alike to answer ecological questions otherwise impossible to address (Conrad & Hilchey 2011; Tulloch et al. 2013). However, obtaining reliable scientific results from participatory science data may require new analytical tools to handle big datasets and issues related to data fragmentation or inaccuracy, monitoring biases, lack of experimental design, or insufficient quality control (Conrad & Hilchey 2011).

Few studies have assessed the impacts of participatory science on ecological research, and those studies have been largely limited in scope to peer-reviewed publications (Conrad & Hilchey, 2011; Dickinson et al. 2012; Chandler et al. 2017). Thus, other types of scientific contributions,

such as grey literature publications (government reports, conference proceedings, conference abstracts, book chapters, theses, and magazine articles) and conservation measures, are largely neglected in the current literature. Yet, these contributions are still critical for the conservation of rare or threatened species. Indeed, when actions are urgently needed to manage a population, the process of peer-reviewed publication may be too long, and raw data or grey literature publications may be more readily accessible and used to take actions, and applied in policy making and programs (Sullivan et al. 2006; Castellanos-Galindo et al. 2011; Guisan et al. 2013). Therefore, peer-reviewed publications, grey literature publications, and conservation measures are all important scientific contributions for the monitoring and conservation of rare and threatened species.

To date, there is no global quantification of participatory science contributions to scientific knowledge and its impact on conservation that includes not only peer-reviewed publication, but also grey literature publications and conservation measures. While there are many examples of datasets collected by participatory science projects that played a crucial role in answering basic and applied ecological questions (Dickinson et al. 2012; Barlow et al. 2015; Gardner et al. 2019), it remains unclear what differentiates successful projects over unsuccessful projects in terms of number of scientific contributions (i.e., peer-reviewed publications, grey literature publications, and conservation measures).

The goal of this study is to assess the scientific contributions of participatory science applied to rare and threatened animals. While opportunistic multi-species monitoring schemes (e.g. eBird, iNaturalist, Christmas Bird Counts, Bioblitzes) are known to make diverse scientific

contributions such as expanding scientific knowledge and scientific literacy (Bonney et al. 2009), we were interested in the growing multitude of participatory science projects that focus on data gaps for rare or threatened animals. We specifically addressed 3 questions: (1) What are the spatial and temporal trends of participatory science projects that focus on rare or threatened animals? (2) What are the scientific contributions those projects produce, as measured by the number of peer-reviewed publications, grey literature publications, and direct contributions to conservation and management measures? (3) What variables predict the success of those projects in terms of the number of scientific contributions? We expected the cumulative number of projects to increase through time and anticipated participatory science projects to contribute more to the grey literature and conservation measures than to peer-reviewed publications. We predicted that a range of factors predict scientific contribution success, such as the project longevity or its data quality index.

Methods

Search for participatory science projects

To explore the spatial and temporal trends of participatory science applied to rare or threatened animals and assess the scientific contributions of such projects, we first created a global database of participatory science projects found online, similar to the ones reported by Theobald et al. (2015) and Pocock et al. (2017). We broadly searched the internet using pre-determined terms such as “citizen science” or “particip*” and “rare” or “threatened”. We selected terms based on studies with a similar method and our knowledge of relevant key words. Specific key words such as “bat” or “chiropter*” were also included in the English search (Table S2.1). Using the Google search engine, we selected the options “pages in English language only” and “personalised dates from

2019 and before”. To expand our search, as advised for global review in conservation in Nuñez and Amano, 2021, we applied the same method to search Spanish and French language pages. While acknowledging that the success of many projects may rely on communication in local languages and dialects, we believe that choosing the most populous languages would be representative at the global scale. We used the Baidu search engine to locate Chinese sites (Table S2.1 for full search terms in English, Spanish, French, and Chinese). We followed the first 100 links produced by the search, which included (but were not restricted to) major participatory science directories, such as scistarter.com, zooniverse.org, and CitSci.org. We used a snowball sampling method, meaning that if a website mentioned a potential participatory science project with its link, then this new website link was followed.

We included in our database, the projects that match the four following criteria. (1) The project managers requested public assistance to monitor animals or otherwise further the scientific process (e.g., sorting images). (2) The focal animals were locally or globally considered as rare, threatened or endangered, as usually mentioned on the website and confirmed via an external source such as the International Union for Conservation of Nature (IUCN) red list, national or local lists (if the program had many focal species, more than half of the species under study needed to be rare or threatened for inclusion). (3) The project’s aim included the monitoring and/or the conservation of those animals (e.g., projects that were exclusively about education and communication were excluded). Finally, (4) the project ran for two years or more. Overall, we screened more than 5600 links in four different languages and found a total of 332 projects fitting those criteria, for which we identified its location, taxa, goal, and type of data collection.

Assessment of the scientific contributions

For each project included in our database, we assessed the following scientific contributions: (1) number of publications in peer-review journals, (2) number of publications in the grey literature, and (3) number of direct contributions to conservation management measures. We assessed those three scientific contributions by surveying participatory science project managers or coordinators and received 119 completed English surveys for a response rate of 51% (out of the 235 English language projects; see Survey S2.1 for the full project survey questions).

We provided a definition for each scientific contribution in the survey to remove any ambiguity of these terms. Publications in a peer-review journals were defined as such, as it is already explicit. Publications in the grey literature included government reports, conference proceedings, conference abstracts, book chapters, theses, and magazine articles. Contributions to conservation management measures was defined as any regulation that minimized direct and indirect negative impacts on valued sites and/or valued species, with the goal of sustaining existence of specific species (Sale 2002). Direct contributions to conservation management measures included official policies or publications, consisting of conservation initiatives, management decisions, or policy actions, such as the assessment of the local or global conservation status of a species and/or land-use restrictions.

To facilitate the survey, we classified scientific contributions into five categories: none, 1, 2–5, 6–10, or >10 scientific contributions. To corroborate and supplement our results, we also visited the websites and searched for additional information on all projects in the candidate list.

This study was conducted under a certificate of ethical acceptability of research involving humans (#2003038) and adhered to guidelines from the McGill University research ethics board.

Assessment of predictors of success

For each surveyed project, we assessed the following predictors: (a) project longevity (time since the project foundation; 1945–2019), (b) location (North America, Central and South America, Africa, Europe, Russia, Asia, Oceania, Arctic/Antarctica, worldwide), (c) scale of data collection (local, regional, national, international), (d) focal taxa (mammal, bird, herps, fish, invertebrate, mixed of more than one taxon), (e) collaboration type (intra-, multi-, inter-, trans-disciplinary), (f) organization type (citizen-driven, non-profit, academic, governmental, industrial, mixed of 2, mix of 3 or more), (g) methodological complexity (for data quality only, assessed as in Pocock et al. 2017) and (h) data quality (see Table S2.2 for more details about predictors).

Collaboration type was defined as follows: (1) intradisciplinary: working within a single discipline (i.e. biology), (2) multidisciplinary: people from different disciplines working together, each drawing on their disciplinary knowledge in an additive manner (i.e. studying bats from the morphology and disease-carrying point of view), (3) interdisciplinary: integration of knowledge and methods from different disciplines using a synthesis of approaches with stronger level of cooperation, and (4) transdisciplinary: creating a unity of intellectual frameworks beyond the disciplinary perspectives to form a new holistic approach.

Data quality was assessed by attributing a score based on the criteria found in Theobald et al. 2015 and Kosmala et al. 2016. These criteria were found to increase data quality by boosting

data accuracy and accounting for bias. We selected seven criteria that were the most important and common to the two studies and easy to understand by our survey's respondents while accurately assessed. Those criteria were the following: protocol freely available, support and training, data entry, metadata, verifiability, validation and data standardization (Table 2.1). For each criterion, we gave a score of 0–1.5 (or not applicable), for a maximum score of 10.5. We then normalized this score to one to create a data quality index ranging from 0 to 1 for each project. We used survey answers and website content to collate data and only included projects with all required information for analyses of predictors of success.

Table 2.1. Data quality criteria and its scoring system used to create the data quality index included in our assessment of predictors of scientific contributions success.

<i>Factors</i>	<i>Scoring</i>
Written protocol freely available	Yes = 1.5, On request = 1, No = 0
Support and Training	In person/personal = 1.5, Hard copy or electronic support = 1, None = 0
Data entry	Systematic = 1.5, Semi-systematic = 1, Non-systematic = 0
Metadata	Environmental conditions = 0.5, Characteristic of volunteers = 0.5, Equipment settings (if) = 0.5, None = 0 (cumulative)
Verifiability	Expert = 1.5, Photo or audio = 1, Optional = 0.5, None = 0
Validation	Yes = 1.5, Partially = 1, None = 0
Data standardization (if data analysis done)	All = 1.5, Some = 1, None = 0, Not applicable

Statistical analysis

We assessed whether trends in the number of projects per year varied significantly by location using a general linear model with a degree 1 polynomial function and a quasi-Poisson distribution, followed by a Tukey test (Table S2.3). We tested the influence of predictors on each scientific contribution success with ordinal logistic regression models (*polr* from the *MASS* package; Venables and Ripley 2002). We then used a global model including the most plausible predictors of success (Table S2.4) and used the “*dredge*” function from the *MuMIn* package (Barton 2019) to generate a model selection table from the selected subset of models combining terms of the global model. We evaluated the candidate models using Akaike’s information criterion corrected for small sample size (AICc) and selected the simplest model with $\Delta\text{AICc} < 2.00$ as the best model. We interpreted predictors as having a significant statistical effect if confidence intervals included 0. We also used linear models (*lm*) to test the influence of predictors on data quality using the model selection process mentioned above (Figure S.1 and Tables S11–14 for results). To reduce the skew in the data, we used a \log_{10} transformation on the longevity and a square root transformation on the data quality index. We used packages listed above to carry all analyses with R 3.5.1.

Results

The cumulative number of projects discovered via our systematic search (90% were still active) increased exponentially for most locations during the last 2 decades (Fig. 2.1). Projects started earlier and grew faster in North America than other locations, with a global acceleration starting in 2010 (Fig. 2.2). We also found computer-based image classification projects starting in 2010.

This type of project constitutes 10% of the projects started in 2010 and after. Projects were focused primarily on mammals, followed by herps (reptiles and amphibians), birds, invertebrates, fishes, and mixed (Fig. 2.2a). Projects were distributed across all continents, with more than half occurring in North America (Fig. 2.2b). From 235 with an English website, we received 119 surveys from project managers, who mostly had >5 years of experience managing the project (Fig. 2.2c) and had a Master’s degree or higher (Fig. 2.2d).

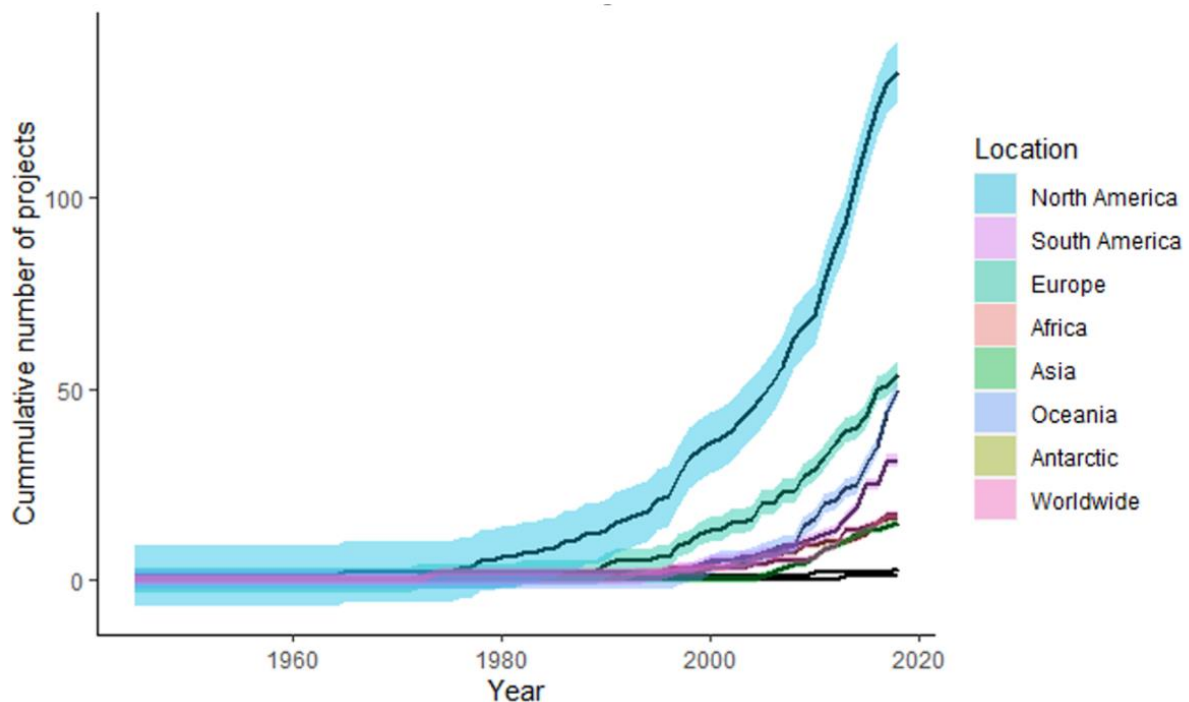


Figure 2.1. Cumulative number of participatory science projects on rare or threatened species over the period 1940–2020 (n = 332). Note that “worldwide” refers to projects that are not primarily restricted to one continent.

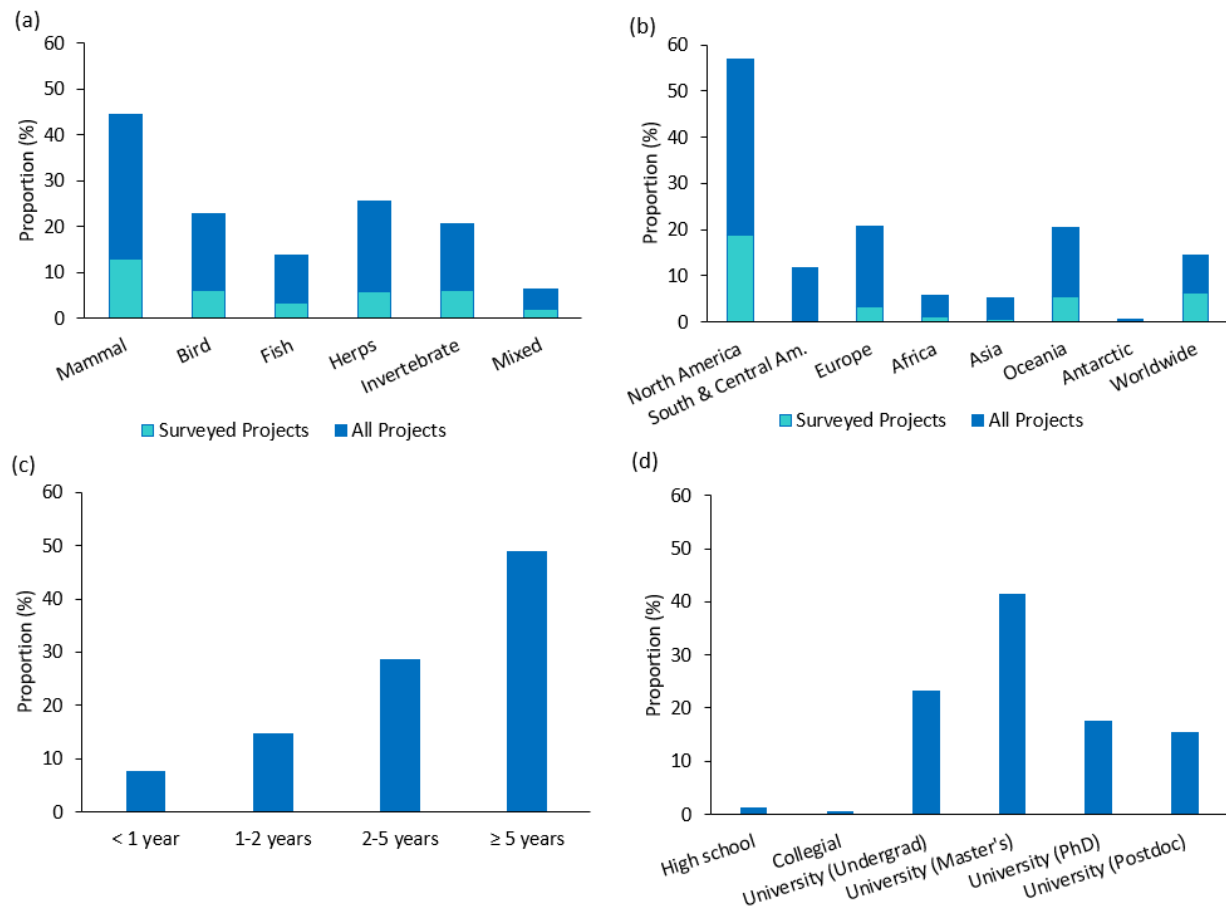


Figure 2.2. Proportion of a) projects found online (N = 332) and surveyed (N= 119) by taxa, b) projects found online (N = 332) and surveyed (N= 119) by location c) surveyed projects by managers year of experience managing the program (N = 119), and d) surveyed projects by managers level of education (N = 119).

Scientific contributions and predictors of success

Surveyed projects mostly generated knowledge on trends and distributions, but also on habitat selection, population dynamics, behavior, effect of threats or conservation measures on the species, and more, generally aiming for knowledge advancement, conservation, and public education. Forty-five percent (45%) of the surveyed projects produced at least one peer-reviewed scientific publication, 64% produced at least one publication in the grey literature, and 64% produced at

least one at least one conservation measure (Fig. 2.3). Several projects provided data to other organizations that then wrote management and mitigation plans or improved policies. Data for certain species was used to evaluate threatened or endangered status at a regional, national, or international level. Data was also used to identify and establish protected or at-risk areas, such as protected breeding grounds and road mortality hotspots. Other projects contributed directly with conservation measures such as habitat restoration or protection, control of invasive species, captive breeding programs, and awareness campaigns.

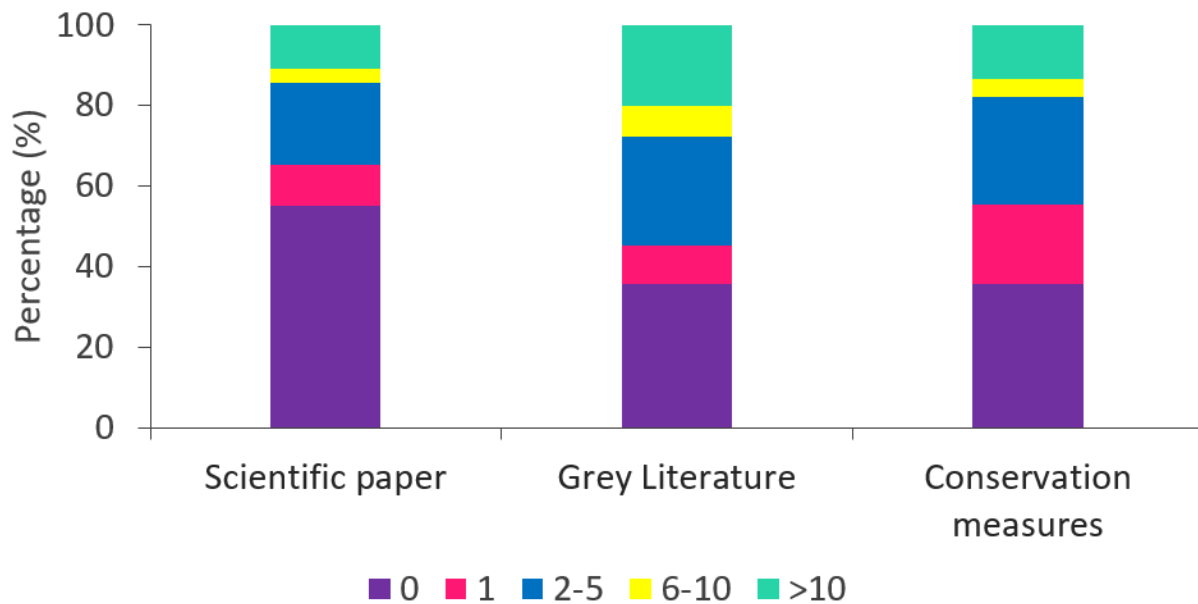


Figure 2.3. Percentage of scientific contributions of participatory science projects applied to rare or threatened species surveyed ($n = 119$) by number of contribution intervals for each type of contribution: peer-reviewed scientific publications, grey literature, and conservation measures.

The model best explaining the number of peer-reviewed scientific papers had a weight of 0.71, a R^2 of 0.43 and included 2 parameters: longevity and data quality index (Table 2.2; See

Tables S5–6 for full list of model selection and predictor outputs). The number of scientific papers produced increased with project longevity (Coef. Value = 2.39, 95% CI 1.32–3.54) and data quality index (Coef. Value = -3.91, 95% CI -6.67 – -1.37; Fig. 2.4). The model best explaining the number of grey literature publications had a weight of 0.58, a R^2 of 0.35, and included 3 parameters: longevity, data quality index, and collaboration type (Table 2.2; see Tables S7–8 for full list of model selection and predictor outputs). The number of grey literature publications increased with project longevity (Coef. Value = 2.22, 95% CI 1.14–3.37), data quality index (Coef. Value = -2.78, 95% CI -5.32 – -0.37), and projects with trans- and inter-disciplinary collaborations (Fig. 2.5). Four models explaining the number of conservation measures had $\Delta AICc < 2$. Of those models, the simplest had a weight of 0.09, a R^2 of 0.66 and included 2 parameters: longevity and the collaboration type (Table 2.2; See Tables S9–10 for full list of model selection and predictor outputs). These 4 models all included a combination of the same 4 factors: longevity, data quality index, collaboration type and taxa, with a cumulative weight of 0.55. The number of conservation measures increased with project longevity (Coef. Value = 2.39, 95% CI 1.30–3.54) and transdisciplinarity (Fig. 2.6).

Table 2.2. Top 5 of model selection of predictors of success on a) scientific paper publications, b) grey literature, c) conservation measures ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). $\Delta AICc$ is the difference between AICc for the current model and the minimum of AICc among all the models. ω_i = Akaike weights.

<i>Models</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>w_i</i>
<i>a) Scientific paper publications</i>			
log(longevity) + $\sqrt{(1\text{-quality index})}$	287.5	0.00	0.689
log(longevity) + $\sqrt{(1\text{-quality index})}$ + location	290.8	3.26	0.135
log(longevity) + $\sqrt{(1\text{-quality index})}$ + collaboration	291.5	3.98	0.094
log(longevity) + $\sqrt{(1\text{-quality index})}$ + organisation	294.4	6.91	0.022
log(longevity)	294.7	7.19	0.019
<i>b) Grey literature publications</i>			
log(longevity) + $\sqrt{(1\text{-quality index})}$ + collaboration	331.7	0.00	0.584
log(longevity) + $\sqrt{(1\text{-quality index})}$	333.9	2.15	0.199
log(longevity) + collaboration	334.5	2.76	0.147
log(longevity)	337.1	5.41	0.039
log(longevity) + $\sqrt{(1\text{-quality index})}$ + collaboration + taxa	340.0	8.28	0.009
<i>c) Conservation measures</i>			
log(longevity) + $\sqrt{(1\text{-quality index})}$ + collab + taxa	318.2	0.00	0.183
log(longevity) + collaboration + taxa	318.8	0.52	0.141
log(longevity) + $\sqrt{(1\text{-quality index})}$ + taxa	319.0	0.78	0.124
log(longevity) + collaboration	319.8	1.52	0.085
log(longevity) + $\sqrt{(1\text{-quality index})}$ + collaboration	319.9	1.69	0.079

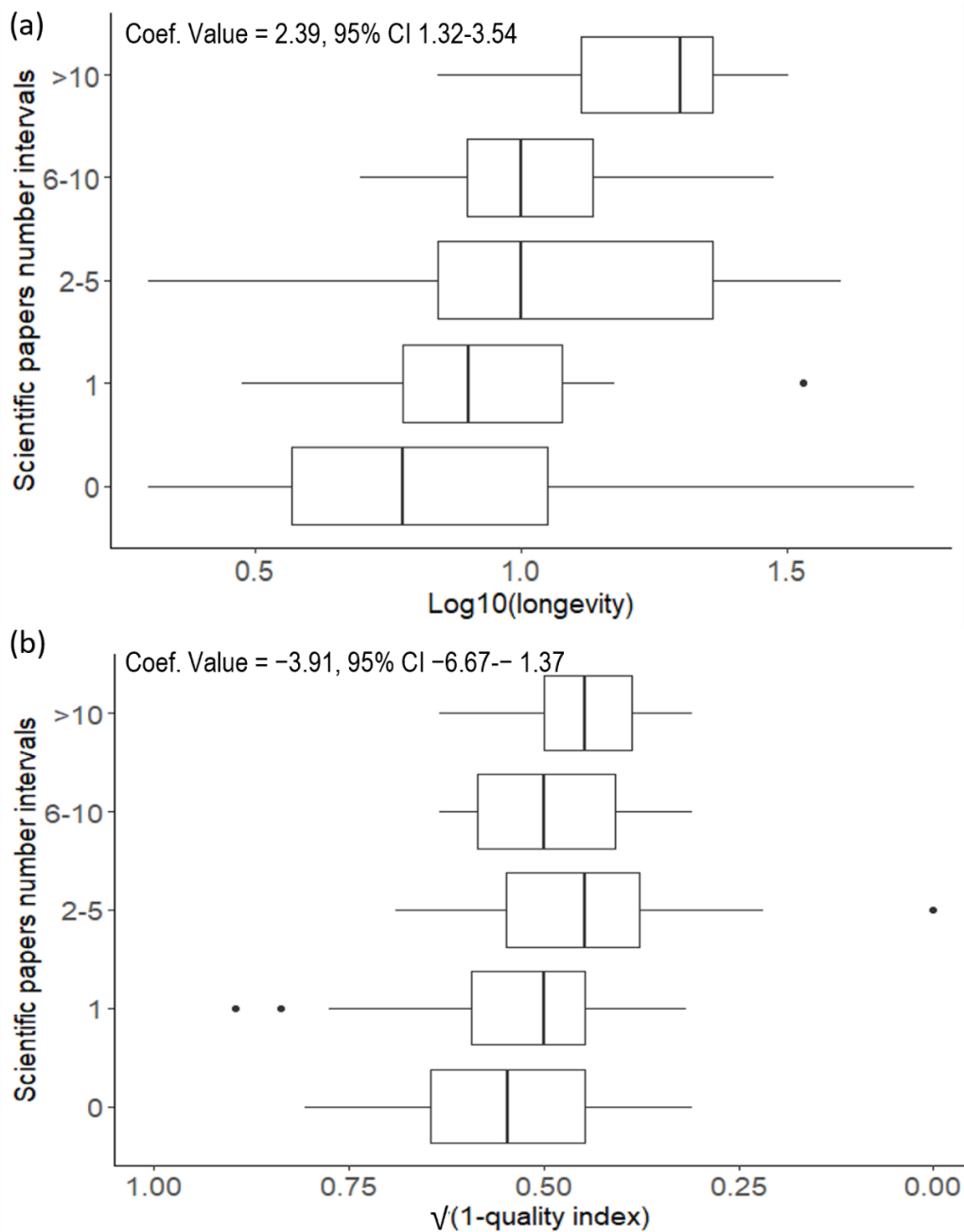


Figure 2.4. Number of scientific papers relative to a) project longevity and b) project data quality index (n = 119). Data transformed to achieve normality. Coefficient and p-value derived from the ordinal logistic regression best model. Low scores on the $\sqrt{(1-\text{data quality index})}$ represent high data quality axis and high scores represent low data quality, as assessed by our data quality index.

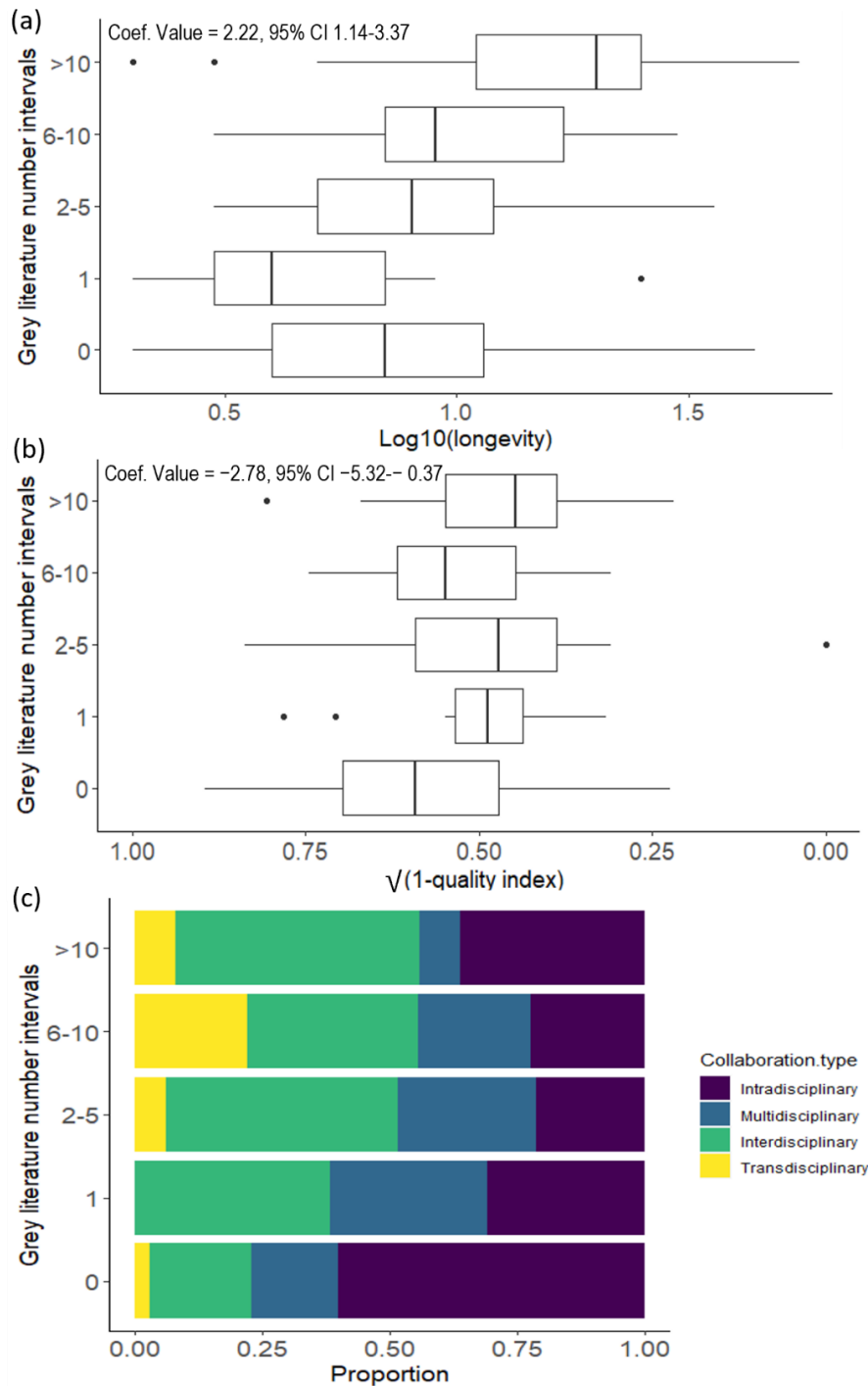


Figure 2.5. Number of grey literature publications relative to a) project longevity, b) project data quality index, and c) project collaboration type ($n = 119$). Data transformed to achieve normality. Coefficient and p-value derived from the ordinal logistic regression best model. Low scores on the $\sqrt{(1-\text{data quality index})}$ axis represent high data quality and high scores represent low data quality, as assessed by our data quality index.

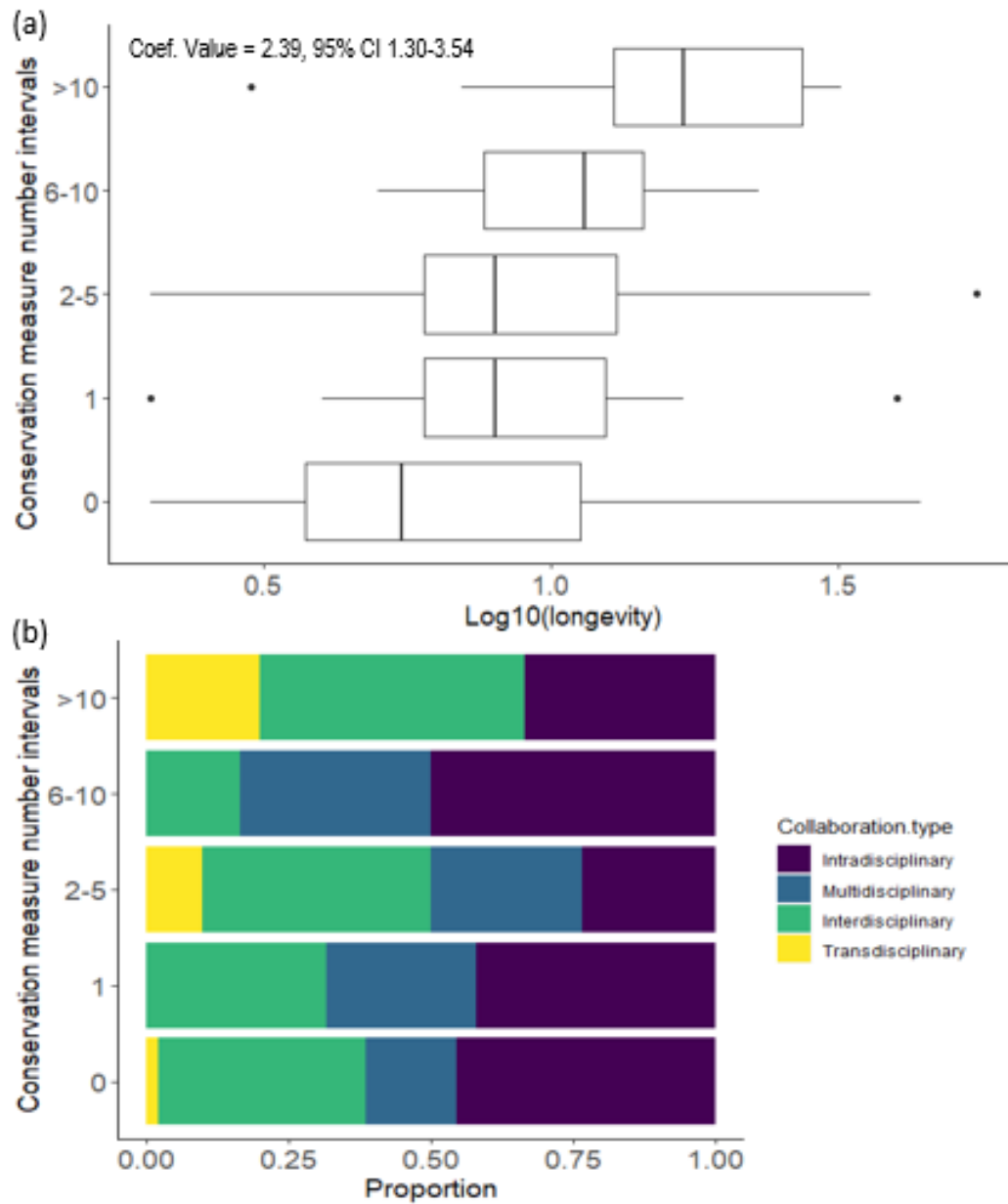


Figure 2.6. Number of conservation measures relative to a) project longevity and b) project collaboration type (n = 119). Data transformed to achieve normality. Coefficient and p-value derived from the ordinal logistic regression best model.

Discussion

Most projects studied mammals, herps, birds, and invertebrates, presumably over-representing “charismatic” and/or easy to access and identify animals. Interestingly, most of the project managers had at least a Master’s degree and five years’ experience, implying considerable technical knowledge. Thus, although a major contribution of participatory science has been the education, involvement and empowerment of non-scientists (Cohn 2008; Wiggins 2012), management is typically led by someone with considerable expertise. This might also explain why many projects did indeed make substantial scientific contributions, as outlined below.

Spatial and temporal trends

The number of participatory science projects studying rare and threatened species increased substantially after 2010, independent of the continent, mirroring a rise in the number of general participatory science projects (Follett & Strezev 2015; Theobald et al. 2015; Kullenberg & Kasperowski 2016). Pocock et al. (2017) list 3 drivers for the growth of ecological and environmental participatory science that could also applied to our set of projects: the rise of technologies, a change in the societal and cultural acceptability of different types of projects, and advances in statistical approaches. For threatened species in particular, the widespread awareness of the global loss of species, exacerbated by increasing human impacts (Manfredo 2008; Joseph et al. 2021), may also have contributed to the rise in the number of participatory science projects.

Of the 332 projects identified by our systematic search, more than half were located in North America, followed by Europe and Oceania. Similarly, Cunha et al. (2017) found that 58% of publications resulting from environmental participatory science projects originated from North

America. Several reasons could explain this result. First, the greater land area of the North America compared to Oceania (second-largest number of projects and 3 times smaller than North America) and Europe (third-largest number of projects and 2 times smaller than North America). Second, the fact that our study focused on rare or threatened wildlife, resulting in the exclusion of several participatory science projects focusing on a whole taxon, biodiversity, or the environment in general. Despite Europe having a long history of participatory science, we found most projects within the continent were in a multispecies setting and so did not fit our selection criteria. We did find, however, that participatory science projects focusing on rare or threatened species occur primarily in rich, developed countries that have the funding available for project managers, advanced websites and associated technology, as well as many volunteers with the time, education and money available to participate. Similarly, participation in large participatory science programs (e.g. eBird, iNaturalist) is much higher per capita in OECD countries, although quickly expanding elsewhere (Christie et al. 2021). The citation rate of conservation research is also higher in wealthy countries (Meijaard et al 2015). As there is a negative spatial relationship between the number of peer-reviewed studies showing evidence in conservation and the number of threatened and data-deficient species (Christie et al. 2021), there is a great potential to expand participatory science outside of North America, Oceania and Europe, where most rare and threatened animals are located (Pocock et al. 2018).

Quantification of scientific contributions

Participatory science has been recognized to contribute substantially to many domains of science, including wildlife conservation, natural resources and environmental science (McKinley et al.

2017). As an example, data collected on bird populations by the Cornell Lab of Ornithology participatory science projects have examined changes in bird distribution over time and space, influences of environmental changes on breeding success, spread of emerging infectious diseases through wild animal populations, and consequences of acid rain (Wells et al. 1998; Rosenberg et al. 1999; Hames et al. 2002; Altizer et al. 2004). However, few studies have quantified participatory science global contributions as a whole (i.e. not just peer-reviewed publications) or are often limited to a specific project or location (e.g. Arthur et al. 2014; Gardner et al. 2019; Poisson et al. 2020). In a survey across several groups of participatory science projects, Newman et al. (2017) found the contribution to management plans to be between 14% for CitSci.org projects and 50% for The Stewardship Network New England projects. Contributory and place-based model of participatory science supported by Earthwatch leads to over 60% of projects annually producing scientific publications as well as input to management plans and/or policies (Chandler et al. 2017).

To our knowledge, we provide the first quantification of the scientific contribution of participatory science focusing on rare or threatened species on multiple continents. As we predicted, projects contributed more to the grey literature and conservation measures than to peer-reviewed papers. Indeed, the monitoring of threatened species often relies on governmental or not-for-profit organizations whose outputs typically include reports or proposed conservation measures. Legal protection for threatened or rare species often relies on the “best available science”, and the contribution of raw data, grey literature, and direct mitigation actions provided by participatory science projects to species conservation should not be underestimated (Sullivan et al. 2006; Hemmi & Graham 2014). Still, almost half of the projects included in our survey produced at least one peer-reviewed paper, although this number included papers only partially

based on participatory science, only partially focusing on rare or threatened species, and sometime focusing on other topics than conservation and monitoring (e.g., a study where citizen scientists provide validated biodiversity data on frogs of Australia, another monitoring humpback whale *Megaptera novaeangliae* behaviour). A similar proportion was found by Theobald et al. (2015) for biodiversity participatory science projects. They found that 12% of environmental participatory science projects were recorded as leading to a peer-reviewed publication based on traditional literature-based methods compared to 45%–60% with a manager survey-based method. Theobald and colleagues proposed that the inconsistent responses to survey questions suggest that project manager respondents may be confused about what constitutes peer-reviewed literature, likely including grey literature and technical reports in self-reported publications. Our results do not support this explanation, as we specifically ask for three different types of contributions, disentangling grey and peer-review publications. Moreover, most of our respondents provided titles and/or links to back up the number of contributions they provided. We therefore propose that traditional literature-based methods underestimate publication rates, most likely due to the lack of direct or prominent advertisement of the project origins in peer-reviewed publications.

Predictors of scientific contribution success

Participatory science is experiencing an explosion in growth, but data use in scientific publications and conservation decision-making has not reach its full potential yet (Newman et al. 2017). Various participatory science project analysis highlights the importance of several factors to successfully contribute to science and conservation. Those include a well thought design and implementation that will match the needs of science and public involvement with the right type of

project and method, a maximized collaboration among all levels involved in the project, from volunteers to decision makers, and integrating cross-disciplinary approaches (Newman et al. 2017, Robinson et al. 2018; Maas et al 2021).

Longevity was the most important factor influencing the number of peer-reviewed, grey literature publications, and conservation measures. This result aligns with those found by Tulloch et al. (2013) and Theobald et al. (2015), who analyzed peer-reviewed publications of birds and biodiversity participatory science projects, respectively. Chandler et al (2017) also found a similar result with longevity of Earthwatch-supported projects highly correlated with the publication rate as well as management plans. Contributions found in this study increased over time, peaking for management plans and policies at 6–8 years, which was earlier than contributions to publications which peaked at 7–9 years of support. Project implementation is complex with a strong element of trial and error, involving human, budgetary and technical constraints. Furthermore, data accumulation takes time, especially for rare or threatened species. As such, long studies may be more likely to lead to scientific contributions because they improve the ability to measure change over space and time (Tulloch et al. 2013; Bird et al. 2014). Scientists and policy makers may also be more aware of well-established participatory science projects than new initiatives, although threatened species' data are often confidential, and therefore, less easily shared.

Successful project longevity may be related to several factors. Given the longevity of support needed to produce project outcomes, a key challenge for participatory science project is maintenance of long-term financial support for programs, particularly when funding cycles often operate on shorter periods (Brightsmith et al., 2008). As such, co-funding is seen as a key element

in a project sustainability (Conrad and Hilchey 2011, Cunha et al. 2017) as well as in its success in terms of publications and policy contributions (Cunha et al. 2017; Chandler et al. 2017). The combination of scientists and concerned public gained by multiple organization type leading the project (e.g. “university + NGOs”, “government + NGOs”, and “university + government + NGOs”) may also provide two major elements which are often lacking individually: recruitment with long-term engagement and scientific rigour (Cunha et al. 2017). The methodology must reflect the goal of the project as well as the motivations and capabilities of the target volunteer profile to avoid bias in the dataset and loss of motivation due to frustration (Couvet et al. 2008; Chandler et al. 2017; McKinley et al. 2017).

Data quality was another important predictor of success in terms of peer-reviewed and grey literature publications, and to a lesser extent, conservation measures. Theobald et al. (2015) were surprised that probability of publication was largely unaffected by the data quality assurance measures they assessed. This difference with our finding may mean that an index combining the most important metrics may better evaluate the data quality than individual metrics, either because the combined effect is greater than the sum of their separate effects or that the variance in our sample was bigger than the earlier study. Data quality is particularly relevant when studying rare and threatened species, as misidentification could have broader legal implications (Ely et al. 2017), than, for instance, biodiversity. When relying on rigorous methods, datasets produced by citizen scientists can reliably produce high quality outputs, on par with those produced by professionals (Kosmala et al. 2016; McKinley et al. 2017). A comment from a project manager reflects this consideration of scientific rigour: “One of our guiding principles is Do - Discover – Influence: Do good survey work, Discover through data analysis, and Influence policy, conservation

management, research priorities, and development assessment processes”. Here, we provide a tool to quantify and compare data quality, which will help managers to better design their project to optimize their scientific productivity (see Appendices S11-15 for data quality’s predictor of success).

Collaboration type influenced the number of grey literature publications and conservation measures, with transdisciplinary projects producing on average more contributions than other approaches. The idea that more holistic projects yield more conservation outcomes is also supported by a study looking at the explicit inclusion of multiple dimensions of “place” in participatory science project (Newman et al. 2017). It is reasonable to say that transdisciplinarity may not be as important to achieve peer-reviewed publications as the first objective of this type of contribution is often knowledge advancement. In contrast, a transdisciplinary approach may be essential to enact conservation measures for 3 reasons. First, a transdisciplinary approach can better tackle “real world” problems, such as endangered species conservation, which involve non-academic stakeholders. Second, powerful new knowledge can be created by merging multiple knowledge streams and different value systems. Third, this approach also increases creativity, as stakeholders’ different state of mind could inspire others, thus suggesting their best solution to a problem (Putra 2017). Interdisciplinary participatory science projects, which also include a strong level of cooperation, are common in the biological domain (Pettibone et al. 2017) and were well represented in our surveyed projects. Transdisciplinary projects were scarcer, meaning that there is an unexploited potential to improve the scientific value of participatory science projects on rare or threatened species. However, this approach takes more time and effort, emphasizing the importance of proper planning to ensure projects last long and reach their full potential. As many

funding agencies focus on short-term deliverables, we advise consideration of the increased benefits of long-term commitment for participatory science projects focusing on rare and threatened species.

We address two potential sources of bias in our study: the process of discovering and selecting projects for analysis and the process for obtaining information about each of the selected projects. We expect under-sampling of: (a) projects in communities speaking other languages than English, Spanish, French, and Chinese for our spatial and temporal trend analysis, as well as projects in communities speaking other languages than English for our scientific contribution analysis, (b) projects without websites (i.e. very local or small-scale), (c) projects fitting the definition of participatory science although not defining themselves as such or founded before the late 2000s, when the terms “citizen science” and “participatory science” became popular, (d) projects not focusing on rare or threatened species but producing scientific contributions on rare or endangered species (e.g. eBird, iNaturalist), and (e) completed projects (Pocock et al. 2015). Moreover, since citizen science is a term more popular in North America, the use of other key words like “participatory science” or “volunteer” extended our search geographically. We have no way of estimating how these other kinds of projects might differ from our project’s subsample. Nonetheless, our search was standardized, repeatable and, we believe an informative examination of this type of project and a valuable starting point for future participatory science projects, allowing for a systematic analysis of participatory science focusing on rare or threatened animals. In addition, bats were overrepresented due to our specific search for this taxon in English (see note in Table S2.1). However, since the results for bats only did not differ from other taxa (preliminary results), we are confident that including bats separately did not bias the overall results of our study.

Conclusion

We showed that participatory science contributes substantially to rare or threatened animals monitoring and conservation in a wide range of ways, from theoretical frameworks in peer-reviewed publication to applied conservation measures. Results gained from this study combining web searches and manager surveys would have been impossible with a traditional literature-based method. To our knowledge, we provide the first quantitative analysis of a large spectrum of scientific contributions of participatory science projects focusing on rare or threatened animals on multiple continents. We also provide indicators to inform the future development of participatory science activities and increase scientific contributions. While this study focuses on the quantification of scientific contributions and identifying factors increasing contribution numbers, it is important to mention that not all contributions are equal in terms of quality and impact for science and conservation. Quantity is not always guarantor of success and future research should take into consideration other indices of success such as the contribution quality (Chandler et al. 2017):-

Participatory science is now recognized as a promising approach to help scientists to address gaps required to ensure effective conservation of rare or threatened species. We call for increased conceptual and methodological development when starting participatory science projects to ensure project persistence, high quality data, and transdisciplinary values in research design and outputs by:

- Carefully matching the needs for science and public involvement with the right type of participatory science project and the right method of public participation when starting the project (McKinley et al. 2017).
- Educate and train project managers since this can influence the time delivery of projects (Brown et al. 2007).
- Finding multiple sources of funding as it is a common and safe way to cope with the risk of cuts in resources (Conrad & Hilchey 2011; Cunha et al. 2017).
- Ensure good data collection and management by integrating factors included in our data quality index or those included in Kosmala et al. 2016.
- Include a diversity of stakeholders in all stages of the project to ensure best practices that link scientific research to conservation interventions.

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Linking Statement

In the previous chapter, I explored participatory science's contributions to the conservation of rare or threatened species to show that it can contribute substantially to conservation biology, through peer-reviewed scientific publications, grey literature publications, and conservation measures. I also explored factors influencing success of this type of project to inform the future development of participatory science activities. In the next chapter, I take the Neighbourhood Bat Watch as an example to illustrate the usefulness of participatory science projects to provide trends for declining bat species in relation to WNS onset and information on where colony exclusions happened. Although the involvement of citizens in counts seems more challenging, citizen inputs were essential to locate maternity colonies. This chapter also provides population trends for two threatened *Myotis* species (highly impacted by WNS) and the big brown bat (only lightly impacted by WNS), therefore facilitating conservation efforts specific to each region and species.

Chapter 3 – The Quebec Neighbourhood Bat Watch participatory science project reveals rapid decline of bats after white-nose syndrome and a high rate of bat colony exclusion

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Abstract

Long-term and large-scale monitoring of wildlife populations is fundamental to answer questions relevant to conservation. Participatory science has become a popular tool to collect additional data and for monitoring trends across larger scales, especially for rare, threatened, or cryptic species, such as bats, for which data can be harder to collect. As the white-nose syndrome, a fungal disease, spreads through North American bat populations, a participatory science project was initiated in 2012, asking the public (“citizen scientists”) to help monitor bat maternity colonies in Quebec, Canada. The project uses public participants to locate roosts, with species identification achieved by professional wildlife biologists, and emergence counts made by both professionals and participants, demonstrating how participatory and professional science can interact synergistically. We examined variation in the distribution and abundance of bat populations in Quebec using the Neighbourhood Bat Watch database on location and emergence counts ($n = 381$) at maternity colonies from 1997-2020. We focused on trends relative to white-nose syndrome (WNS) progression and maternity colony exclusions from buildings. Colony size of *Myotis* species declined during the first three years after WNS onset (declined by 77 % - 98 %), while mixed and big brown bat colonies changed only slightly after WNS onset. Out of the 287 colonies with known fate recorded from 1997-2020, 102 (36 %) have subsequently been excluded from buildings. The probability of exclusion was higher in the north than the south, and in houses compared to barns, garages, and sheds, but did not vary significantly with habitat type. The Neighbourhood Bat Watch participatory science project provided trends for declining bat species and information on where colony exclusions happened, thereby facilitating habitat restoration efforts for these declining *Myotis* species.

Introduction

Long-term and large-scale monitoring of wildlife populations is fundamental to answer questions relevant to conservation, such as species range shifts, phenology, changes in community composition and ecology of infectious disease (Dickinson et al. 2010). The collection of data relating to the natural world by members of the general public (“citizen scientists”; OED 2020) can contribute to a diversity of outcomes and has become a popular and valuable tool to obtain additional data and for monitoring trends in wildlife across larger scales (Whitelaw et al. 2003; Devictor et al. 2010). Participatory science, also called citizen science, is largely used for assessing changes in species distribution and population size in a number of taxa including birds, butterflies, reptiles and mammals (Dickinson et al. 2010; Penone et al. 2013; Wright et al. 2013; Horns et al. 2018; Gardner et al. 2019).

Participatory science can be especially useful to survey rare, imperiled, or cryptic species, as opportunistic detections from citizen scientists mitigate the large amount of effort required to collect enough data to identify conservation needs and track population trends (Strien et al. 2013; Crawford et al. 2020). Global biodiversity inventories as well as projects specifically focusing on rare or threatened species can contribute to a diversity of scientific outcomes (Fontaine et al. under review?). Examples include the revision to the wintering distribution and habitat use of the Kirtland’s warbler (*Setophaga kirtlandii*) using eBird (Cooper et al. 2019) and revealing contrasting migration and survival rates of horseshoe crabs (*Limulus polyphemus*) using the New York Horseshoe Crab Monitoring program (Bopp and al. 2019).

Bats are a taxon well suited for participatory science. Indeed, bats represent one-fifth of all mammal species, yet because of their cryptic habits, relatively little is known about the abundance

and population dynamics for many species. A recent study showed that 80% of bats assessed needed either conservation or research attention (Frick et al. 2019). Estimating numbers of bats, distribution changes and landscape occupancy, at both small (i.e. specific colonies) and large scales, is critical for assessing short-term and long-term conservation of bats and documenting the impact of stressors (Kunz et al. 2009; Jones 2011).

In 2006, *Pseudogymnoascus destructans* (Pd; Ascomycota) was introduced in North America, leading to the appearance of white-nose syndrome (WNS). This fungal infection spread rapidly across the continent (Froschauer and Coleman, 2012), inducing high mortality in cave-dwelling bats during hibernation, with a decline of more than 90% for several severely impacted species (Cheng et al. 2021). The species most affected are *Myotis* species (spp.), including the little brown bat (*Myotis lucifugus*) and northern long-eared bat (*Myotis septentrionalis*). Big brown bats (*Eptesicus fuscus*) share hibernacula with *Myotis* spp. and have also been diagnosed with WNS (Blehert et al. 2009), but exhibit evidence of resistance with only mild WNS symptoms (Frank et al. 2014; Moore et al. 2018). When some species decline, others might benefit from a release in competition for foraging resources and roosting sites (Perkins 1996; Carter et al. 2004; Thalken et al. 2018). Thus, species like big brown bats may benefit from the decline in *Myotis* spp. due to WNS (Morningstar et al. 2019; Faure-Lacroix et al. 2020, Johnson et al. 2021).

Although WNS is currently the greatest threat to cave-hibernating bats in North America, they are also subject to other stressors resulting from anthropogenic activities. Habitat modification, caused by urban development, decreases the abundance of natural roosts such as cavities in old and large snags traditionally used by females to raise their young during the summer (Fabianek et al. 2015). Nonetheless, some species adapt to urban areas and use buildings as

maternity roosts, which offer large and warm permanent structures. In big brown bats, fidelity to buildings is higher than to tree cavities, likely because buildings offer a warmer and more stable microclimate (Lewis 1995; Brigham 1991), leading to greater long-term reproductive success for building-roosting bats (Lausen and Barclay 2006). While natural roosts become scarcer, and modern materials make houses wildlife proof, roost loss through building renovation or bat control operations may be an additional threat to those cavity-dwelling bats using buildings as maternity roosts. Educating citizen scientists through participatory science and investigating what factors affect the risk of maternity colony exclusions from buildings could potentially improve mitigation methods for bat-human conflicts as well as improve bat populations persistence following WNS.

Given the growing threats facing North American bats, a participatory science platform was created in 2014 by the Ministère des Forêts, de la Faune et des Parcs of Quebec, with the collaboration of the Quebec Centre for Biodiversity Science and the University of Winnipeg, and was later expanded to cover Ontario, Manitoba, Saskatchewan, Alberta and Yukon. This Canadian initiative called the Neighbourhood Bat Watch (www.batwatch.ca or Chauves-souris aux abris; www.chauve-souris.ca) aims to involve citizen scientists in bat monitoring. As few winter roosts are known in Canada, evening emergence counts at maternity colonies provide a non-invasive, simple and reliable method for estimating regional population declines for species dwelling in human structure. Rigorous protocols of the Neighbourhood Bat Watch allow participants and scientists to upload colony locations and counts of bats occupying maternity colonies located on anthropogenic structures, such as privately owned attics, cottages, barns or sheds.

Using the Bat Watch colony and emergence count databases, we examine the variation in the distribution and abundance of Quebec bat populations in relation to WNS onset and maternity

colony exclusions from buildings. We hypothesize that if WNS negatively affects *Myotis* population trends immediately following its regional onset, then we should observe a decline in colony sizes. We also expect an eventual increase in big brown bat populations following WNS onset due to competitive release from *Myotis spp.* We also hypothesize that the risk of colony exclusion is a significant threat for bats that varies among regions, habitat types, and roosting structures. Accordingly, we predict that the probability of colony exclusion should be higher (i) in the south than north, where wilderness areas are more common, (ii) in urban and modified habitats than natural habitats and (iii) in houses and cottages than in other structures that are uninhabited by humans, like barns, garages, and sheds.

Study Area

Maternity colonies were located across the province of Quebec, Canada. Quebec is divided in 17 administrative regions varying in area, climate and land cover classes, with most human populations and anthropogenic landscapes in the south (Table S3.1). Average temperatures vary from south to north, between 31 ° C and 5 ° C in summer, and between −10°C and −25°C in winter. The onset of WNS, which was monitored by administrative regions, was first detected in the south-west of the province in 2010, gradually spreading to the north-east in 2019. The WNS may still be spreading in remote locations, such as on Anticosti Island and the eastern Côte-Nord. We divided the administrative regions into four groups based on their geographic location and climatic conditions (north, east, south, and west; Figure 3.1). Three species of bats were detected in anthropogenic structures in Quebec: the little brown bat, the northern long-eared bat, and the big brown bat. The *Myotis spp.* have high susceptibility to WNS and are present in all regions, while the big brown bat has low susceptibility to WNS and is not present in the north.

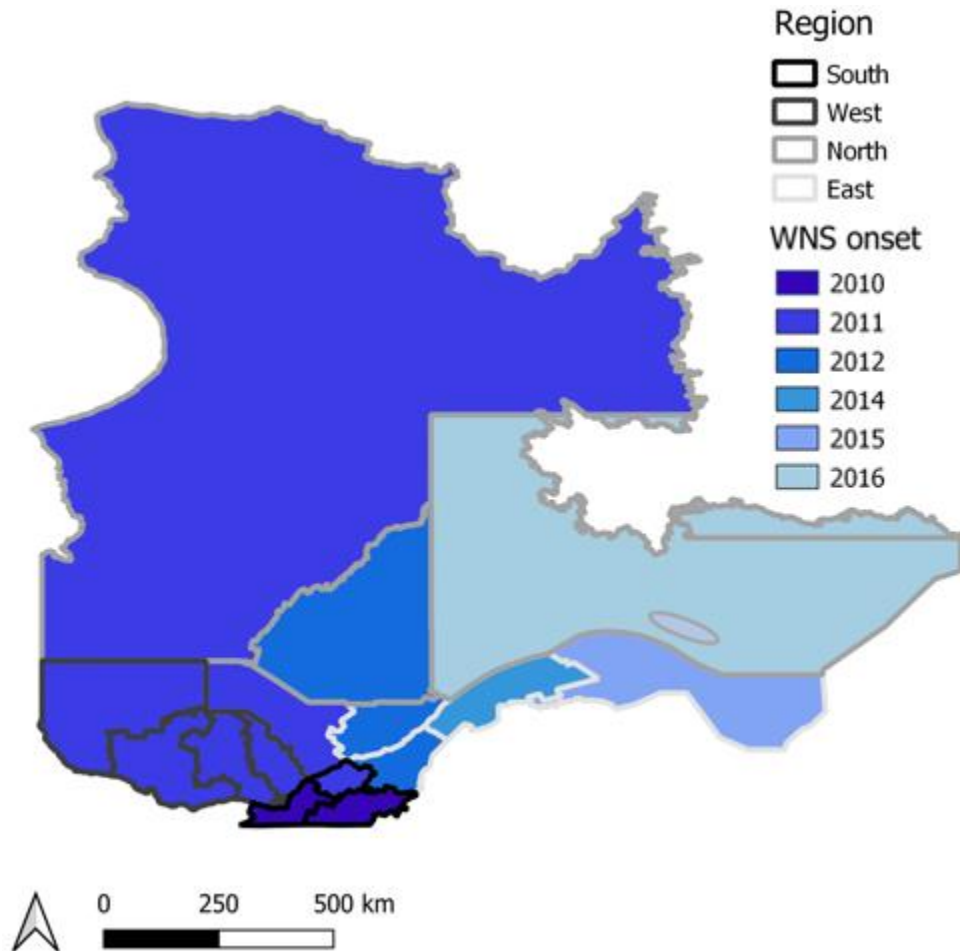


Figure 3.1. Administrative regions of Quebec, Canada, with their respective year of WNS onset. Also shown are the four geographic regions represented by the different colors with their respective number of counts. Map from <https://donneesquebec.ca>, modified with QGIS 3.4.4. software (www.qgis.org).

Methods

Data Collection

The Bat Watch project was initiated in 2012, two years after WNS arrived in southern Quebec, but includes historical data for some maternity colonies as early as 1997. We therefore have information about colonies and emergence counts from 15 years before WNS onset to 11 after

WNS onset, depending on the region and colony. At the end of 2021, there were more than 525 maternities registered on the Bat Watch website in Quebec and more than 696 counts had been completed at 193 different maternity colonies (1 to 25 counts per maternity colony). Participants were either citizen scientists (mostly owners of buildings used by bats) or biologists from academic, governmental, and non-governmental organizations.

We provided detailed protocols for maternity colony validation and emergence counts to all participants (available on the Bat Watch website: www.batwatch.ca/content/protocols). Counts of bats that emerge from the colony to go foraging (emergence counts) started 15 minutes before sunset and ended 30 minutes after the last bat exited the roost and occurred under warm and dry weather conditions (temperature: > 15°C, wind: < 20 km/h, and no continuous rain). Through online forms, we collected information about the colony maternity and counts, including: date, environmental conditions at time of counts, participant names and status (citizen scientist, provincial wildlife ministry team or scientific or non-governmental organization), as well as photos of the roost when feasible. When possible, bat calls were recorded during emergence counts using acoustic detectors (mostly Anabat SD2). Trained professionals identified the species based on typical shapes and frequency range of calls along with whether a species was known to use buildings and its geographical distribution at the time of the count (O'Farrel et al. 1999). The little brown bat and the northern long-eared bat were grouped as *Myotis spp.* as their calls overlap in frequency range and have similar shapes. Three classifications were therefore possible: *Myotis spp.*, big brown bats, or a mixed of *Myotis spp.* and big brown bats.

Data Selection and Statistical Analysis

Impact of White-nose Syndrome.— To measure the effect of WNS onset on maternity size, we first selected emergence counts associated with colonies for which species was identified (*Myotis spp.*, Mixed, or big brown bat). We then grouped all counts that occurred before WNS onset as “year -1”, as they act as a pre-WNS population level baseline. If more than one count from the same colony was available before the onset of WNS, we kept only the most recent count to avoid temporal autocorrelation. We excluded counts that occurred after major disturbances of the roost, such as major renovations of the building or bat control operations. Similar to the approach developed to describe population trends in breeding birds (Fewster et al. 2000) and bat populations (Roche et al. 2011, Barlow et al. 2015), we used a generalized linear mixed model (glmm) with a Poisson distribution to evaluate how the number of individuals in maternity colonies was influenced by time since the onset of WNS (T_{wns}), regions and species identity, as well as their possible interactions. We also tested the non-linear effect of T_{wns} (logarithmic or quadratic relationships) to better fit the declining trends of *Myotis* species. We added reproduction period at time of the count as a fixed effect (i.e. pre- or post-volancy period) and the colony identity as a random effect. Counts conducted during the post-volancy period could inflate the number of individuals counted. This period started around July 10 in southern regions, with a two-week lag for the north region (Fontaine 2022). We selected the best model based on the Akaike information criterion corrected for small sample sizes (AICc).

To examine trends before and after T_{wns} , we used the subsample of 24 colonies with at least six years of counts (range: -12 y to +11 y from T_{wns}). To identify whether trends differed among colonies, we used piecewise regressions applied to each colony using the segmented package in R

(Muggeo 2008). In segmented regressions, the independent variable is segmented into a predetermined number of intervals and a separate regression is fitted for each interval, which allows the estimation of “breakpoints”; that is, regressor values at which the relationship changes. We allowed a breakpoint two years before WNS onset or later. We fitted regression models with segmented relationships between the number of individuals per colony and T_{wns} , and the reproductive period at the time of the count using generalized linear models with a Poisson distribution.

Impact of maternity colony exclusions.— We evaluated the number of exclusions based on maternity colonies with known fate recorded from 1997 to 2020, meaning colonies for which we knew if the colony had been excluded or not. We then used a generalized linear model to test the effect of the region, habitat type and roosting structures on the probability of colony exclusion. We estimated the effect of each factor, using the effects package in R (Fox and Weisberg 2019), applied to a logistic regression with “excluded” or “not excluded” as a binary response variable and regions, habitat types, and structures as explanatory variables. For all analyses, we used a significance threshold of ≤ 0.05 .

Results

Impact of White-Nose Syndrome

Our final dataset consisted of 453 counts from 121 colonies. Forty-seven *Myotis spp.* colonies with at least one count were recorded into the north, east, west, and south regions ($n = 175$ counts). Sixteen mixed colonies with at least one count were recorded into the east, south, and west ($n =$

78 counts). Sixty big brown bat colonies with at least one count were recorded into the east, south and west (n = 200 counts).

The most parsimonious model looking at the effect of T_{wns} on colony size included an interactive effect of the $\ln(T_{wns})$, species, and region (Figure 2; Table S3.2 for model selection). *Myotis spp.* decreased during the first three years by 62 % in the north, 88 % in the east. A steep decline of 98 % also occurred in the south during the last five years. The mixed colonies slightly decreased in the south, were stable in the east, and increased in the west, while the big brown bat colonies decreased in the south and the west and were slightly increased in the east. Reproductive period also impacted the number of individuals, with 3.7 % more individuals during the post-volancy period than during the pre-volancy period.

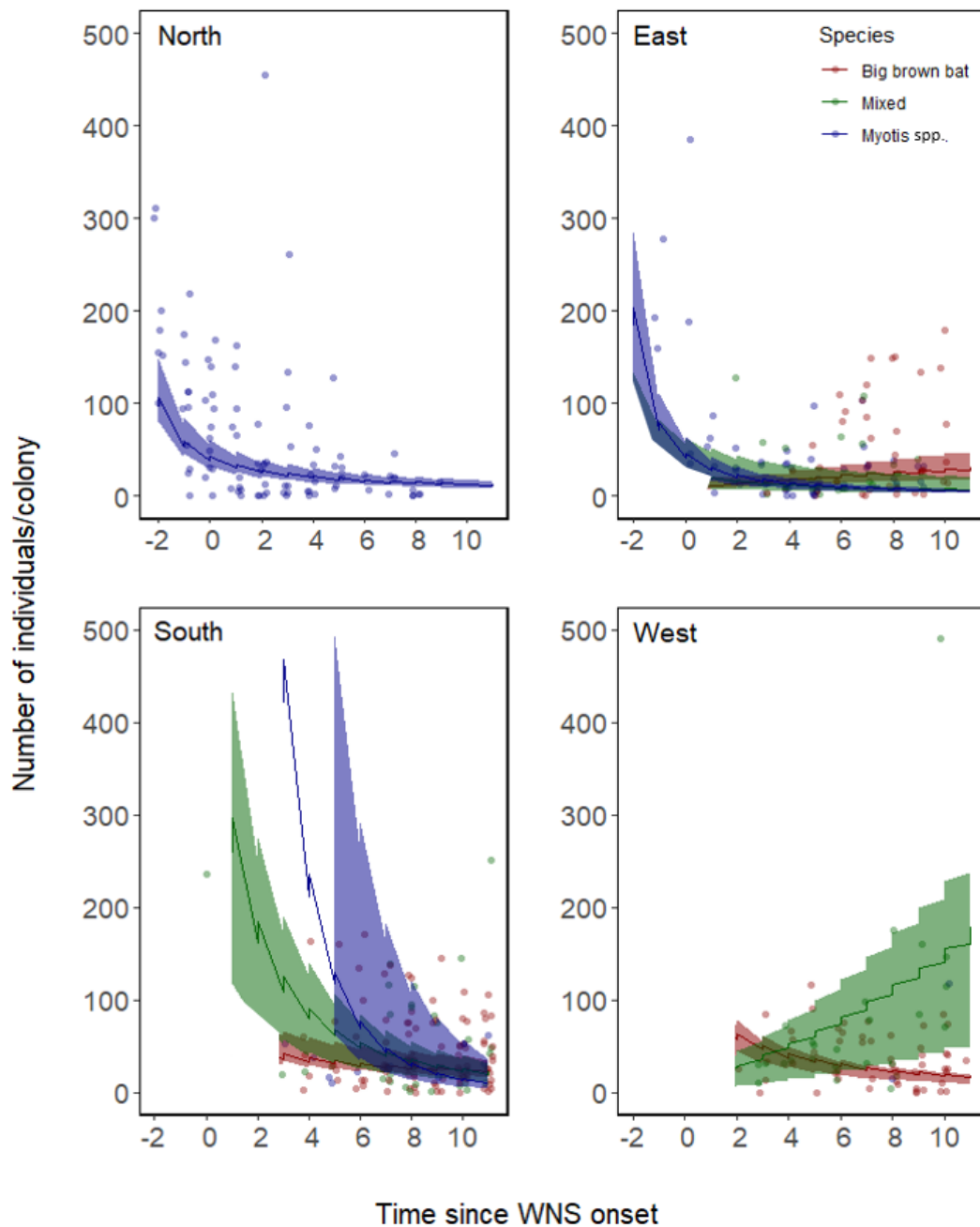


Figure 3.2. Model predictions for the number of individuals by maternity colony in response to an interaction of $\ln(\text{time since WNS onset})$, species, and region in the province of Quebec, Canada. The predictions are based on a generalized linear mixed model with a Poisson distribution accounting time since WNS onset, species, regions, reproduction period at time of the count and colony identity. Shaded areas indicate 95% confidence intervals and points show raw data for each count coloured by species from 2 years before to 11 years after WNS onset.

Piecewise regressions applied on the subset of long-term monitored colonies showed that all *Myotis spp.* colonies with substantial pre-WNS data had a significant breakpoint occurring near the official T_{wns} (range: -2 y to +2.5 y; Figure 3.3), except for two colonies that only strongly decreased. Those colonies were relatively stable or increased before the breakpoint (slope ranging from 0.14 – 3.77) and crashed after the breakpoint (slope ranging from -0.24 – -3.08). The four *Myotis spp.* colonies with only a few years of pre-WNS data had first a strong decrease (slope ranging from -1.68 – -0.39), then stabilized or increased (slope ranging from -0.04 – 0.81). Mixed and big brown bat colonies, with counts only after the official WNS onset, showed more stable trends. Most colonies had no break point or no significant breakpoint (8/12 colonies), with only slight increases or declines in colony size (slope ranging from -0.22–0.22).

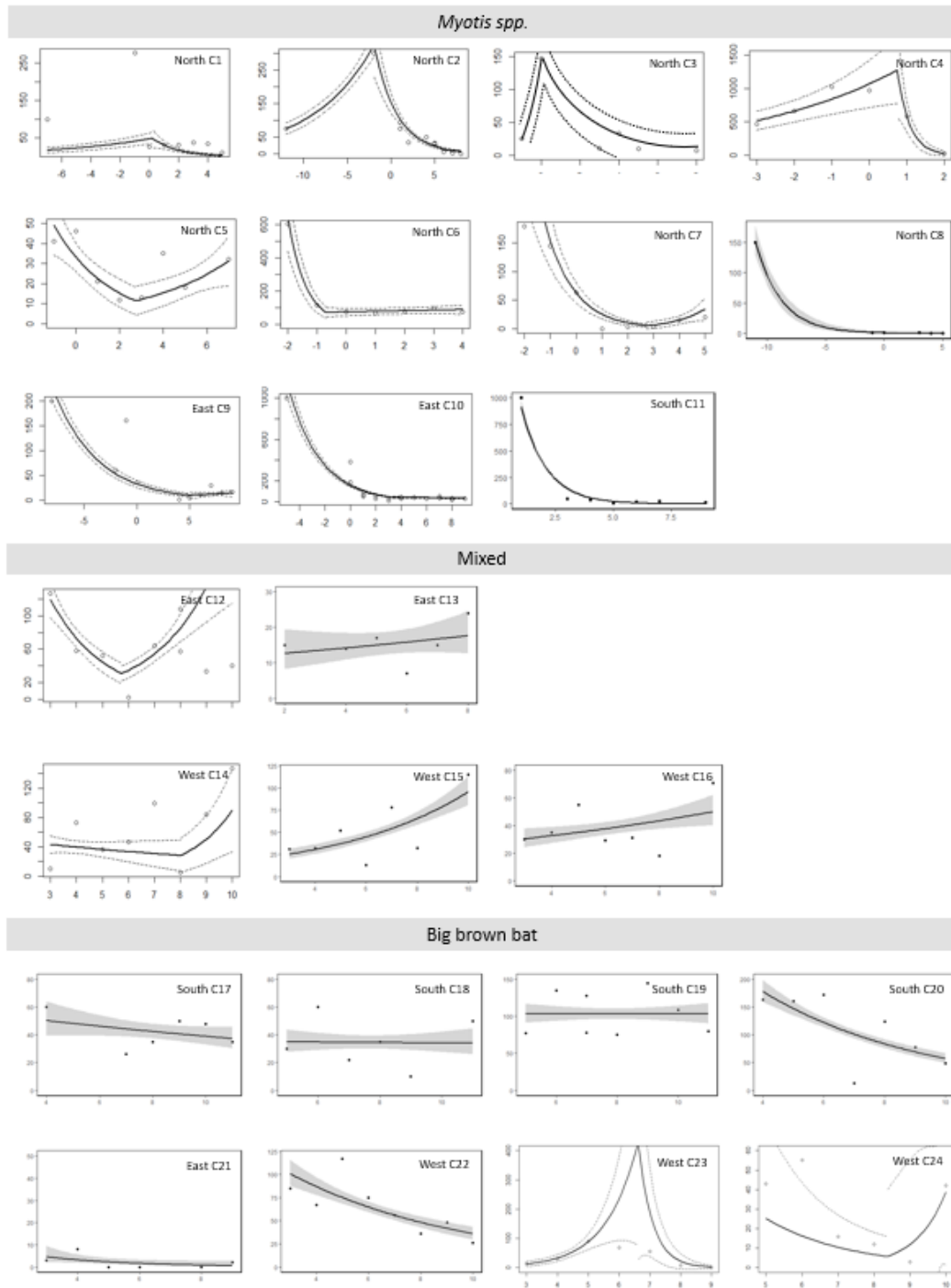


Figure 3.3. Trends for long-term monitored maternity colonies in Quebec, Canada, by species, from 5 years before to 11 years after WNS onset. Trends with confidence intervals with dotted lines are from piecewise regressions with significant breakpoints. Trends with shaded confidence intervals are from linear models with no breakpoint.

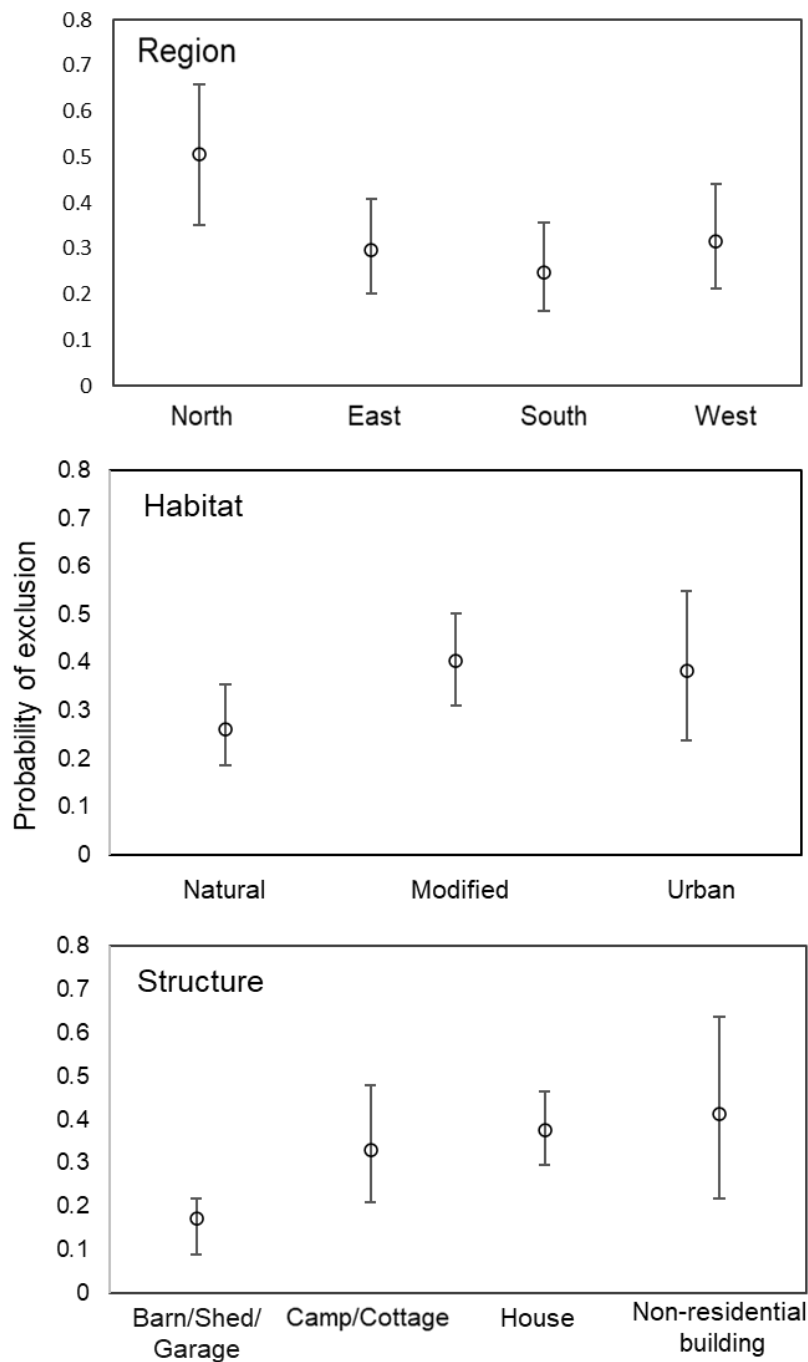


Figure 3.4. Probability of exclusion of bat maternity colonies in Quebec, Canada, by region, habitat type and structure. Estimates and their 95% standard error bars generated from a generalized linear model including the binomial probability of exclusion (excluded or not excluded) in response to region, habitat type and structure.

Impact of Maternity Colony Exclusions

Out of the 287 colonies with known fate recorded from 1997-2020, 102 (36 %) have since been excluded. Of those 102 excluded colonies, 44 (43 %) have been provided with an alternative roost as compensation. From those 44 colonies, 10 have been temporarily colonized (only a few individuals or during only the first season) and seven of them have been permanently colonized. The probability of exclusion varied among the different regions and structures, but not significantly among habitat types (Figure 3.4). The probability of exclusion was significantly higher in the north (0.52; 95 % CI 0.36, 0.67) compared to the south (0.23; 95 % CI 0.15, 0.35). The risk of exclusion was lower in natural habitats (0.26; 95 % CI 0.18, 0.35) than modified and urban habitats (0.33; 95 % CI 0.33, 0.54 and 0.39; 95 % CI 0.24, 0.57 respectively). The probability of exclusion was significantly higher in houses (0.38; 95 % CI 0.30, 0.48) compared to barns, garages, and sheds (0.17; 95 % CI 0.09 0.29). The risk of exclusion was similarly high for camps, cottages and other buildings (0.44; 95 % CI 0.24, 0.68 and 0.34; 95 % CI 0.22, 0.50 respectively).

Discussion

Impact of White-Nose Syndrome

Colony size of *Myotis spp.* decreased by 62 % – 98 % during the first three years after WNS onset. However, the latter estimate is based on only one colony with more than 1000 individuals before WNS onset and fewer than 50 individuals three years after WNS onset. Those estimates are similar to those found from hibernacula counts and transect acoustic surveys in Quebec. *Myotis spp.* declined by 88 % – 100 % at five Quebec hibernacula four to five years after WNS onset (Équipe de rétablissement des chauves-souris du Québec 2019). *Myotis spp.* activity sharply declined after

the onset of WNS, down by 79% after three years (Faure-Lacroix et al. 2020). Regional declines of bat populations in the eastern United States suggest declines from peak levels in regional relative abundance by 2011 of $71\% \pm 11\%$ in *M. lucifugus* and $31\% \pm 18\%$ in *M. septentrionalis* (Ingersoll et al. 2013). Population trajectories in some areas suggest that declines likely resulted from the WNS, but also other unknown threats (Ingersoll et al. 2016). As such, other threats not considered in our analysis may also contribute to declines of several species in Quebec maternity colonies.

As time since WNS onset was based on first official detection in each administrative region, real WNS onset may vary among colonies, particularly in the north, a region covering a large area. That variation may have partially concealed declines, by deflating the population level baseline in the north, as long-term monitored colonies in the north have negative slopes of similar magnitude than colonies in the east. The steepest decrease of *Myotis spp.* and low post-WNS onset colony size in the east, compared to the north, may also be due to big brown bats colonizing the east region soon after the WNS *Myotis spp.* colony crashes. The establishment of big brown bats in the east may be due to competitive release from *Myotis spp.* but could also be caused by the natural expansion of the big brown bat range, likely because of climate change (Sherwin et al. 2013). Mixed colony size was stable in the east, slightly decreased in the south, and increased in the west. Trends from long-term monitored mixed colonies also varied considerably. We only have post-WNS for mixed colonies. In some instances, *Myotis spp.* may have been replaced by big brown bats. *Myotis spp.* individuals may also have decreased after WNS, but may now be stable. More work to estimate the proportion of *Myotis spp.* and big brown bats in those colonies will help to draw clearer conclusions about those trends.

Although big brown bat colonies may benefit from exploiting prey resources previously shared with *Myotis spp.* and a higher availability of roosting and hibernating locations (Thalke et al. 2018; Morningstar et al. 2019), our data shows no significant increase in big brown bat colony size following the decline in *Myotis spp.* colony size. Unlike an increase in big brown/silver-haired bat activity over the three years following WNS onset, possibly due to competitive release found in Faure-Lacroix et al. 2020, big brown bat colonies were generally stable. This trend was also confirmed by the long-term monitoring, with most maternity colonies slightly increasing or decreasing. These differences may be explained by the discrepancy in data collection periods, with my data being mostly collected several years after theirs and only after the arrival of WNS onset. Other threats unrelated to WNS onset such as habitat loss and agricultural pesticides could outdo the competitive release from *Myotis spp.* (Thomas 1995; Jones et al. 2009; Clark 1988). Another explanation may hold in sex-specific responses to WNS establishment, with male abundance being more positively impacted than female abundance, therefore this overall increase would not be detected with maternity colony surveys (Barclay 2012; Simonis et al. 2021).

Due to roosts being detected almost only in non-natural structures, maternity colony counts are biased towards a subset of the whole populations that are closely associated with structures that are easily accessible to humans and located in more disturbed habitats. Roost counts are indices of a greater system, and minor changes in counts must be interpreted with caution. Nonetheless, changes in colony sizes in our study, particularly those for *Myotis spp.* are of a different magnitude and are likely attributable to WNS.

Impact of Maternity Colony Exclusions

In our study, 36 % of all the colonies recorded from 1997-2020 have since been excluded. Almost half of the colonies were excluded with compensation, although often this alternative roost was not used by bats in the long-term. As predicted, the risk of exclusion was higher in urban and modified habitat than in natural habitats. Surprisingly, the probability of exclusion was higher in the north and lower in the south. Perhaps the proportion of old buildings surrounded by a suitable habitat, appropriate for bat maternity colonies, is higher in the north than in the south (Hayward and Roy 2019) or the lack of suitable natural roosts in the north due to small tree sizes increase bat-human conflicts (Thomas and Jung 2019). Whatever the cause, education in urban and modified habitats, particularly in the north, where only endangered *Myotis* species are present, could help to reduce exclusion rates.

The risk of exclusion was also higher in houses than in uninhabited structures like barns, garages, and sheds. Exclusions may be difficult to avoid in houses, since guano droppings often bother the owners, and the close proximity of the bats brings fear of disease transmissions (IDPH 2018). In such cases, we encourage letting bats use a small and closed section of the original roost or providing other structures, like bat boxes, as an alternative roost. Although bat boxes are frequently touted as a successful conservation measure, and several documents exist for guidance on construction and installation, current designs are mainly ineffective in urban and suburban northern areas (Neilson and Fenton 1994; White 2004; Mering and Chambers 2014; Arias et al. 2020, but see Michaelsen et al. 2014). Recent research on bat boxes designs could potentially mitigate negative impacts of bat exclusions from buildings and reduce human-bat conflicts

(Wilcox and Willis 2016; Hoeh et al. 2018; Fontaine et al. 2020). Nonetheless, more work needs to be done to find effective roost alternatives.

The impact of exclusion on bats that inhabit buildings is still unclear. Radio-tracking studies (Brigham and Fenton 1986) revealed that in eastern Canada, big brown bats excluded from a building moved to another building < 1 km away. For this species, exclusion may reduce reproductive output, but does not necessarily increase mortality (Brigham and Fenton 1986). Effective alternative roosts are especially important for WNS-impacted species such as little brown and Northern long-eared bats because healing from WNS-associated wing damage, in addition to the immune reconstitution inflammatory syndrome response itself, is likely to be energetically expensive (Fuller et al. 2011). As there is no cure to WNS, improving survival and reproduction during the active season by providing suitable roosts should help population sustainability (Maslo et al. 2015).

Conclusion

The Bat Watch project demonstrates how data collected synergistically by science professionals and participatory science can be integrated within the same program and co-inform each other. Most of the colonies were found by participants. Without this information, the sample size to measure changes in the relative abundance and distribution of maternity colonies would have been much smaller and results would have included more uncertainties. However, only up to one third of the counts per year included participants. Their participation in counts may be more challenging. Many participants welcomed Bat Watch partners for counts, but fewer had the time and the will to get out at night to count bats of their colony. Several bat participatory projects showed successful

participant implications with acoustic static and transect surveys, as well as with rock climbing surveys (Barlow et al. 2015; Border et al. 2017; Davis et al. 2017). As opposed to those projects, most participants of the Bat Watch did not choose to participate, but participated because bats chose their property to roost. Motivation is therefore not the same and more effort from project managers is required for their participation (He et al. 2019). By participating in the Bat Watch project, participants improve knowledge on bat demography, ecology, and behavior, but also facilitate exchanges between conservation scientists and those hosting colonies, providing the possibility to promote roost conservation or mitigation. The Bat Watch project also contributes to facilitating the collaboration among provincial and national bat researchers and modifying the official provincial status of bat species.

Our study reveals trends in bat maternity colonies, which are of prime conservation concern. We found an important decline in *Myotis spp.* following the WNS onset, while evidence that big brown bat maternity colonies benefited from the decrease in *Myotis spp.* was weak. The impact of maternity colony exclusions from buildings has been poorly studied so far. We found a high maternity colony exclusion rates, which likely harmed population recovery of WNS-affected species. With the increase of urbanization, including its modern wildlife proof dwellings, exclusions will likely become an important source of concern for species using buildings. Education could likely reduce the exclusion rate and increases the rate of roost compensation when an exclusion is unavoidable. Although beyond the scope of this study, threats other than WNS and maternity colony exclusions are likely to contribute to the declines of many species. For example, Faure-Lacroix et al. (2020) report a relationship between bat activity and climate variability, suggesting the possible influence of climate change in the future. Immediate intervention on threats

more amenable to management than WNS could alleviate synergistic or interacting effects that may be compounding threats to bats and ameliorate other stressors to make bats more resilient to the WNS (Harvell et al. 2002; Kannan et al. 2010). Conservation and management for WNS-affected bats have long been focused on improving survival during hibernation, but active-season habitat management including foraging and roosting habitat may also hold a key for successful reproduction and recovery of remnant post-WNS populations.

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Linking Statement

In the last chapter, using the Neighbourhood Bat Watch participatory science project, I provided trends for declining bat species and information on where maternity colony exclusions happened, thereby facilitating habitat restoration efforts for these declining *Myotis* species. Knowledge of the size or density of a population is an essential prerequisite to managing wildlife populations effectively. Determining and understanding factors influencing the reproductive rate of a population is also crucial, as the growing rate of a population is dependent on those parameters. This is particularly true for species that reproduce slowly such as bats, since they usually take longer to adapt through the process of natural selection and that population recovery takes a long time. Small and cryptic species like bats are challenging to study and in-hand examination is usually required to determine reproductive parameters. In the next chapter, I use a subsample of five maternity colonies to evaluate if PIT tags detection patterns can be used to determine reproductive status, parturition date and time away from the roost of female *Myotis*. I show that with good conditions, an assessment of reproductive activity is possible for most of the females. To further evaluate the potential of this method to improve our understanding of bat population ecology, I take the Domaine Joly colony as a case study and evaluate how environmental and individual factors influence female reproductive parameters and time away from the roost.

Chapter 4 – Using PIT tags to infer bat reproductive status and parturition date: Busy nights during lactation

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Abstract

The population dynamics and life-history traits of cryptic species can be challenging to study due to their limited potential for direct observation, which is compounded for small animals because they are too small to be tracked by many biologists. In some cases, these issues can be overcome by using Passive Integrated Transponders (PIT tags) to mark individual animals for identification and infer behaviour. We recorded detections of PIT-tagged little brown (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) at the entrance of five maternity roosts from 2017-2021 to evaluate if this system could be used to determine reproductive status, parturition date and time away from the roost of individual bats. To further evaluate the potential of this method to link behaviour and demographics, we chose one maternity roost as a case study and investigated factors affecting parturition date and time away from the roost. We were able to estimate reproductive status for most of tagged individuals (63 to 100%) at three of five roosts and failed at the two other roosts. Similarly, we were able to estimate parturition date for 42 to 82% of tagged individuals at two of the five roosts and failed at the three other roosts. Proportion of gestating bats with several identifiable bouts away from the roost was higher at the two roosts with successful assessment of reproductive parameters compared to the other three (52-93% vs. 0-50%, respectively). Failures to infer reproductive parameters from PIT tag detection patterns were mainly caused by the use of alternative roosts or entrances by bats. Early individual arrival date and warm spring mean temperature at night led to early parturition dates while longer nights, warmer temperatures, and heavy rainfall at night increased time away from the roost of gestating females. Through this study, we demonstrated that, with an appropriate set up, PIT tag systems may be useful to detect changes in activity patterns of reproductive female bats and infer individual reproductive parameters for female bats, including reproductive status and parturition date. Using this method, the impact of intrinsic and extrinsic factors on reproductive parameters can be investigated to improve understanding of bat population dynamics and, hopefully, population management decisions.

Introduction

Demographic studies investigating population growth rates, lifespan, reproductive histories and social associations require a capacity to identify individuals in permanent and reliable ways while limiting impacts on behaviour, and survival (Barclay and Bell 1988, Kunz and Weise 2009). Several new technologies emerged during the last few decades to track wild animals, yet only a few tools are suitable for small animals exhibiting cryptic behavior. The Passive Integrated Transponder (PIT) is one tool that is small enough to be applied to small vertebrates and has become a popular means of permanently marking individuals (Fiedler 2009; Rigby et al. 2012; Omeyer et al. 2019). A PIT tag is a small microchip encased in inert glass that is usually inserted subcutaneously and when excited by an electromagnetic field emits a unique code. PIT tags have been used on many taxa to answer questions about animal physiology, behaviour, social interactions, phenology, movement, and population dynamics (Gibbons and Andrews, 2004; Nomano et al. 2014; Soanes et al. 2015; Schorr and Siemers 2021).

PIT tags have been particularly valuable for research on bats, a challenging group to study considering their small size, nocturnal habits, ability to fly, and long lifespan. Studies using PIT tags provided valuable information about bat population dynamics, including phenology, apparent survival, site fidelity, relative abundance, and colony size (O'Shea et al. 2011; Law et al. 2020; Santo-Moreno et al. 2021; Schorr and Siemers 2021). Still, such studies are limited in their inference of reproductive success and timing of parturition, and still requires pairing with conventional captures or roost inspections several times a season or through multiple years to assess reproductive status (Zahn 1999; O'Shea et al. 2010; Francl et al. 2012). Finding ways of simplifying the collection of information relative to reproductive success would contribute to improved knowledge of bat ecology.

PIT tag detection patterns may be an efficient means to assess individual reproductive status and parturition date. Reproductive females of several bat species greatly modify their nightly activity budget depending on whether they are gestating or lactating (Anthony et al. 1981; Maier 1992; Horn 1998; Henry 2001). Roost fidelity is variable among bat species and among individuals and is mostly related to the type of roost occupied (Lewis, 1995). As such, species having high

intra- and inter-annual roost fidelity, such as the little brown bat (*Myotis lucifugus*) using buildings as maternity roosts, (Norquay et al 2013; Schorr et al. 2021), should be a good candidate to evaluate individual changes in patterns that arise during the reproductive period through PIT tag detections.

Anthony et al. (1981) were the first to document changes in time budgets of reproductive little brown bats based on observations inside a maternity roost coupled with periodic captures. Using infra-red automatic counter that was used on bats, Maier (1992) also found a unimodal nightly activity pattern in pregnant pipistrelle bats (*Pipistrellus pipistrellus*), changing to a bimodal pattern in lactation, and returning to a unimodal pattern in post-weaning. Another study based on periodic captures, telemetry and videos of little brown bats at a maternity roost entrance showed that gestating females usually have two foraging bouts separated by one resting bout outside the roost. On the other hand, lactating females typically have two or three bouts away from the roost separated by one or two returns to the maternity roost, likely to feed their pup (Henry 2001). Even with an imperfect PIT tag detection caused by having only one antenna for multiple roost exits, the nightly time budget of 199 PIT-tagged little brown bats showed clear and repeatable patterns illustrating several bouts away from the roost per night during the lactation period (Horn 1998). Therefore, using PIT tag detections to infer individual reproductive status and parturition date may minimize stress on individuals while improving understanding of factors influencing variation in reproductive parameters.

Bats from temperate zones experience strong seasonal cycles that impact all aspects of their life histories, especially reproduction. Torpor is one strategy used by insectivorous bats to cope with the costs of maintaining a high body temperature while environmental conditions are unfavorable. Although beneficial to save energy, entering torpor during summer may also delay female reproduction by slowing fetal development and reducing milk production (Racey 1973; Wilde et al. 1999). Therefore, late spring and adverse weather are known to reduce pregnancy rates and delay parturition and juvenile growth (Racey and Swift 1981; Grindal et al. 1992; Lewis 1995; Linton and Macdonald 2018). For healthy populations, the consequences of delayed spring on reproductive output are part of environmental stochasticity and likely have little impact on long-term demographics (Gaillard et al. 2000; Doak et al. 2005). However, for declining populations

that face several threats, such as North American bats with white-nose syndrome (Cheng et al. 2021), it becomes important to estimate reproductive fitness while minimizing disturbances.

To successfully reproduce, females modify their foraging bouts during gestation and lactation since these periods are energetically costly (Kurta et al. 1989; McLean and Speakman 1999). Therefore, time spent foraging can vary both daily and seasonally in relation to reproductive status, but also with night length, weather conditions, food resources, and animal health (Anthony et al. 1981; Allen et al. 2011; Dzal and Brigham 2013). Foraging bouts are usually assessed using radio telemetry, which can be logistically challenging and often have low temporal resolution unless manual telemetry is used. Although females can spend small amounts of time in non-foraging activities while away from the maternity roost, time away from the roost may still be used as a proxy for foraging bout, reflecting energy demands (e.g., Wilkinson and Barclay, 1997).

The main goal of this study was to evaluate if a PIT tag system is an effective method to accurately detect changes in nightly activity (exit and entrance) patterns, from which inference on incidence and timing of reproduction in bats might be drawn, as well as time away from the roost. Specifically, PIT tag detection patterns should allow the inference of individual reproductive status and parturition date from the behavioural change from gestation to lactation of female little brown bats using artificial roosts, as showed in several bat studies (i.e., lactating females interrupt time away from the roost multiple times each night, to feed their pups at the roost; Antony et al. 1981, Maier 1992; Horn 1998, Henry 2001). We tested these predictions at four maternity roosts in Quebec equipped with the Biomark PIT tag system and validated it with one roost in Newfoundland PIT-tagged with the Trovan technology.

To further evaluate the potential of this method at improving knowledge on bat population ecology, we chose the maternity roost at the Domaine Joly (Québec, Canada) as a case study. We analyzed five years of PIT tag data from 41 little brown bats (*M. lucifugus*) and eight northern long-eared bats (*M. septentrionalis*). We investigated whether variation in parturition dates of females inferred from PIT tag detection pattern changes could be explained by annual weather conditions and arrival date at the roost. We predicted that individuals that arrived late to maternity roosts would have later parturition dates, especially during wet, cold and windy springs (Racey

and Swift 1981; Ransome and McOwat 1994). Over the five years of monitoring, we expected to find individuals having consistently earlier parturition date compared to others due to intrinsic factors such as body size, body condition, and age (Holroyd 1993). We also evaluated if time away from the roost varied in function of nightly weather conditions (temperature, rainfall, and wind speed), night length, and estimated reproductive status. We predicted foraging on nights with low temperature, high amount of rain, and high wind speed to be energetically expensive, resulting in shorter time away from the roost. As bats are nocturnal, we also expected shorter night lengths (time between sunset and sunrise) to constrain bats to have shorter foraging bouts, and therefore, shorter time away from the roost (Rydell et al. 1996; Talerico 2008). Finally, because reproduction is energetically costly, reproductive females should forage for a longer period during the gestation period than non-reproductive female. Alternatively, non-reproductive females could stay away from the maternity roost for a similar period than reproductive females, using cooler night roosts to save energy (Grinevitch et al 1995).

Methods

Study area

We PIT tagged bats at five maternity roosts, four in Québec and one in Newfoundland, Canada (Fig. 4.1). The Domaine Joly roost was the attic of a historical building, converted into a restaurant and surrounded by 19th century park-garden of 138 hectares on the south shore of the Saint Lawrence River, in a central part of Québec (46.66677, -71.84898). The Spodumène roost was a condemned camp in the boreal forest, beside a small lake (~1 km²) and a well-lit mine located in northern Québec (51.68698, -75.82339). Anna Lake and Cailloux Lake roosts were both derelict camps surrounded by a boreal forest and a small lake (~ 500 m²) located on Anticosti Island, in eastern Quebec (49.87091, -64.14379 and 49.77001, -63.83035, respectively). The roost in Newfoundland was in Salmonier Nature Park and included 11 bat boxes positioned within 1 km² (47.26270, -53.28488). All sites had a cold temperate climate, the warmest being the Domaine Joly with a mean temperature in June of 16°C, while other sites were around 10–12 °C.

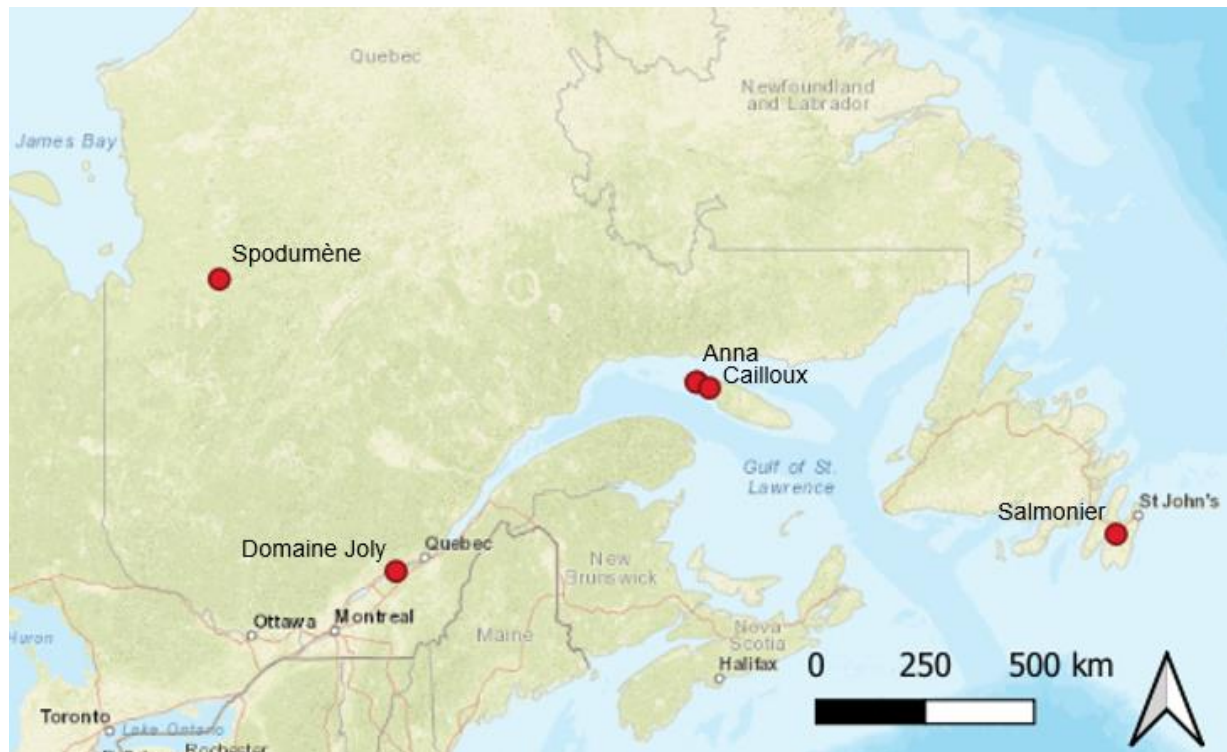


Figure 4.1. Map of the five maternity roost locations where we PIT-tagged bats and recorded their detections, from 2017-2021 in Quebec and Newfoundland, Canada. Map derived from ESRI Standard <https://server.arcgisonline.com>, modified with QGIS 3.4.4. software (www.qgis.org).

Bat PIT tagging

We captured and marked little brown and Northern long-eared bats before and after parturition (June and July respectively), when young were believed to be born, but not volant at the Domaine Joly roost in 2016 and 2017. We marked bats once a year in 2018 at all the roosts in Quebec, while we marked bats several times per year since 2012 at the Salmonier roost. For each bat captured, we recorded the species (*M. lucifugus* or *M. septentrionalis*), mass, and sex, and assessed the individual's reproductive condition by palpating the abdomen or examining the nipples (Haarsma 2008). We marked bats with GPT12 (12.5 mm) PIT tags (Biomark, Inc., Boise, Idaho) in Quebec and with ID-100s PIT tags (Trovan, Ltd., Netherlands) in Newfoundland. We inserted tags subcutaneously below the scapula, and we sealed insertion sites with a biomedical glue (Vetbond Tissue Adhesive; 3 M Science, St. Paul, Minnesota).

At the Domaine Joly and Anna Lake roosts, we detected tagged bats using a 0.8 m × 0.3 m window-style PIT tag antenna framing the main entrance with a HPR plus reader (FS2001; Biomark, Inc.). At the Cailloux Lake roost, we used a 0.2 m racket-style PIT tag antenna with a HPR plus reader (FS2001; Biomark, Inc.). At the Spodumène Lake roost, we detected tagged bats using a 7.6 m cord PIT tag antenna system (IS1001; Biomark, Inc.) that was stretched under the eaves. At the Salmonier roost, we used window-style PIT tag antennas that were fitted to the bat house's entrances (Trovan Ltd.). All antennas and reader systems detected PIT tag signals from the day of capture and in the following years, generally from mid-May to mid-September. We constrained to 30 seconds the time allowed between two consecutive detections for a given individual. Based on previous knowledge, this interval between two detections of a given individual was the best compromise to avoid recording too many detections of a same individual resting near the antenna, without missing 'independent' detections. At the Domaine Joly, we used household AC power to record data, with DC batteries as back up in case of power failure, while at other roost, we power data recorders with DC batteries connected to a solar system. We installed antennas in early spring (usually at the end of April) and removed them in fall (usually in mid-October).

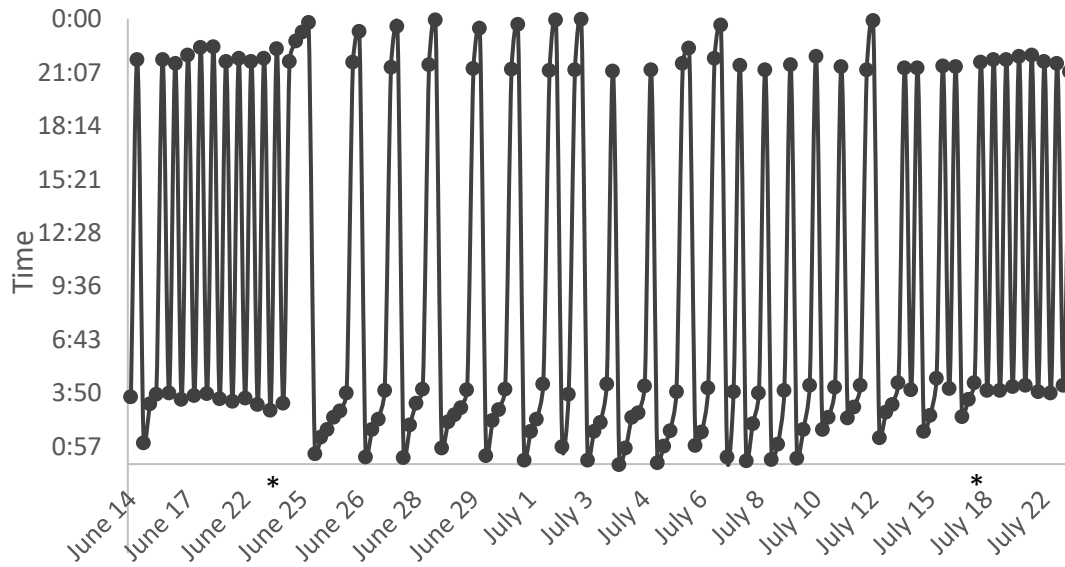
Estimating reproductive status, parturition date, time away from the roost, and weather conditions

We sorted PIT tag detections by individual. As bats sometimes wait beside the antenna and are recorded several times before exiting or after entering the roost, even with our 30-second interval setting, we kept only one detection by sequence of consecutive detections (i.e., within a 15-minute interval). We kept the last detection when the bat left the roost for the first time at night, and the first one when it entered the roost for the last time in the early morning. We cleaned detection sequences between the first exit and the last entrance, alternating with exits and entrances.

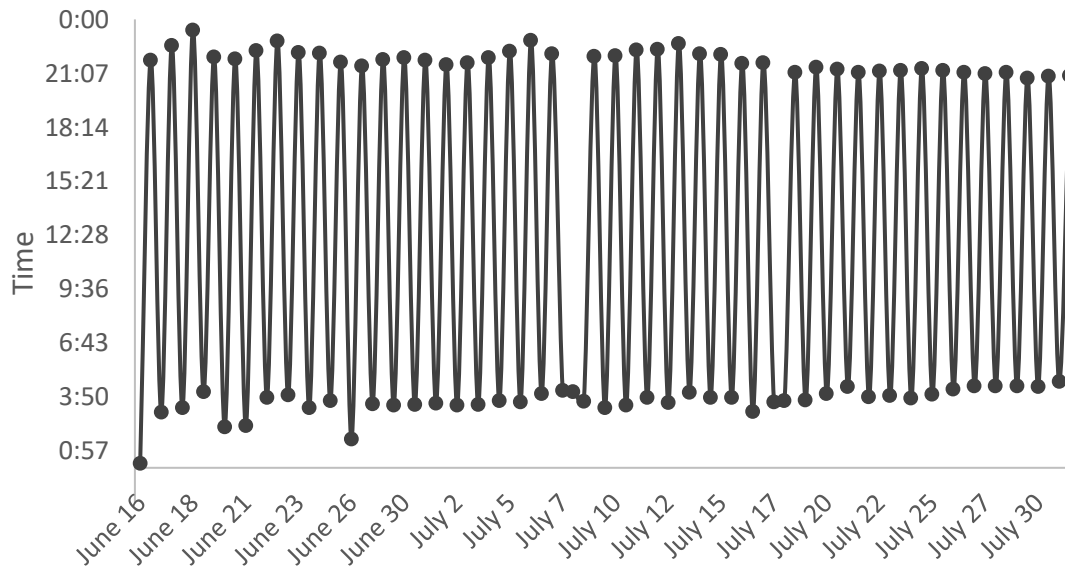
We estimated reproductive status from the temporal pattern of PIT tag detections. Specifically, we identified a female as reproductive if detection patterns changed from a single exiting/return sequence per night to two or more exiting/return sequences per night. To be more specific, we verified whether no midnight return was recorded for an individual for the seven days preceding a change in detection patterns, followed by two or more exiting/return sequences per

night, without a single exiting/return sequence, in the seven following days (Fig 4.2a). When we failed to detect a clear change of detection pattern and found a single exiting/return sequence per night throughout the entire reproductive season, we assessed that there was no evidence that the individual was reproductive and for discussion, label them as non reproductive (Fig 4.2b). We assessed an individual as unknown reproductive status if it stopped being recorded before the end of the mean parturition date or if both periods contained too much variability.

For females identified as reproductive, we estimated the parturition date as the date when there was a change in the activity pattern: i.e., at least three consecutive nights with only one exit and one return followed by at least three consecutive nights with two or more exits and returns. We defined parturition date as the night where the female started to come back to the roost twice or more instead of once per night (e.g., Fig 4.2). When possible, we estimated apparent weaning onset following the same logic. As nightly activity pattern was found to be unimodal during the post-weaning period (Maier 1992), we defined weaning onset, or the change in parental care intensity, as the date where the female started to leave the roost all night, likely with its young, instead of coming back to the roost several times a night.



a)



b)

Figure 4.2. Examples of a) reproductive activity pattern for the pit-tagged female 3D9.1C2D61E021, changing from one to several visits to the roost per night at the Domaine Joly maternity roost (Quebec, Canada) in 2017. The estimated parturition and weaning onset dates, represented by asterisks, are estimated to June 24 and July 18, respectively, and b) absence of activity pattern changes for the pit-tagged female 3D9.1C2D61ECE1, identified as non-reproductive, at the Domaine Joly maternity roost (Quebec, Canada) in 2019.

Although time away from the roost during the gestation period may include other activities of undetermined location and duration than foraging (e.g., rest), this parameter appeared to be assessed more accurately during gestation than lactation. Full sequences of time away from the roost (i.e., presumably all exits and returns per night for a given individual) during lactation were scarcer, as one missing detection or inaccuracy in data cleaning may have biased the estimate. Therefore, we estimated time away from the roost only during gestation. We estimated individual mean time away from the roost in minutes based on days with full sequences during the 14 days preceding the parturition for each individual. To compare non-reproductive with reproductive individuals, we considered the 14 days preceding the mean estimated parturition date of the colony at a given year.

To investigate parameters affecting our estimated parturition date, and time away from the roost of females, we achieved a case study for the Domaine Joly colony. At this roost, we calculated mean and minimal temperature (°C), mean rainfall (mm), rain duration (hour), and mean wind speed (km/h) at night using the hourly data from Deschambault meteorological station of Environment Canada, located 9 km from the roost (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). We considered nightly weather being from 21h00 to 04h00. Spring weather included data from March 1 to June 30. We calculated night lengths in minutes from sunset to sunrise data from Quebec City, located 15 km north of the roost (<https://www.sunset.com/fr/sun/canada/quebec>). We evaluated spring arrival to and fall departure from the study maternity roost, acknowledging that females could have arrived before or returned after to a nearby alternative roost that is not monitored.

Statistical analysis

We calculated the proportion of bats for which we could assess the reproductive status, parturition date, and time away from the roost for all individuals recorded at least once for each roost (n=5) and years (n=3-5). For the Domaine Joly roost case study, we used the subsample of females with estimable reproductive status, parturition date, and time away from the roost. We evaluated if variation in parturition date was influenced by spring weather conditions and time of arrival at the roost with a linear crossed mixed model (LMM). We first built a subset of global models to test

and compare different correlated metrics and relationships to see what would best fit the data as temperature, rainfall, and arrival date metrics. Those metrics and relationships were tested based on the literature and visual inspection of the data and included: mean temperature, mean temperature at night, number of hours in the optimal temp range of 15–32 °C, number of hours in the optimal temperature range of 21–32 °C, number of days with maximal temperature between 15–32 °C at night, number of days with maximal temperature between 21–32 °C, total rainfall, number of days with rainfall between 2.5–25 mm, and arrival date with varying intercepts. We selected the best global model based on the Akaike's information criterion corrected for small sample size (AICc; Table S4.1).

Our global model included parturition date as response variable, arrival date, spring mean temperature at night, number of days with rainfall between 2.5–25 mm during spring, and spring mean wind speed as fixed factors and individual identity and year as random factors. We then used the “dredge” function of R package MuMIn (Barton 2019) on our global model to generate a model selection table including a subset of models with combinations of fixed effect terms of the global model (Table S4.2). We select the most parsimonious model of this subset based on AICc and used it as a final model to interpret the effect of the different factors. Our final model, used to analyze the data, included parturition date as response variable, arrival date, spring mean temperature at night, and spring mean wind speed at night as fixed factors and individual identity and year as random factors.

We evaluated if time away from the roost during gestation varied in function of daily weather conditions, night length, and reproductive status using a LMM. Again, we first built our global model by comparing different correlated metrics of temperature and rainfall using AICc (Table S4.3). Our global model included time away from the roost as response variable, reproductive status, night length, mean nightly temperature, total rainfall at night, and mean nightly wind speed as fixed factors, while individual identity and year served as random factors. Again, using the dredge function, we selected our final model used to analyze the data, that included time away from the roost as response variable, night length, mean nightly temperature, and total rainfall at night as fixed factors, and individual identity and year as random factors (Table S4.4). We used

lme4 package in R (Bates et al. 2015) for all analysis and used confidence intervals to verify the significance of variables, i.e., if the 95% confidence intervals around the slope did not include zero.

Results

Estimation of reproductive status, parturition date and time away from the roost

From the 39 PIT tagged bats that were detected at least once during the same year of their in-hand capture or recapture, reproductive status (lactating, gestating, non-reproductive, or unknown) of 92 % of them were correctly assessed with PIT tag detections compared with in-hand assessment. The 8 % remaining were assessed as unknown because the number of days of detections was too low to reliably assess reproductive status. Using PIT tag detection patterns, we identified the reproductive status for 73–94 % of PIT-tagged females detected at least once during a year at the Domaine Joly roost ($n_{\text{tot}}=22-33$), 0 % at the Spodumène Lake roost ($n_{\text{tot}}=12-14$), 71–100 % at the Cailloux Lake roost ($n_{\text{tot}}=2-7$), 25–50 % at the Anna Lake roost ($n_{\text{tot}}=2-8$), and 63 % at the Salmonier nature park roost ($n_{\text{tot}}=60$; Table 4.1). Estimated parturition date from PIT tag detection patterns was identifiable only at the Domaine Joly and Salmonier nature park roosts, with 42–82 % and 57 % of individuals with known parturition date respectively. The proportion of gestating bats with identifiable time away from the roost varied between 52–93 % at the Domaine Joly roost, 0–14 % at the Spodumène Lake roost, 29–50 % at the Cailloux lake roost, 0 % at the Anna Lake roost, and 73 % at the Salmonier nature park roost. In some cases, full detection sequences were not registered. This problem may come from antennas not detecting PIT-tagged bats, or from bats using alternative entrances. Rates of full detection (i.e., presumably all entrances and exits) sequences per individual ranged from 0–100% with means ranging from 9–44 % depending on the year and location. Full sequences were higher for individuals detected throughout the whole season. For those individuals, full sequences were higher during the gestation period. For example, the mean rate of full sequences was 70 % during gestation compared to 44 % during the whole season at the Domaine Joly roost.

Table 4.1. Percentage of PIT-tagged bats with estimable reproductive status, parturition date, and time away from the roost by sites and years in Eastern Canada from 2017–2021.

Site	Year	Number of PIT-tagged bats before parturition	Return rate (number of bats detected after being tagged)	Percentage of bats with estimable reproductive status	Percentage of bats with estimable parturition date	Percentage of gestating bats with identifiable time away from the roost
1. Domaine Joly's attic	2017	36	33	85 %	42 %	52 %
	2018	46	31	94 %	55 %	61 %
	2019	53	29	93 %	62 %	93 %
	2020	53	22	86 %	73 %	77 %
	2021	53	21	81 %	71 %	81 %
2. Spodumène Lake's camp	2019	26	14	0 %	0 %	14 %
	2020	26	12	0 %	0 %	0 %
3. Cailloux Lake's camp	2019	30	7	71 %	0 %	29 %
	2020	30	2	100 %	0 %	50 %
4. Anna Lake's camp	2019	12	8	25 %	0 %	0 %
	2020	12	2	50 %	0 %	0 %
5. Salmonier's bat houses	2017	1425	60/879*	63 %	57 %	73 %

*879 bats have been detected at Salmonier's bat houses in 2017, but a subsample of 60 bats for which at least one record on at least 40 days between June 1 and July 31 have been analysed.

Determinants of Domaine Joly colony's parturition date and time away from the roost

From 2017-2021, females arrived at the Domaine Joly maternity roost from April 30th to June 15th, gave birth from June 4th to July 13th. Apparent weaning, or decreased nightly parental care, occurred from July 6th to August 3rd, and females left from July 8th to September 15th (Table 4.2). The proportion of individuals for which there was no evidence of reproduction at the Domaine Joly roost varied from 4-15 % between 2017 to 2021.

Table 4.2. Phenology of reproduction estimated from PIT tag detections for female little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) at the Domaine Joly maternity roost in Quebec, Canada from 2017–2021.

Year	Arrival date range	Parturition date range	Weaning onset range	Departure date range
2017	May-13/June-15	June-24/July-01	July-06-July-21 (n=7)	July-08/Aug-05
2018	May-05/June-05	June-21/June-29	July-14/July-23 (n=9)	July-12/Aug-24
2019	May-05/June-03	July-04/July-13	July-23/Aug-03 (n=15)	July-19/Sept-16
2020	May-15*/June-01	June-24/June-30	July-14/July-27 (n=12)	July-18/Sept-04
2021	April-30/May-29	June-18/June-27	July-10/July-21 (n=9)	July-09/Aug-24

*First arrival date assumed to be prior to the date of installation. Delayed installation date due to Covid-19.

There was a significant effect of arrival date and spring mean temperature at night on parturition date (Fig. 4.3). Using the best linear crossed mixed model (conditional r-square = 0.94), we predicted that a female arriving at the roost 10 days later than its conspecifics give birth approximately three days later (Coef. Value =0.20, 95% CI 0.09 – 0.28; Fig. 4.3a). We also predicted that an increase of 1°C in spring mean temperature at night resulted in females giving birth five days sooner (Coef. Value =-5.59, 95% CI -9.47 – -1.72; Fig. 4.3b).

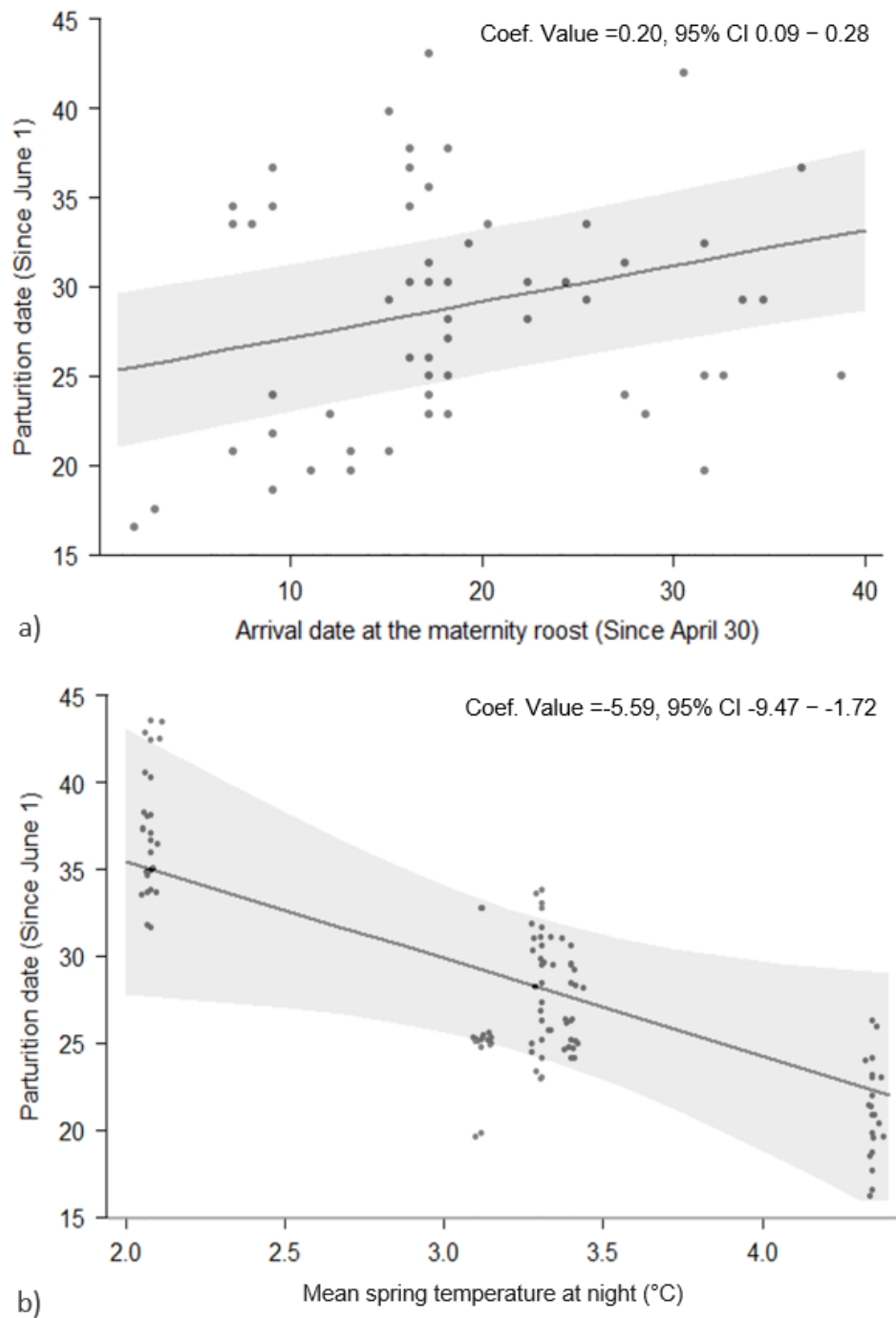


Figure 4.3. Effect of a) arrival date at the maternity roost and b) spring mean temperature at night on parturition date of female little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) at the Domaine Joly's roost from 2017–2021 (Quebec, Canada). The predictions are based on a linear crossed mixed model including the arrival date, spring mean temperature, and mean wind speed, with individual identity and year as random factors. Shaded areas indicate 95% confidence intervals and points show raw data of parturition date.

Variation in parturition date among years at Domaine Joly roost were generally greater than within year inter-individual variation with much later parturition date in 2019 and sooner parturition date in 2021. Although a few individuals seemed to consistently give birth sooner (e.g., 3D9.1C2D62859C, 3D9.1C2D626F0F, and 3D9.1C2D62094E) or later (e.g., 3D9.1C2D625939, 3D9.1C2D61ECEE, and 3D9.1C2D61DAB2), most individuals displayed little consistency among years (Fig. 4.4).

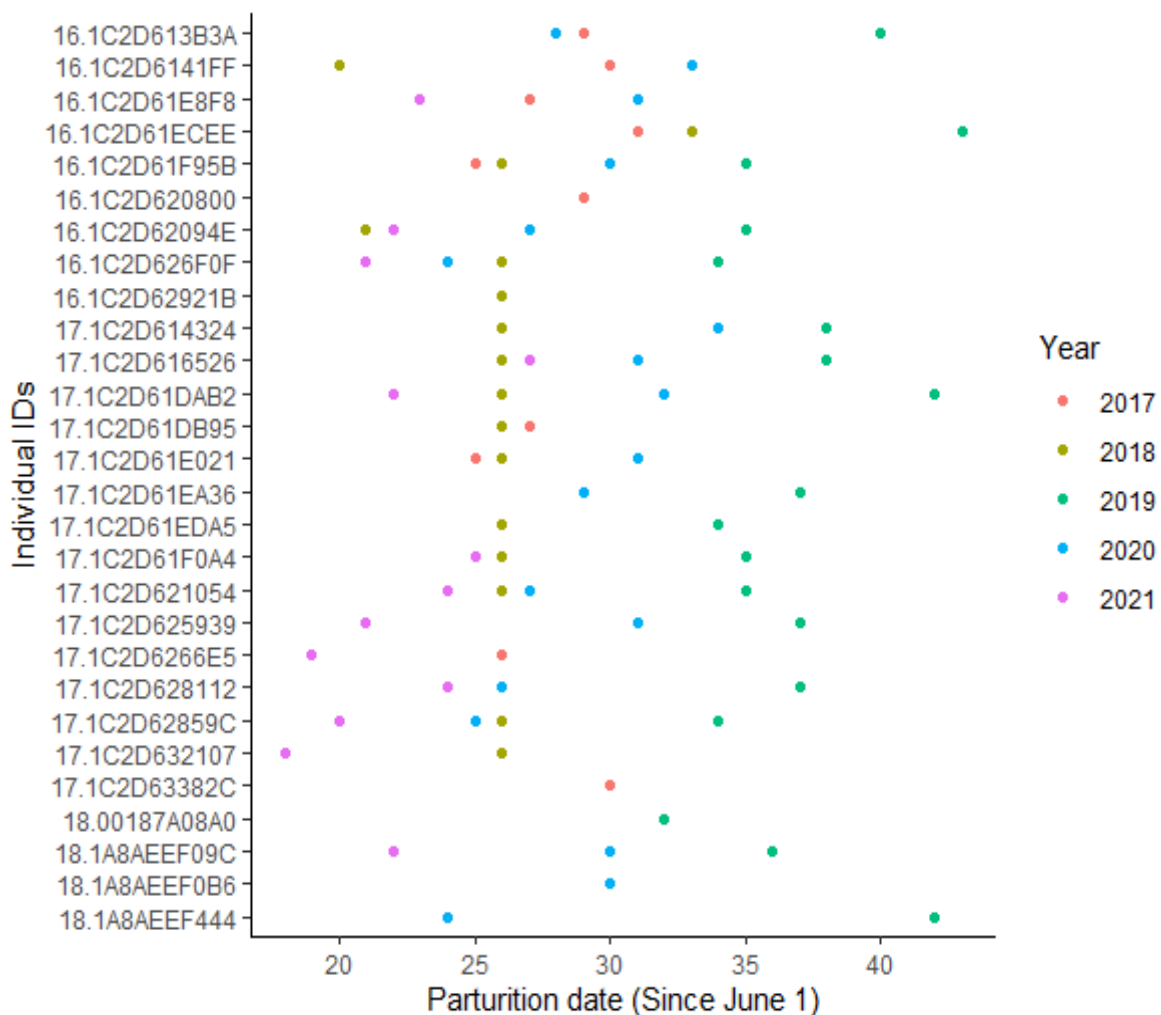


Figure 4.4. Estimated parturition date of PIT-tagged female little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) at the Domaine Joly roost from 2017–2021 (Quebec, Canada).

Night length, mean rainfall, and mean wind speed at night significantly influenced time away from the roost, an index of foraging bout length in gestating females (Fig. 4.5). The influence of reproductive status on time away from the roost was not significant. However, time away from the roost of reproductive females were, on average, 13 minutes shorter than for non-reproductive females, for which time away from the roost varied greatly. Based on our final linear crossed mixed model (conditional $r^2 = 0.26$), we predicted that every increase of 10 minutes in night length and 10 °C in the mean temperature at night resulted in an increase of 15 and 13 minutes, respectively (Night length Coef. Value =1.34, 95% CI 0.32–2.33; Fig. 4.5a; Temperature Coef. Value =1.35, 95% CI 0.52–2.15; Fig. 4.5b). Similarly, an increase of 20 mm of rainfall at night resulted in an increase of 25 minutes in time away from the roost (Coef. Value =1.16, 95% CI 0.32–2.03; Fig. 4.5c). Finally, time away from the roost was longer in 2017 2018, and 2021 (400, 407, and 406 min respectively) than in 2019 and 2020 (380 and 388 min respectively).

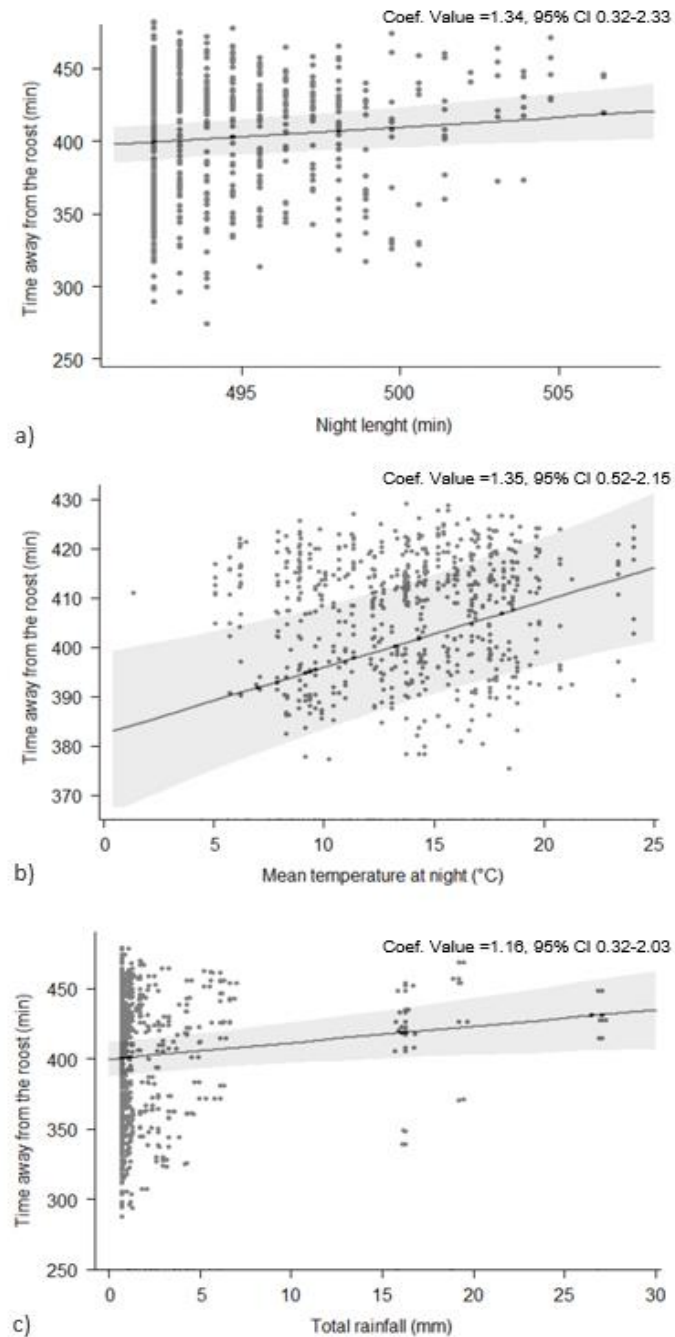


Figure 4.5. Effect of a) night length, b) mean temperature at night, and c) total rainfall at night on time away from the roost of gestating female little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) at the Domaine Joly roost from 2017-2021 (Quebec, Canada). The predictions are based on a linear crossed mixed model including night length, mean temperature at night, and total rainfall at night, with individual identity and year as random factors. Shaded areas indicate 95% confidence intervals and points show raw data of time away from the roost.

Discussion

We evaluated the potential of PIT tags to detect nightly activity pattern change in reproductive female bats, to ultimately estimate individual reproductive status and parturition date of female bats at maternity roosts, removing the need for multiple recaptures of individuals to obtain this information. We were able to accurately detect nightly activity patterns, and therefore estimate reproductive status, for most individuals at the Domaine Joly, Salmonier Nature Park, and Cailloux Lake roosts. We estimated parturition date and time away from the roost of most gestating females from the Domaine Joly and Salmonier Nature Park. In the Domaine Joly roost case study, parturition date was influenced by individual arrival date and spring mean temperature at night, with important variation in mean parturition date among years. A few females seemed to consistently give birth sooner or later, but the most noticeable trend was the late mean parturition date associated with cold spring temperature in 2019. Night length, mean temperature at night, and total rainfall at night also affected time away from the roost of gestating females.

Estimation of reproductive status, parturition date, time away from the roost

Several studies used long-term periodic captures or inspections of the roost to assess reproductive population trends (Zahn 1999; Francé et al. 2012; Linton and MacDonald 2017) but few were able to determine individual parturition, lactation, and pup weaning dates (reduced parental care; e.g., Henry 2001). Our study demonstrates, for the first time, the possibility to estimate individual reproductive status and parturition date from PIT tag detections without the need to recapture individuals. Our investigation was based on behavioural patterns of reproductive female bats reported in the literature (Antony et al. 1981, Maier 1992; Horn 1998, Henry 2001) using permanent maternity roosts, and confirmed by our in-hand captures at the Domaine Joly roost (n=39). Our successful estimation of these reproductive parameters at the Domaine Joly and Salmonier Nature Park occurred because all entrances were covered by an antenna and individuals had high fidelity to monitored roosts. Unfortunately, not all roosts have equally high fidelity, particularly when alternative roosts are present in the vicinity. The Spodumène Lake roost has been highly disturbed by recent changes in mining activity in close proximity to the roost. Moreover, although the main roost (i.e., a barricaded windows) was covered by the antenna, bats

were able to use alternative roosting locations in the camp. The use of alternative entrances or locations not covered by antennas reduced the number of PIT tag detections, and therefore, our capacity to estimate reproductive status and parturition date. The same issue likely occurred for the Cailloux Lake and Anna Lake roosts, on Anticosti Island. The arrival of white-nose syndrome on Anticosti Island during the study also decreased population size and return rate of PIT-tagged bats, reducing the sample size and, therefore, the statistical power for those two sites.

Although several limitations remain, such as PIT tag loss, antenna interferences with metallic structures, power supply issues, or inability of antennas to read several tags passing through at the same time, PIT tags have allowed innovative investigations into numerous ecological fields (Gibbons and Andrews 2004; Schorr and Siemers 2021). Recapture of bats using antennas that continuously read PIT tags allows rigorous estimation of bat population parameters that can elucidate trends in phenology, reproduction, abundance, and survival (O'Shea et al. 2010; Schorr and Siemers 2021). We demonstrated here, using two different systems, that PIT tag detections also allow successful estimation of reproductive status and parturition date for the majority of adult females. Reproductive status and parturition date found with PIT tag detections fitted what we found for the subsample of bats captured by hand during the same year. This non-invasive recapture method is valuable for detecting elusive species, improving estimates of population parameters, reducing stress to organisms and stress-induced bias, as well as, reducing the behavioural response bats can have to capture and that response's impact on detection probability (Ellison et al. 2007; Rigby et al. 2011). However, although there is no evidence that PIT tags alter bat long-term stress, we advise they are only used where there is a reasonable chance of long-term monitoring as the first capture and tagging can cause temporary desertion of the roost and is still considered as an invasive method. If reproductive parameters are of interest, we also advise they are only used for species and location where nightly activity pattern change in reproductive female bats is known.

Determinants of reproductive status, parturition date and time away from the roost

After hibernation, females begin gestation and must raise their pup within a timeframe that matches the development of resources in spring and summer (Fleming and Eby 2003; Jonasson and

Guglielmo 2016). Female *Myotis* in Canada traveled up to 647 km during seasonal movements from winter to summer grounds (median distance: 463 km), suggesting high energetic demands (Norquay et al. 2013). The positive relationship between individual arrival date and parturition date in our study suggests that early arrival allows a longer breeding season that likely translate into fitness advantages for females and their pup (Frick et al. 2010). Difference in arrival and parturition date may also be explained by variations in female body condition in early spring, local conditions at hibernating and summer roosting sites, or migration distance from the hibernaculum to the maternity roost (Pettit and O’Keefe 2017; Linton and MacDonald 2018; Sommers et al. 2019).

Determining the extent to which key life history traits, such as reproductive status and parturition date, are influenced by environmental conditions and climatic variation is crucial for predicting the consequences of climate change on long-term population dynamics and stability. During “late” springs, with prolonged suboptimal conditions, breeding females face a trade-off between the short-term benefits and long-term negative consequences of employing torpor to delay parturition. Gestation length in a colony of pipistrelle bats in Scotland varied by 10 days in two consecutive years, with gestation being extended by cold and wet weather during the early stage (Racey and Swift 1981). Similarly, early births followed warm springs in a population of horseshoe bats (*Rhinolophus ferrumequinum*) in England, where mean birth date was 18 days earlier following a rise of 2°C in spring temperature (Ransome and McOwat 1994).

We observed that spring weather conditions influenced breeding phenology, with warm temperature leading to earlier parturition dates than colder conditions. Spring 2019 was colder than any other year observed in our study, while 2021 was the warmest. This important climatic variation possibly contributed to a delayed mean parturition date of 12 days in 2019 compared to other years. As 2019 was not extremely wet nor windy, and as those factors were not significant in our analysis, we argue that the effect of spring rainfall and wind speed on parturition date is likely minor compared to temperature in a northern temperate environment. Parturition date in our study varied by 7-10 days. In Massachusetts, little brown bat pups were born within a 23-day period (Burnett and Kunz 1982). The tighter parturition period of the Domaine Joly colony

supports that higher climate-related resource availability constraints are present in colder temperate regions (Arlettaz et al. 2001; McKinnon et al. 2012). We found interannual variations to be more important than interindividual ones. Interindividual variation detected in our dataset may nonetheless be related to age or body condition (Linton and MacDonald 2017), two unknown parameters.

Night length positively affected time away from the roost. A similar relation was found for little brown bats in Yukon, where fluctuations in night length are large (Talerico 2008). As our study only included the gestation period, variability in night length was less than previous studies. Nevertheless, we still documented a positive influence of night length on time away from the roost, supporting important constraints related to light conditions. Little brown and northern long-eared bats feed primarily on small flying insects, such as *Diptera* and *Lepidoptera* (Anthony and Kunz 1977; Brack and Whitaker 2001; Clare et al. 2011; Dodd et al. 2012), for which a peak of abundance occurs around dusk. Little brown and northern long-eared bats may therefore be constrained from exploiting most of the evening peak in aerial insect abundance, presumably because earlier emergence would result in higher predation risk at higher light levels (Jones and Rydell 1994; Rydell et al. 1996).

Foraging efficiency can be reduced by low temperatures, precipitation, and strong winds (Rydell 1989; Grindal et al. 1992; Burles et al. 2009). These adverse conditions increase the thermoregulatory costs during foraging bouts and decrease prey availability for insectivorous bats (Anthony et al. 1981; Racey and Swift 1981). Moreover, increases in precipitation and wind in early spring are associated with a higher probability of torpor use with longer and deeper bouts (Besler and Broders 2019). As predicted, time away from the roost for the Domaine Joly's gestating females increased with mean temperature at night. However, time away from the roost also increased with total rainfall at night. As such, females may need more time to forage due to reduced efficiency associated with light and constant rainfall. Bats may also need to rest in an alternative roost more often or for a longer period of time if sudden downpours occur. Unlike previous studies, we did not find an effect of wind speed on time away from the roost (Blake et al. 1994; Verboom and Spoelstra 1999). Wind speed in June may not be high enough to significantly

reduce foraging efficiency at our study site. Other factors not included in this analysis may also influence time away from the roost, as the variance explained by our final model was relatively low ($r^2 = 0.26$).

Conclusion

To conclude, in addition to providing population parameters, such as apparent survival, we demonstrated that PIT tag recapture methods can detect individual pattern changes, and consequently, be used to infer individual reproductive status and parturition date of female bats using permanent maternity roosts. Effective assessment of reproductive activity requires covering all roost entrances, using reliable technologies, and ensuring the absence of alternative day-roost in the vicinity. Estimates provided by this new method will contribute to better understand populations while less fastidious for researchers and less stressful for bats than any other current methods (i.e., Racey and Swift 1981; Ransome and McOwat 1994). Through our case study at the Domaine Joly roost, located in a northern temperate region, we also underlined the influence of arrival date and spring temperature on breeding phenology, as well as the effect of night length, temperature, and rainfall on the time that gestating little brown bats and northern long-eared bats spend away from the roost. In the face of massive mortalities caused by the white-nose syndrome over the last decades, assessing reproductive success and its constraints can help biologists understand how climatic variability may jeopardize bat conservation efforts. This method can also provide detailed phenology of reproduction, and as such, improve management actions and refine research protocols by identifying optimal timing for bat surveys.

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Linking Statement

In the previous chapter, I demonstrated that in addition to providing population parameters such as survival and fidelity, PIT tag recapture methods can inform on individual reproductive parameters. This new methodology allows researchers to evaluate individual reproductive status, as well as parturition date, and ultimately to better understand populations while easier for researchers and less stressful for bats than any other current methods. My case study also demonstrated that weather conditions were major factors affecting breeding phenology and time away from the roosts. Bats must therefore carefully choose suitable maternity roosts that reduce their energetic expenditure to successfully reproduce. Bat boxes are widely used as a conservation tool in case of colony exclusions from buildings or habitat enhancement. However, the colonization rate of bat boxes is often low in urban or suburban northern temperate environments. Most studies on bat box suitability occurred in temperate and warm climates, and few researchers have adapted bat boxes to northern temperate conditions. For the last chapter, I work on the improvement of an existing conservation tool, bat boxes, to better fit reproductive female bat requirements living in northern temperate regions. Working in collaboration with engineers and architects, I use passive solar concepts to improve bat box thermodynamics and demonstrate its energetic advantage over a traditional bat box model with bioenergetic modeling.

Chapter 5 – Using mounting, orientation, and design to improve bat box thermodynamics in a northern temperate environment

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Abstract

Wildlife managers design artificial structures, such as bird houses and bat boxes, to provide alternative nesting and roosting sites that aid wildlife conservation. However, artificial structures for wildlife may not be equally efficient at all sites due to varying climate or habitat characteristics influencing thermal properties. For example, bat boxes are a popular measure employed to provide compensatory or supplementary roost sites for bats and educate the public. Yet, bat boxes are often thermally unstable or too cold to fulfill reproductive females needs in northern temperate environments. To help improve the thermodynamics of bat boxes, we tested the effect of (1) three mountings, (2) four orientations, and (3) twelve bat box designs on the internal temperature of bat boxes. We recorded temperatures in bat boxes across a climate gradient at seven sites in Quebec, Canada. Bat boxes mounted on buildings had warmer microclimates at night than those on poles and those facing east warmed sooner in the morning than those facing west or south. Our best new model based on passive solar architecture (Ncube PH1) increased the time in the optimal temperature range (22–40 °C) of targeted species by up to 13% compared to the most commonly used model (Classic 4-chamber) when mounted on a building with an east orientation (other designs presented in the Supplementary Information). Based on bioenergetic models, we estimated that bats saved up to 8% of their daily energy using the Ncube PH1 compared to the Classic 4-chamber when mounted on a building with an east orientation. We demonstrate that the use of energy-saving concepts from architecture can improve the thermal performance of bat boxes and potentially other wildlife structures as well.

Introduction

Artificial dens, roosts, or nests for wildlife can help mitigate threats to animal conservation associated with habitat loss, climate change and direct human disturbance. Artificial roosts can be used to supplement available habitat, compensate for habitat lost, provide sites used during the nesting or gestation period, protect prey from predators, or shelter species from adverse weather (Priddel and Carlile 1995; Burton et al. 1996; Chambers et al. 2002; Lausen and Barclay 2006; Kelm et al. 2008). Apart from direct conservation, artificial roosts can also facilitate the study or monitoring of wildlife populations (Priddel and Carlile 1995), as well as enhance citizen education and stimulate public involvement toward conservation (Agnelli et al. 2010). Many investigators have reported the occupancy rates of artificial roosts, but fewer have explicitly studied the underlying causes influencing the selection of some models over others (Brittingham and Williams 2000; Lambrechts et al. 2012; Rueegger 2016). To avoid artificial roosts being used despite being suboptimal for successful reproduction or becoming periodically unsuitable with worldwide increasing extreme weather events (Easterling et al. 2000; Welbergen et al. 2008; Adams 2010), it is important to understand how design, location, and mounting influence the roost microclimate, and ultimately, the preference and health of animals (Ratti and Reese 1988; Flaquer et al. 2014; Griffiths et al. 2017b; Rowland et al. 2017; Bideguren et al. 2019). For example, the same box used on sites with different environmental conditions can unequally affect the energy budget of individuals, especially at critical life cycle stages, such as migration or reproduction (Zahn 1999; Ruczyński 2006; Wilcox and Willis 2016; Griffiths et al. 2017b; Bideguren et al. 2019).

Wildlife living in temperate zones must adapt to a wide range of temperatures, which can vary considerably throughout the year. For instance, in Quebec, Canada, while the average summer high temperature ranges from 25 to 30 °C, temperatures during the night are sometimes under 0 °C. For insectivorous bats and birds, the negative effect of ambient temperature on food availability compounds this problem (Thiollay 1988). Torpor, a state of decreased physiological activity including low body temperature and metabolic rate, is one strategy used by insectivorous bats to cope with the costs of maintaining a high body temperature (Ransome 1989; O'Shea et al. 2010). Although beneficial to synchronize birth to the peak of resources (Nurul-Ain et al. 2017) or allow bats to save energy on cool days when insects are not available, entering torpor during summer may also delay female reproduction by slowing fetal development and reducing milk production (Racey 1973; Racey and Swift 1981; Wilde et al. 1999), with negative consequences on the probability of survival throughout hibernation for both mother and offspring (Beer and Richards 1956; Pagels 1975; Ransome 1989; O'Shea et al. 2010). To reduce torpor use and optimize their fitness, female little brown bats (*Myotis lucifugus*) inhabit warm roosts close to feeding sites (home range within 20–30 ha; Henry 2002). The thermoneutral zone of little brown bats is 32–37 °C (Studier et al. 1976), meaning that an individual can maintain internal temperatures with minimal metabolic regulation within this range. For bats, it is also meaningful to determine at which temperature, although outside of that ideal range, that females can manage to maintain adequate temperatures without entering torpor or suffering from detrimental effects. When roost temperature falls below 20 °C in gestation, or below 22 °C in lactation, females little brown bat use torpor 50–70% of the time (Henry 2001). On the other hand, when temperature reaches 40 °C, individuals exhibit behavioral thermoregulation, moving from upper to lower areas

of houses' attics, most likely to avoid the detrimental effects of overheating (e.g., dehydration, heat stroke, or death; Flaquer et al 2014; Henry 2001). Although not functionally equivalent to the thermoneutral zone, a temperature range of 22–40 °C is likely suitable for breeding females to remain homeothermic without altering their behavior, therefore minimizing energy expenditure while maximizing reproductive success (Zahn 1999; Henry 2001; Ruczyński 2006; Wilcox and Willis 2016).

North American insectivorous bats are important pest consumers, yet this ecological and economical services are becoming scarcer, as more than half of North American insectivorous bat species are declining due to anthropogenic pressures, exacerbated more recently by exposure to White-Nose Syndrome (WNS; Mickleburgh and al. 2002; Boyles and al. 2011). Bats have long life expectancy and reproduce slowly, which makes population recovery slow (Barclay et al. 2003). For example, the little brown bat can live up to 30 years in the wild and females give birth to only a single pup per year (Keen and Hitchcock 1980). As bats spend over half of their lives within roosts (Kunz et al. 2003), providing suitable roost sites can aid population recovery for species that are declining and known to use bat boxes (Wilcox and Willis 2016). Experiments have occurred since the 1980s to test bat boxes effectiveness as conservation measures. The bat box's microclimate, especially the internal temperature, is one of the most important selection criteria for bats (Campbell et al. 1996; Entwistle et al. 1997; Kerth et al. 2001; Lourenço and Palmeirim 2004; Webber and Willis 2018). The internal temperature is influenced by many factors, including bat box orientation, mounting, sun exposure, colour, design, construction material, and the number of occupants (Kerth et al. 2001; Lourenço and Palmeirim 2004; Griffiths et al. 2017b; Bideguren et al. 2019). Proximity to water, species-specific habitat type, proximity to an existing roost site,

time since installation and clustering of bat boxes also increase the probability of bat box colonization (Lourenço and Palmeirim 2004; Rueegger 2016). Colonization success also rises when using multiple narrow chambers that allow bats to roost side-by-side and employing an open bottom design that reduces colonization risk of non-target species (e.g., birds, small mammals, wasps) and feces accumulation (Rueegger 2016). Finally, height above ground, form and size of the bat box can also influence the colonization success but vary widely among roost types and species, with vespertilionids roosting in tree cavities and buildings most commonly using bat boxes (Mering and Chambers 2014; Rueegger 2016).

Despite attempts by conservationists to address the causes of variability listed previously, the colonization rate of bat boxes varies widely (White 2004; Mering and Chambers 2014; Mackintosh 2016; Rueegger 2016; Griffiths et al. 2017b; López-Baucells et al. 2017), often with low rates in urban or suburban northern temperate environments (e.g. occupancy rate of 1-48% in Canada, Northern United States, Poland, and England (Neilson and Fenton 1994; Brittingham and Williams 2000; White 2004; Mering and Chambers 2014, but see Michaelson et al. 2014). Most studies on bat box suitability occurred in temperate and warm climates, such as in the Central and Southern United States and the Mediterranean region, and few researchers have adapted bat boxes to northern temperate conditions, where the average temperature in June is equal or less than 20 °C (Kerth et al. 2001; Bartonicka et al. 2007; Michaelsen et al. 2014). Knowledge gained during the last few decades on passive solar architecture, used to heat or cool residential houses, could be transposed to bat boxes (and other forms of wildlife artificial roost development) to improve their thermodynamics and be suitable for a colder and larger range of climatic conditions (Sodha et al. 1986; Ralegaonkar et al. 2010; Morrissey et al. 2011). Passive solar designs take advantage of a

building's geographic location and climatic conditions, building's shape, orientation, construction materials, openings, and more to minimize energy use for heating and cooling to maintain thermal conditions that are suitable for its inhabitants (Ralegaonkar et al. 2010). These design principles reduce heating and cooling loads through energy-efficient strategies, such as using thermal masses to store the heat, which are redistributed through radiation at night (Morrissey et al. 2011).

The present study aimed to improve the thermal properties of artificial bat boxes to better meet the thermal preferences of reproductive female little brown bats living in Quebec, as estimated via the extended optimal temperature range of 22–40 °C (EOTR). First, we tested the impact of three mountings (poles, non-heated buildings, and heated buildings) and four orientations (south, east, and west for buildings and south, east, and south-east for poles) on the thermodynamics of the most commonly used bat box model, the Classic 4-chamber. We then evaluated the impact of bat box design on its thermodynamic by testing four commonly used bat box models and eight newly designed models (Table S5.1). As newly designed models were improved over the years, we only present results comparing the thermodynamics of our best newly designed model, the Ncube PH1, to the most commonly used model, the Classic 4-chamber in the main manuscript. Finally, we modelled daily energy expenditure of gestating and lactating little brown bats using these two boxes. We predicted that external factors, such as an east-facing orientation and mounting on a heated building, could improve thermal properties of bat boxes and favour time spent in the EOTR of 22–40 °C of reproductive female little brown bats. We also expected that integrating concepts of energy saving and passive heating into bat box designs would improve the thermal properties and increase the amount of time within an EOTR of 22–40 °C compared to traditional designs. Finally, we expected that thermal improvements to bat boxes, as

measured during our field experiments, should lower the modelled daily energy expenditure of reproductive female little brown bats. We expected bats to save energy especially at night and in the early morning, when reproductive females are thermally challenged as they rewarm after nightly torpor bouts.

Results

Mounting

During 122 days, from mid-May to mid-September 2017, we recorded 2928 temperature data points for each of the 18 Classic 4-chamber bat boxes, which were either mounted on poles (n=6), non-heated buildings (n=6), or heated buildings (n=6) at two sites in Quebec, Canada. Based on a generalized additive mixed model, we estimated that average daily temperatures of Classic bat boxes varied among mounting types, sites, and with time of day (Fig. 5.1, Tables S5.2, and S5.3). At night, the Classic bat boxes average temperature was between 1–1.5 °C warmer when mounted on heated or non-heated buildings than poles while the opposite occurred during the day (Fig. 5.1). The percentage of time below, between, and above the EOTR were relatively similar among mounting type. Temperature varied from 6.5–44 °C in Classic bat boxes on poles, from 6.5–48.5 °C in Classic bat boxes on non-heated buildings, and from 7–49 °C in Classic bat boxes on heated buildings. The minimal and maximal temperature of Classic bat boxes were generally similar among mountings at the same site, varying from 0.5–5 °C (Table 5.1).

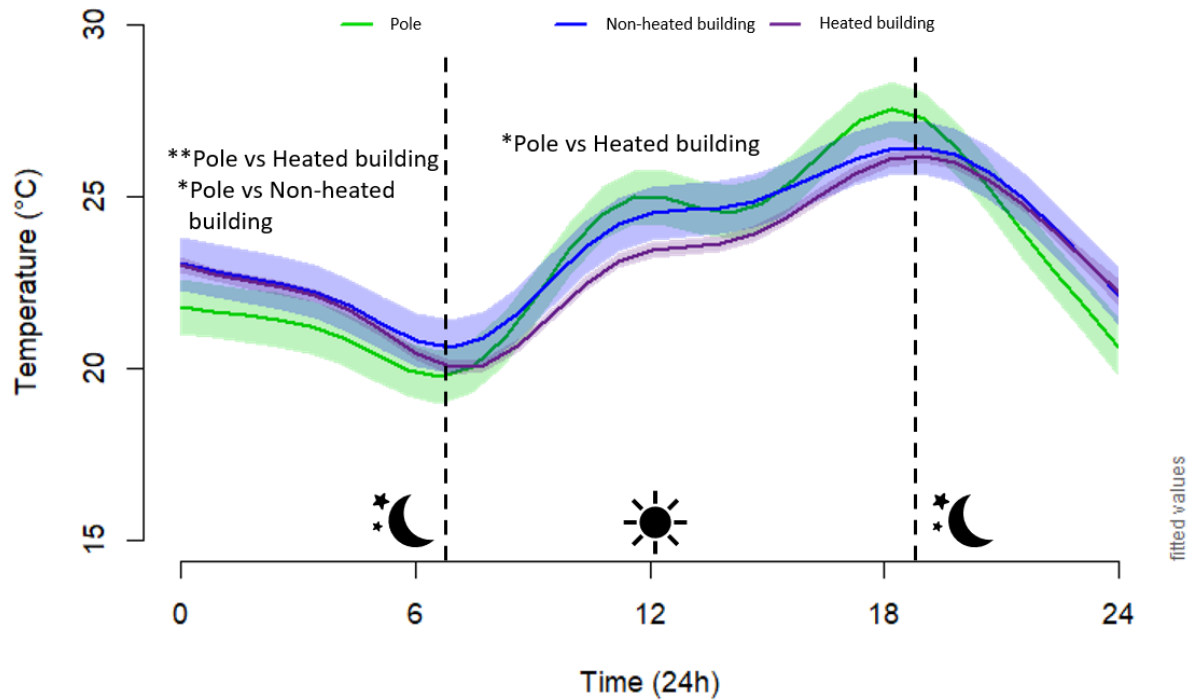


Figure 5.1. Estimated hourly patterns for the different Classic bat box mountings in Quebec, in 2017 (pole: $n = 6$, non-heated building: $n = 6$, and heated building: $n = 6$). The estimated values are based on a generalized additive mixed model, accounting for time, date, orientation, external temperature, site, and individual bat box identity. Values of fixed factors have been set to: date = July 6, orientation = east, external temperature = 18 °C. The asterisks (*) represent significant differences between structures during the day and night. P = pole and B = building.

Orientation

During 122 days, from mid-May to mid-September 2017, we recorded 2928 temperature data points for each of the 18 Classic bat boxes, which were either facing east ($n=4$), south ($n=4$), and west ($n=4$) on buildings, or facing east ($n=2$), south ($n=2$) and south-east ($n=2$) on poles, at two sites in Quebec, Canada. Based on a generalized additive mixed model, we estimated that average daily temperatures of Classic bat boxes varied among orientations, mounting types, sites, and with time of day (Fig. 5.2, Tables S5.4, and S5.5). On buildings, west-facing Classic bat boxes were significantly warmer in the early evening and colder in the early morning than those facing east.

During the day, temperatures in east-facing Classic bat boxes were significantly different than those facing south or west, being warmer especially in the morning (Fig. 5.2). On poles, the only significant difference was at mid day, when south-facing Classic boxes were warmer than those facing east. The percentage of time below, between, and above the EOTR varied among orientations. The highest percentage of time in between the EOTR occurred for Classic bat boxes with an easterly orientation, while the highest percentage of time above the EOTR occurred for bat boxes with an east and west orientation at the warmer site. Temperature varied from 6.5–49 °C in Classic bat boxes facing east, from 6.5–44 °C in Classic bat boxes facing south-east, 6.5–41 °C in Classic bat boxes facing south, and from 6.5–49 °C in Classic bat boxes facing west. The minimal and maximal temperature of Classic bat boxes were generally similar, among orientations at the same site, varying from 0.5–5 °C (Table 5.1).

Table 5.1. Percentage of time below, between, and above the extended optimal temperature range of 22–40 °C, and minimal and maximal temperature inside and outside of Classic bat boxes from mid-May to mid-September 2017 at intermediate and warmer sites in Quebec, Canada presented per mountings and orientations.

Orientation	Measures	Intermediate 1 site			Warmer 2 site		
		Heated building	Non-heated building	Pole	Heated building	Non-heated building	Pole
East	Time below 22 °C (%)	59	54	53	50	47	55
	Time between 22–40 °C (%)	41	46	47	47	52	45
	Time above 40 °C (%)	0	0	0	3	1	0
	T _{min}	7	7.5	7	8	7.5	6.5
	T _{max}	38	38.5	39	49	45	43.5
South-East	Time below 22 °C (%)			59			54
	Time between 22–40 °C (%)			41			45
	Time above 40 °C (%)			0			1
	T _{min}			6.5			7
	T _{max}			35			44
South	Time below 22 °C (%)	62	58	55	47	53	55
	Time between 22–40 °C (%)	38	42	45	53	47	45
	Time above 40 °C (%)	0	0	0	0	0	0
	T _{min}	7	7.5	7	9.5	8	6.5
	T _{max}	40	38	38	40	41	41
West	Time below 22 °C (%)	61	59		52	52	
	Time between 22–40 °C (%)	39	40		45	46	
	Time above 40 °C (%)	0	1		3	2	
	T _{min}	7	6.5		8.5	7.5	
	T _{max}	39	41.5		49	48.5	

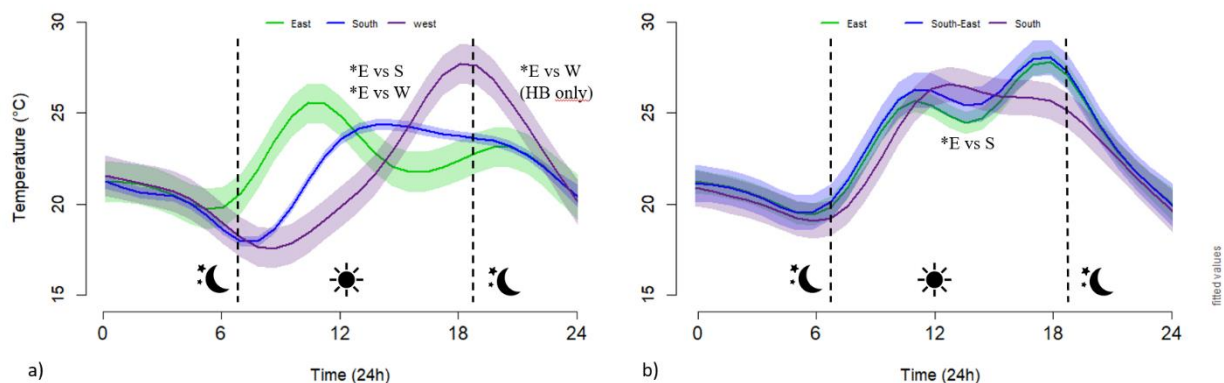


Figure 5.2. Estimated hourly patterns for the different bat box orientations in Quebec, in 2017. Bat boxes facing east ($n = 4$), south ($n = 4$), and west ($n = 4$) on buildings (a), and facing east ($n = 2$), south ($n = 2$) and south-east ($n = 2$) on poles (b). The estimated values are based on a generalized additive mixed model, accounting for time, date, external temperature, structure, site, and individual bat box identity. Values of fixed factors have been set to: date = July 6, external temperature = 18 °C. The asterisks (*) represent significant differences between orientations during the day and night. E = east, S = south, W = west, and SE = south-east. HB = heated building.

Design

From mid-May to mid-September 2016-2019, we recorded 2928 temperature data points per year and per bat box at seven sites in Quebec, Canada. We tested in total 12 bat box designs mounted on poles and buildings facing east, but only present results comparing the thermodynamics of our best newly designed model, the Ncube PH1, which included a main and a lower chamber ($n=8$), to the Classic 4-chamber ($n=11$). Based on a generalized additive mixed model, we estimated that average daily temperatures varied between the Classic and the main chamber of the Ncube PH1 model, (Fig. 5.3, Tables S5.6, and S5.7, see Fig. S5.1 for all models). Temperatures in the Classic and Ncube PH1 were significantly warmer than the outside temperature during both night and day. The main chamber of the Ncube PH1 was significantly warmer than the Classic during both night

and day, being on average 3.5 ± 1.5 °C warmer during the night, 3 ± 1.5 °C warmer in afternoon, and similar in the morning from 700 to 1100.

Bat boxes were installed at seven sites separated into cooler ($n=2$, $T_{\bar{x}}$ in June= 11 °C), intermediate ($n=3$, $T_{\bar{x}}$ in June= 16 °C), and warmer sites ($n=2$, $T_{\bar{x}}$ in June= 19 °C). For comparative purposes, we present the percentage of time below, in between, and above the EOTR for bat boxes on buildings at intermediate sites only; results at warmer and cooler sites being similar with a higher and lower mean temperature respectively (Table 5.2, see Fig. S5.2 for all models). The Classic was in the EOTR 46% of the time and above the EOTR 2% of the time. Considering the bats can use the lower chamber when above 40 °C in the main chamber, the Ncube PH1 was in the EOTR 58% of the time and never above the EOTR, therefore increasing by 12% the amount of time in the EOTR compared to the Classic.

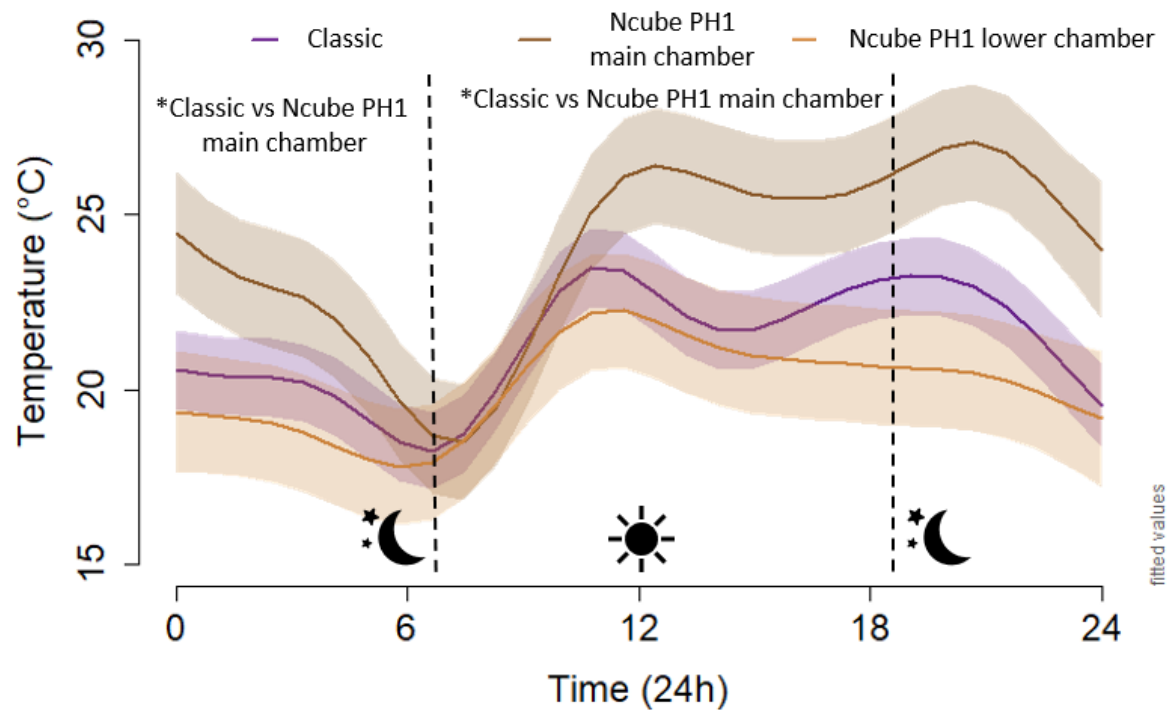


Figure 5.3. Estimated hourly patterns for the Classic ($n = 11$) and the Ncube PH1 models (main and lower chambers, $n = 8$). The estimated values are based on a generalized additive mixed model accounting for time, week, year, structure, external temperature, site, and individual bat box identity. Values of fixed factors have been set to: week = first half of July, year = 2019, structure = building, external temperature = 18 °C. The asterisks (*) represent significant differences between models during the day and night.

Table 5.2. Percentage of time below, between, and above the extended optimal temperature range of 22–40 °C, and minimal and maximal temperature in Classic bat boxes, Ncube PH1 bat boxes, and outside (external temperature) from mid-May to mid-September 2019 in Quebec, presented per climatic and mounting types.

Models	Measures	Building			Pole		
		Cooler	Intermediate	Warmer	Cooler	Intermediate	Warmer
Classic	Time below 22 °C (%)	72	52	36	79	53	45
	Time between 22–40 °C (%)	28	46	60	21	46	51
	Time above 40 °C (%)	0	2	4	0	1	4
	T _{min}	-4.5	2	7	-1	2	5
	T _{max}	45.5	48	55	31	43.5	47.5
Ncube PH1 : main chamber	Time below 22 °C (%)	59	42	32	51	47	42
	Time between 22–40 °C (%)	39	54	58	49	53	57
	Time above 40 °C (%)	2	4	10	0	0	1
	T _{min}	-3	1.5	7	0	4.5	6.5
	T _{max}	47	49	53	34.5	38	47
Ncube PH1 : lower chamber	Time below 22 °C (%)	77	64	51	79	61	50
	Time between 22–40 °C (%)	23	36	49	21	39	50
	Time above 40 °C (%)	0	0	0	0	0	0
	T _{min}	-4.5	2.5	6	0	4	7
	T _{max}	38.5	40	41	31.5	43.5	43.5
External	Time below 22 °C (%)	92	74	63	92	74	63
	Time between 22–40 °C (%)	8	26	37	8	26	37
	Time above 40 °C (%)	0	0	0	0	0	0
	T _{min}	-5	-2	5	-3	-2	5
	T _{max}	29.5	31.5	42.5	28.5	31.5	42.5

The minimal temperature of the Classic and the Ncube PH1 were similar (2 °C and 1.5 °C respectively) but the maximal temperature differed given the use of the lower chamber of the Ncube PH1 (48 °C and 40 °C respectively; Table 5.2). From mid-May to mid-September 2019, daily minimum temperatures recorded in the Classic were slightly warmer than external temperatures, but slightly colder than the Ncube PH1 main chamber at both cooler 1 and warmer 2 sites (Fig. 5.4). Daily maximum temperatures in the Classic were warmer than external temperatures, similar to the Ncube PH1 lower chamber, and colder than the Ncube PH1 main chamber at the site cooler 1. At the site warmer 2, daily maximum temperatures in the Classic were warmer than the Ncube PH1 lower chamber, but similar to the Ncube PH1 main chamber, both overheating frequently, with 50 and 54 days with daily maximum temperatures over 40 °C

respectively (Fig. 5.4). Overheating events occurred only once at warmer sites for the Ncube PH1 lower chamber on buildings, which spent <1% of the time above 40 °C (one two hours long overheating bout; Table 5.2). Overheating events occurred at warmer and intermediate sites for the Classic model, which spent 4% of the time above 40 °C at warmer sites (52 1–6 hours long overheating bouts in 2019) and 2% at intermediate sites (12 1–6 hours long overheating bouts in 2019).

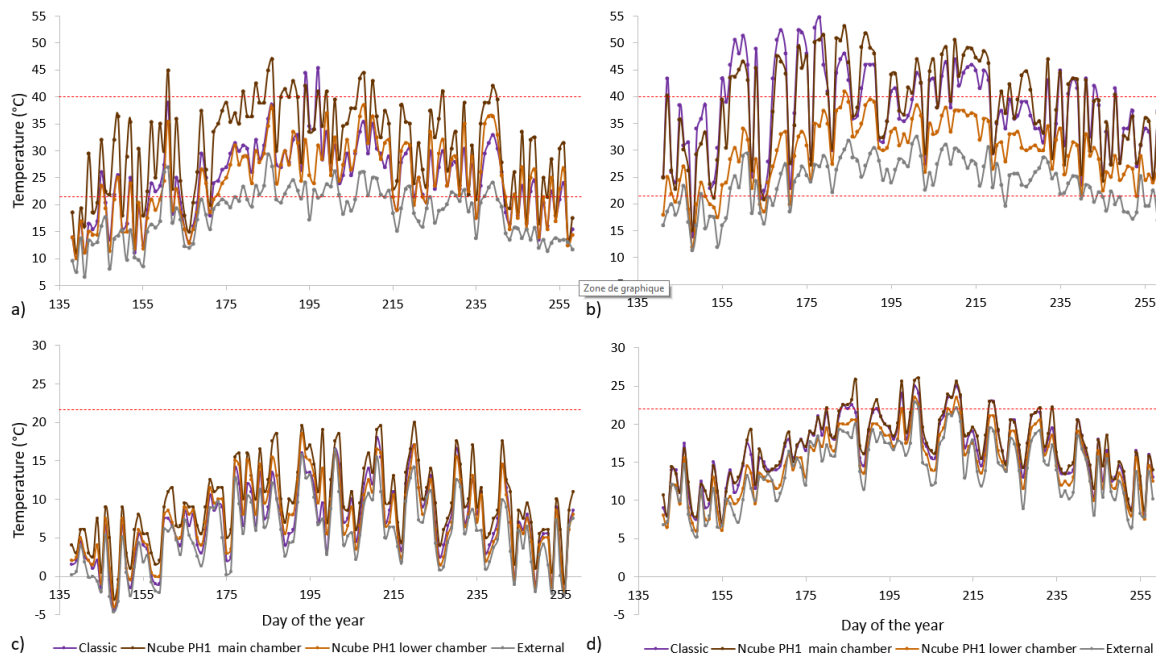


Figure 5.4. Daily minimum and maximum temperatures in the Classic and the Ncube PH1 bat boxes on buildings and the external temperature in 2019 at cooler and warmer sites, in Quebec. (a) daily maximum temperatures at the cooler site, (b) daily maximum temperatures at the warmer site, (c) daily minimum temperatures at the cooler site, (d) daily minimum temperatures at the warmer site. The red dotted lines represent the extended optimal temperature range of 22–40 °C.

Bioenergetic modeling

We estimated average daily thermoregulatory energy expenditures using bioenergetic modeling for a female little brown bat during the gestation and lactation period based on internal temperatures recorded in 2019 in a Classic 4-chamber versus a Ncube PH1 bat box on building at cooler, intermediate, and warmer sites in Quebec, Canada. We selected the internal temperature of the Ncube PH1 main chamber when equal or lower than 40 °C and the lower chamber when above 40 °C. The internal temperature of the Classic was based on the middle chamber (chamber 3 from the front) at all times (see the methods for more details). Predicted average daily energy expenditure was reduced by 3–8% during gestation in the Ncube PH1 compared to the Classic bat box model (Fig. 5.5). During lactation, energy savings varied between 5–7%. Energy saving differences were higher in cooler sites compared to warmer sites but were significant at all sites and reproductive periods, except during gestation at warmer sites.

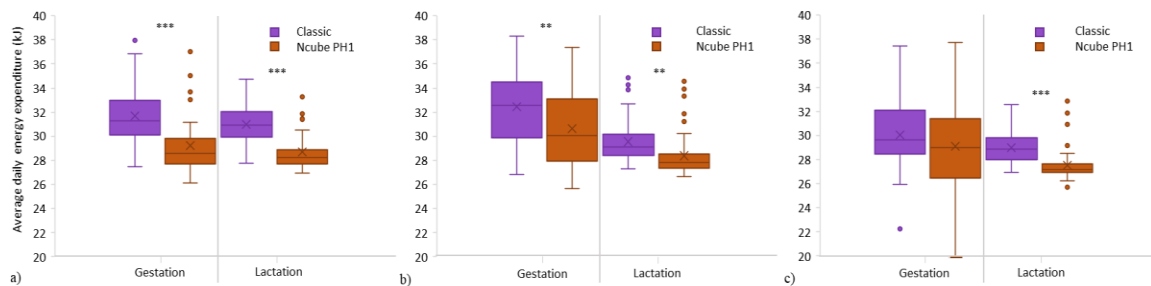


Figure 5.5. Average daily thermoregulatory energy expenditure (in kilojoules) from bioenergetic modeling for a female bat during the gestation and lactation period in a Classic versus Ncube PH1 bat box on building at: a) cooler, b) intermediate, and c) warmer sites in Quebec, in 2019.

Discussion

To be a valuable conservation measure, artificial roosts must be adapted to the species' needs and location (Griffiths et al. 2017a). At our study sites, an easterly orientation and mounting on a building improved the thermodynamics of bat boxes: it increased temperature at night and in the morning and provided a better thermal stability, likely favouring the reproductive success of little brown bats. Although it is impossible to always be in the EOTR with concepts of passive heating and heat conservation in a northern temperate environment, those concepts improved the thermodynamics of our newly designed Ncube PH1 model over the Classic model by increasing the amount of time within EOTR by 7–13% and remaining on average 4.5 °C warmer at night. Finally, we confirmed that thermal improvements of bat boxes could minimize the energetic costs and decrease daily energy expenditure for reproductive females little brown bats who occupy them in a northern temperature environment. Average daily energy expenditure differences were greater during lactation than gestation and at cooler than warmer sites, with an average saving up to 8%.

Mounting

Although well covered for birds, few studies have evaluated the effect of mountings on roost use for bats (Mering and Chambers 2014; Arias et al. 2020). A review by Mering and Chambers 2014 stated that bat boxes are placed on a variety of structures, most commonly on trees, poles, and buildings, but that bat boxes had highest occupancy rates or are most frequently used when mounted on buildings and poles than on trees (Kiser 2004; White 2004; Tuttle et al. 2005; Flaquer et al. 2006; Long et al. 2006). However, none of these studies evaluated how mounting type influences the thermodynamics of the box. On our study sites, mounting on buildings, heated or

not, resulted in warmer bat box internal temperatures than on poles during the night with the reverse during the day. The temperature variance was slightly higher for bat boxes on poles than those on buildings. This can be explained by a longer solar exposure (from sunrise to sunset) for bat boxes installed on poles than buildings, as the latter were shaded by the building walls for part of the day. Buildings protect bat boxes from the wind coming from behind and partially from the wind coming from the sides. Buildings also enhance heat retention, providing more stable conditions than those on poles in our study area. We detected no difference between heated and unheated buildings, day or night. The non-heated buildings tested in our study were brick or insulated buildings, so perhaps if we had tested non-insulated buildings, that have a lower heat retention capacity, such as old barns or sheds, we would have obtained different results.

Orientation

Several studies report that the orientation of bird and bat boxes influences occupancy rates, with south or east-facing boxes being favoured in a northern temperate environment (Dillingham et al. 2003; Ardia et al. 2006; Long et al. 2006; Horncastle et al. 2008). Few investigators have explicitly examined whether nest orientation preference appeared correlated with bird nest temperatures (Hooge et al. 1999; Wiebe 2001; Ardia et al. 2006). For little brown bats established maternity colonies in artificial roosts that received ≥ 7 hours of sunlight in Pennsylvania (Brittingham and Williams 2000). In Australia, the effect of colour on box temperatures was influenced by a range of factors, including orientation. They found that the box maximum daytime temperature, and the difference between the box and the ambient maximum daytime temperature, were most pronounced for bat boxes facing north and west, the orientations that receive the greatest amount of solar radiation during the hottest period of the day (Griffiths et al. 2017b) Also in Australia, a

study reporting bat box orientation preferences by Gould's wattled bats (*Chalinolobus gouldii*) showed that orientation influenced box temperature, with west-facing boxes being coolest (Godinho et al. 2020).

In our study, the effect of bat box orientation on internal temperature depended on the mounting type, the influence being stronger on buildings than on poles. On buildings, bat boxes facing east warmed sooner in early morning. Moreover, an easterly orientation enhanced the time in the optimal temperature by up to 6% compared to a westerly orientation at the intermediate site. Estimated temperatures for south-facing boxes on buildings were surprisingly lower or equal to those estimated for east or west-facing boxes. Our south-facing boxes should have benefited from longer solar exposure during the warmest period of the day and should have recorded higher temperatures than bat boxes facing east or west; others did find that black-coloured and south-facing boxes recorded the highest temperatures (Bideguren et al. 2019). We suspect that roof eaves facing south and north created shade for a significant amount of time. Orientations tested in this study had little influence on bat box temperature when mounted on poles without differences in temperature increase in the mornings. At night, we suspect insufficient heat retention on poles, while during the day, one side is always fully exposed to the sun. We argue that an east-facing orientation is generally preferable in a northern temperate environment as in Quebec. An east-facing orientation, especially on buildings, maximizes the time in the EOTR, while also warming up sooner in the cooler early mornings.

Design

Design is one of the most important characteristics determining attraction of bats or birds to structures, and design refinement improves the frequency use of nest and bat boxes (Summers and Taylor 1996; Goldingay et al. 2015; Rueegger 2016). Review of Mering and Chambers 2014 identified more than 48 type of bat boxes varying in their materials, size, and shape. However, the authors noted that only a few studies explain how structural characteristics of bat roosts influence internal temperatures. In Portugal, temperatures of artificial roosts painted black (vs. white or gray) were most comparable to building roosts and had the highest use by (Lourenço and Palmeirim 2004). In the USA, the “rocket” box, which was the largest roost, remained within the critical temperature thresholds the greatest proportion of time (Hoeh et al. 2018). In Australia, Rueegger et al. 2020 found that bat box colour, chamber sequence, construction materials, and vents influenced internal temperatures. In Canada, bats preferentially selected heated over non-heated bat boxes (Wilcox and Willis 2016).

Out of the 12 models we tested, including traditional and newly designed models, the Ncube PH1, improved thermal performance both on poles and buildings by increasing time in the EOTR and being warmer at night without overheating during the day. Such improved thermal performance is likely attributed to: 1) a passive heating zone that improves heat gain and retention of the bat box, 2) a thick insulation buffering against temperature fluctuations, 3) a reduced chicane entrance that decreases air exchange and heat loss, and 4) an additional cool chamber at the bottom, where bats can easily and safely go when the main chamber overheats. Still, at warmer sites, the Ncube PH1 on buildings spent a few hours above 40 °C on sunny days, when external temperatures exceeded 28 °C around noon. We suggest three different ways to reduce overheating of the Ncube

PH1 at sites similar or warmer than our warmer sites depending on the specific environmental conditions of the site: 1) a modification of the passive heating zone, from fully juxtaposed with the main chamber to a halfway position to reduce heat diffusion, 2) a wider entrance to increase the air flow and heat loss, or 3) a lighter colour (green, brown, or grey) that minimises heat absorption (Griffiths et al. 2017b). Black has low reflectance and is commonly acknowledged as the best colour to use in northern regions (where the average high temperature in July is $\leq 29^{\circ}\text{C}$) to increase the internal temperature (Campbell et al. 2010). However, black also increases the number of overheating events, even in temperate climates (Bideguren et al. 2019). Therefore, we advise local testing to find what colour best fits local conditions.

Four criteria guided the elaboration of the newly designed models: 1) thermal preferences and requirements of little brown bats minimizing torpor use: EOTR of $22\text{--}40^{\circ}\text{C}$ (Pagels 1975), 2) a passive heating design including a passing heating zone, a reduced opening, and insulation, 3) a relatively light weight, and 4) a low cost. Thanks to a transdisciplinary approach integrating knowledge related to biology/ecology (bat scientist) and material properties and thermodynamics (architects and engineers), we translated energy saving concepts from human eco-housing to bat boxes and created a versatile passive heating design well adapted to a wide range of northern temperate environments. The Ncube PH1 can easily be installed by two people (one person to hold the box and one person to fix the box in place) with a screwdriver and screws on a building or with U-bolts with plates and hex nuts on a pole. However, while prioritizing the optimization of the thermodynamics of the bat box, we failed to keep a low cost. Its price of ~\$800 CAD (including carpenter time fees) is around four times higher than a Classic 4-chamber and almost twice the

price of a regular rocket bat box from local retailers. We still consider that such investment could be justifiable when applied as a compensation measure to roost exclusion or habitat destruction.

Bioenergetic modeling

Roosts have the potential to influence energy expenditure considerably (BCI 2021) through thermoregulation and/or passive rewarming from daily torpor (Geiser and Drury 2003; Turbill et al. 2003). This is especially true for reproductive females that select warm roosts and use shorter and shallower torpor bouts compared to non-reproductive individuals to optimise pup growth during gestation and milk production during lactation (Brittingham and Williams 2000; Kerth et al. 2001; Dzal and Brigham 2013). Patterns of torpor use suggest that bats in buildings save more energy than rock-roosting individuals by roosting in the warmer microenvironments of buildings (Lausen and Barclay 2006). Energetic modeling assuming that bats re-warm from torpor passively as the internal temperature of the heated bat box rises to 32 °C in the morning, demonstrates major energy savings compared to active rewarming in regular roosts (Wilcox and Willis 2016). Although the warmer temperatures recorded in the morning in the Ncube PH1 did not allow passive rewarming, a warmer temperature at night and a quicker increase in the morning most likely results in shallower and less-frequent use of torpor and lower energy costs of rewarming after torpor bouts. Those energetic advantages should therefore favor earlier births and faster juvenile growth, which should increase the fitness of both mother and pup (Speakman et al. 2003; Lausen and Barclay 2006).

Female bats using the Ncube PH1 2019 rather than the Classic model would save between 3.2–7.8%, with the highest saving at cooler sites, underlining the importance of efficient bat boxes

adapted to a northern temperate environment. The Ncube PH1 would be likely beneficial in particular north of the 50 °N, where suitable natural roost availability is scarce and basic bat boxes, similar to the Classic model, are frequently used as maternity colonies. Some parameters in our bioenergetic models, such as time in torpor and foraging flight time, are flexible and depend on weather, sex and reproductive status (Besler et al. 2019). Furthermore, the number of bats in a box will also influence individual energy expenditure (Willis and Brigham 2007). Nonetheless, our model estimates reflect the bioenergetic advantages of our newly designed model and fit those reported in the literature for little brown bats (Kurta et al. 1989; Wilcox and Willis 2016).

Conclusion

We recommend erecting bat boxes facing east and mounted on buildings when safe cohabitation with humans is possible. We also advise bat box designs that include insulation and a passive heating zone similar to the Ncube PH1 that buffers against suboptimal temperatures and increases the time in the EOTR (see Figs. S5.3-S5.6 for the original design plan and batwatch.ca for the improved 2020 design plan). Insulated models could retain heat generated through social thermoregulation better than uninsulated designs, which should also be considered in future studies. Moreover, a cool open chamber at the bottom is a good addition to any bat box model in case of overheating events. We tested the Ncube PH1 model across a range of temperatures in Quebec and demonstrated its thermal advantage for female little brown bats in a northern temperate environment. Despite the better thermal suitability of the Ncube PH1 compared to the Classic model, offering several alternatives to bats is still recommended. There is evidence that box deployment in clusters is important to accommodate individuals of different sexes and

reproductive status throughout the whole season and to a larger range of meteorological conditions (Boye and Dietz 2005; Willis and Brigham 2007; Fukui et al. 2010; Ruegger 2016). A cluster of different bat box models and/or orientations also provide opportunities for roost switching (Lewis 1995) and social interactions (Kerth and Konig 1999). Little brown bats roosting in natural habitat, have also been observed to prefer forest stands surrounded by a large number of snags allowing roost switching (Fabianek et al. 2015).

Our Ncube PH1 better meets the little brown bat (federally listed as Endangered in Canada due to White-Nose Syndrome) requirements than most commonly used bat box models, such as the Classic 4-chamber, and can serve as an alternative roost for bats excluded from dwellings or to enhance high quality habitats where roost availability is limited (Rowland et al. 2017). Nonetheless, assuring an abundance of natural roosting sites remains desirable for bat conservation, especially for tree-roosting species. When installing bat boxes, we encourage local testing and careful consideration of the habitat, availability of suitable roosts in the environment, species present in the local bat assemblage, target species, structure, and orientation, although the first two parameters are difficult to measure. Since this study showed the theoretical value of our newly designed bat box, the next step is to test its colonization success and its functionality for bats on a larger scale. Artificial structure optimization using human architecture concepts shows a great potential to improve conservation tools for other taxa like birds or other hollow-dependent mammals.

Materials and methods

Mounting experiment

For our first experiment, we tested the effect of mountings on bat box thermodynamics with 18 bat boxes mounted on 1) metal poles (diameter = 6 cm; n = 6), 2) non-heated buildings (n = 6), and 3) heated buildings (n = 6; Fig. 5.6) at two sites in Quebec, Canada (Fig. 5.7). We used the most common bat box model, the Classic 4-chamber (<https://www.batcon.org/wp-content/uploads/2020/09/4-Chamber-Nursery-House-Plans.pdf>; paint in black with no vents to be adapted to a northern temperate environment). We recorded bat box internal temperatures (T_{int}) every hour using iButtons (<https://www.ibuttonlink.com/products/ds1921g>) from mid-May to mid-September 2017.

Orientation experiment

For our second experiment, we tested the effect of orientations on bat box thermodynamics at the same two sites, using again 18 bat boxes facing east (n=4), south (n=4), and west (n=4) on buildings, and facing east (n=2), south (n=2) and south-east (n=2) on poles. We installed the same commonly used Classic 4-chamber bat box and recorded internal temperatures every hour (T_{int}), from mid-May to mid-September 2017, using iButtons.

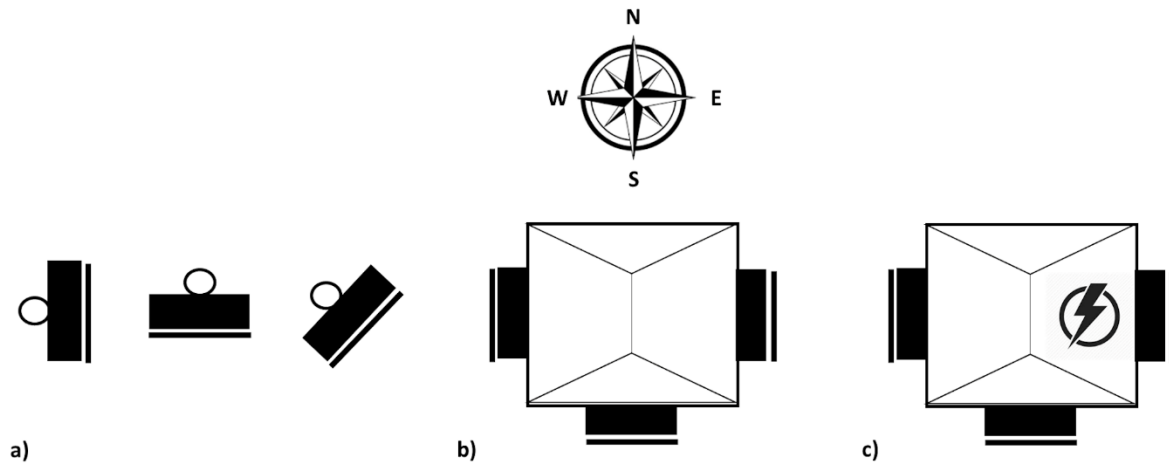


Figure 5.6. Schematic view of the experimental design for the orientation and mounting as tested for bat boxes on two sites in Quebec, in 2017 on a) poles, b) non-heated buildings and c) heated buildings.

Design experiment

Our third experiment aimed to test the effect of design on bat box thermodynamics using 12 models of bat boxes, mounted facing east on poles and buildings at seven sites (Fig. 5.6). As Quebec mean summer temperatures can vary up to 26°C from south to north, we separated sites into cooler ($n=2$, $T_{\bar{x}} \text{ in June} = 11^\circ\text{C}$), intermediate ($n=3$, $T_{\bar{x}} \text{ in June} = 16^\circ\text{C}$), and warmer sites ($n=2$, $T_{\bar{x}} \text{ in June} = 19^\circ\text{C}$). The two warmer sites and two intermediate sites had pole and building mountings, the other sites had either pole or building mountings. We recorded bat box internal temperatures (T_{int}) every hour using iButtons from mid-May to mid-September 2016-2019. The 12 bat box models tested included a Classic 4-chamber, an European fibrocement 1-chamber model, two Insulated rocket models (with and without a solar heated system), and eight new models based on passive solar concepts (Table S5.1). Four criteria guided the elaboration of the newly designed models: 1) thermal preferences and requirements of the endangered little brown bat minimizing torpor use:

EOTR of 22–40 °C (Henry 2010), 2) a passive heating design including a passing heating zone, a reduced opening, and insulation, 3) a relatively light weight, and 4) a low cost (less than \$500 CAD). The last two criteria were selected to facilitate large-scale implementation of an improved model assuming its success at the first criterion. We painted all bat boxes were black to maximise solar radiation absorbance (Griffiths et al. 2017b). The newly designed bat box was conceptualized based on thermodynamics principles used in solar passive architecture, such as heat transfer (radiation, conduction, and convection), thermal load, and heat conservation (insulation and reduced openings that reduce heat loss). We present results on temperatures recorded in the newly designed model, the Ncube PH1 tested in 2019 ($n_{\text{classic}}=11$, $n_{\text{ncube PH1}}=8$), comparing them to temperatures recorded in the most commonly used model, the Classic 4-chamber. Results from the 10 other models are presented in the Supplementary Information 5 only.

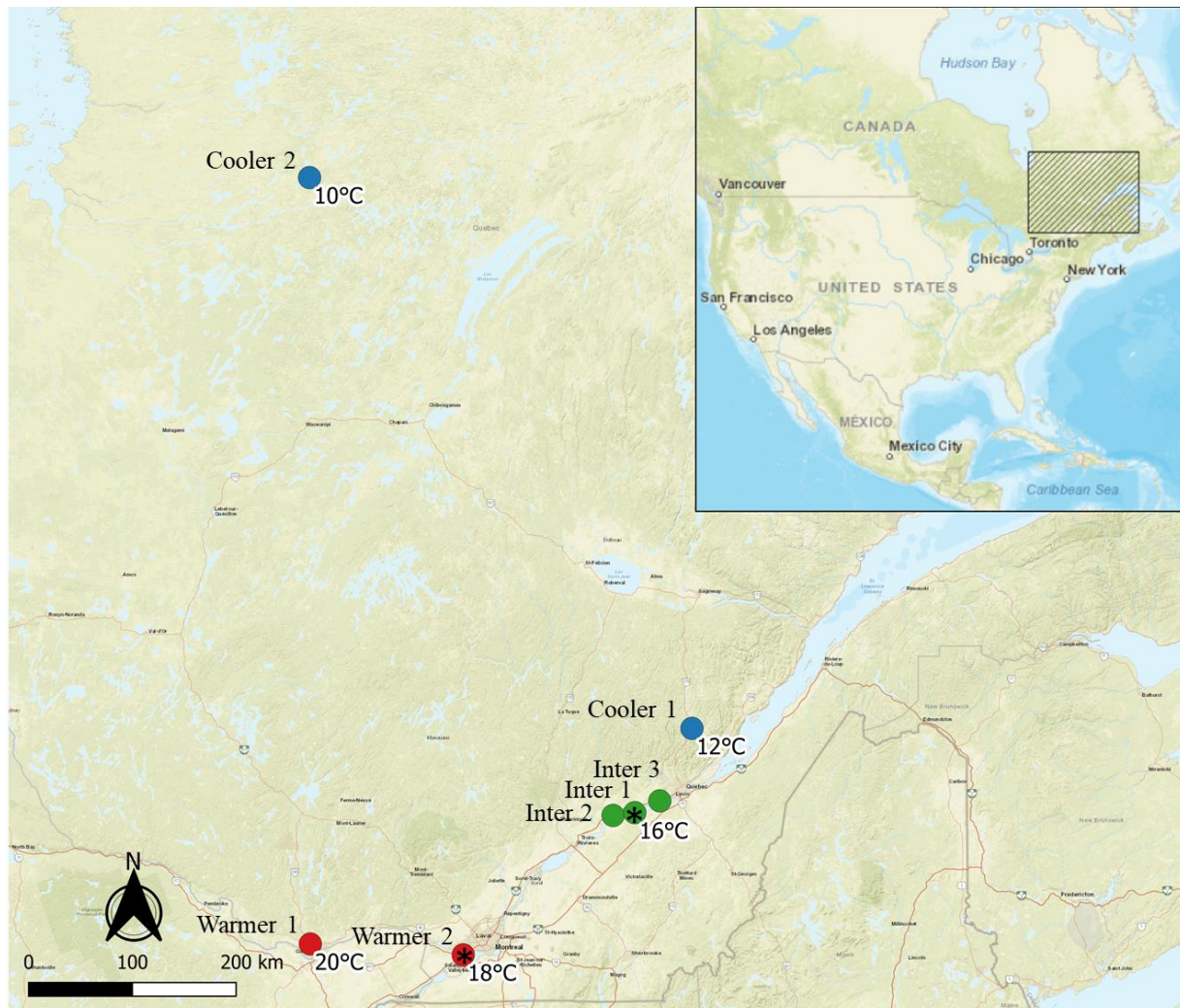


Figure 5.7. Location of the bat box installation sites at cooler (blue), intermediate (green) and warmer (red) sites in Quebec, Canada, from 2016 to 2019 with mean temperature in June. The Montmorency forest is considered a colder site due to its high elevation of 750 m. Structure and orientation tests occurred at sites represented by a star. Map derived from ESRI Standard <https://server.arcgisonline.com>, modified with QGIS 3.4.4. software (www.qgis.org).

For all the experiments, the area around bat box sites was free of trees or any object causing shade, although roof fringes may have caused shade in the second experiment for the southern orientation. We installed bat boxes at the same heights (3–4 m high). We used external temperatures (T_{ext}) from either an *in situ* meteorological station (<https://www.davisinstruments.com/product/vantage-vue-wireless-weather-station/>) or the nearest

Environment Canada station (maximum distance = 1 km; see Table S5.8 for the name and location of the station used). As bats tend to roost at the top of bat boxes, iButtons were placed in the top quarter of each bat box (one in the third chambers from the front in the Classic and two in the Ncube PH1 in the main and lower chambers). The vertical temperature gradient in bat boxes was only verified in the Rocket PH1, the longest model, expected to be more susceptible to vertical temperature gradients. Temperature varied (up to 7.5 °C) between the upper and lower part of the rocket box, but this variance decreased as the internal temperature increased. At high temperatures, this variance was often near zero and highest vertical temperature differences occurred mostly during the night, between 2000 and 0000 (Fig. S5.7). We also recorded temperature variation among the four chambers of the Classic model in 2017 at two sites on poles. The average hourly temperature in the four chambers did not vary during the night but varied during the day, with the second and third chambers being colder than the first and fourth chambers (Fig. S5.8).

Bat boxes were monitored at least every month to verify the absence of bats in boxes (monitoring; guano, bat sighting or hearing) to ensure a colony did not occupy bat box permanently, which would have affected the internal temperatures of bat boxes. During the four years of monitoring, no colony inhabited the bat boxes and we only detected two individuals in two different bat boxes. The occasional presence of individual bats would not change the overall internal temperature profiles of the bat boxes as those individuals were likely males or non-reproductive females that often use torpor to save energy (Hamilton and Barclay 1994; Grinevitch et al. 1995; Dietz and Kalko 2006). Furthermore, we carefully investigated the data for signatures of anomalous increases in temperature indicative of bat presence which we did not find.

Statistical analysis

To compare non-linear daily temperature profiles and evaluate differences among treatments of each experiment (orientations, mountings, and designs), we used general additive mixed models (GAMMs). We modeled internal temperature differences among orientations for Classic models by including bat box T_{int} facing south, south-east, east, and west as response variables, orientation, time, date, T_{ext} , and structure as fixed effects, and location and bat box identity as random factors. We modeled internal temperature differences among structures for Classic models by including bat box T_{int} mounted on poles, heated, and non-heated buildings as response variables, structure, time, date, T_{ext} , and orientation as fixed effects, and location and bat box identity as random factors. We evaluated differences in internal temperature between the Classic and the Ncube PH1 models by including bat box T_{int} of the Classic and the Ncube PH1 as a response variable, time, model, week, T_{ext} , and structure as fixed effects, and location and bat box identity as random factors (see Table S5.9 for statistical model descriptions).

Because of the high daily temperature variance among sites and years in the design dataset, we used mean hourly temperatures over 14 days instead of every day to reduce confidence intervals, which helped to detect differences among bat box models. We equally divided time between day (700–1800) and night (1800–700), which allows a finer investigation of bat box thermal patterns with and without sun exposure (presumably warmer during the day and colder during the night). This division also roughly corresponded to periods when females are more likely to be in the roost (day) and partly away (night). We used *mcgv* package in R for all analysis and used a significance threshold of ≤ 0.05 for all tests. To show the temperature variation among bat

boxes, we also provided the percentage of time below, between and above EOTR, and minimal and maximal internal temperatures ($T_{\text{int-min}}$, and $T_{\text{int-max}}$) for each experiment.

Bioenergetic modeling

Reproductive female little brown bats select roosts that reduce energy expenditure, increase time spent in normothermia and facilitate torpor in the early morning (Barclay 1982; Dzal and Brigham 2013). We used bioenergetic models to predict energy expenditure of the little brown bat in Classic and Ncube PH1 models, based on their respective T_{int} and T_{ext} recorded at cooler, intermediate, and warmer sites. As shown in other studies (Henry 2001; Lourenço and Palmeirim 2004), we assumed that once temperatures reached 40 °C or higher, bats would exhibit behavioral thermoregulation and systematically go down to select a cooler space to avoid detrimental effects of overheating. Therefore, we selected the T_{int} of the Ncube PH1 main chamber when equal or lower than 40 °C and the lower chamber when above 40 °C. T_{int} of the Classic was based on the middle chamber (chamber 3 from the front) at all times since external chambers acted as insulation, reducing overheating during the day while similar to the other chamber temperatures during at night (Fig. S5.8).

We estimated daily energy expenditure during gestation and lactation periods based on the reproductive phenology, activity budgets, foraging flight costs, mean torpor duration per day and typical diet of the little brown bat in Quebec (Kurta et al. 1989; Henry 2001; Speakman et al. 2003; Wilcox and Willis 2016). We calculated daily energy expenditure (Table 5.3; converted into kJ h^{-1}) from the sum of 1) normothermic energy expenditure (E_{norm}), 2) energy expenditure during torpor (E_{tor}) including cooling and torpor phases, and 3) energy costs of active arousals from torpor

(E_{ar}). We then added the energy expenditure for foraging flights (in kJ h^{-1}) to the estimates. After visually assessing for data normality, we used a Welch's paired t-test in R to determine if there was a significant difference in daily energy expenditure between the Classic and the Ncube PH1 2019 during gestation and lactation at cooler, intermediate, and warmer sites using a significance threshold of ≤ 0.05 .

Table 5.3. Bioenergetic modeling to estimate the theoretical energy expenditure of reproductive female bats using the Classic and Ncube PH1 bat boxes.

Parameters used in the bioenergetic models to quantify energy expenditure of little brown bats in Classic and newly designed Ncube PH1 bat boxes		
Energy parameters	Value	Reference
Mass (Mb)	8.47 g	Jonasson and Willis (2011)
Basal metabolic rate (BMR)	1.44 ml O ₂ g ⁻¹ h ⁻¹	Willis et al. (2005)
Minimal torpid metabolic rate (TMR _{min})	0.03 ml O ₂ g ⁻¹ h ⁻¹	Hock (1951); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Normothermic temperature (T _{norm})	35 °C	Thomas et al. (1990); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Lower critical temperature (T _{lc})	32 °C	Stones and Wiebers (1965); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Upper critical temperature (T _{uc})	37 °C	Studier et al. (1976); Wilcox and Willis (2016)
Minimal torpid temperature (T _{tor-min})	2 °C	Hock (1951), Hock (1951); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Normothermic conductance below the lower critical temperature (C _{lnorm})	0.2638 ml O ₂ g ⁻¹ °C ⁻¹	Stones and Wiebers (1965); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Normothermic conductance above the upper critical temperature (C _{unorm})	0.4978 ml O ₂ g ⁻¹ °C ⁻¹	Hock (1951)
Torpid conductance (C _{tor}) or (C _{lct})	0.055 ml O ₂ g ⁻¹ °C ⁻¹	Hock (1951); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Change in torpid metabolic rate (TMR) over a 10°C change in T _a (Q ₁₀)	$1.6 + 0.26T_a - 0.006 T_a^2$	Hock (1951); Humphries et al. (2002, 2005); Wilcox and Willis (2016)

Specific heat capacity of tissue (S)	0.131 ml O ₂ g ⁻¹ °C ⁻¹	Thomas et al. (1990); Humphries et al. (2002, 2005); Wilcox and Willis (2016)
Little brown bat reproductive parameters	Value	Reference
Gestating mean torpor duration per day	133 min	Dzal and Brigham (2013); Wilcox and Willis (2016)
Lactating mean torpor duration per day	334 min	Dzal and Brigham (2013); Wilcox and Willis (2016)
Gestation period	May 15-June 30. We used a 2 weeks delay for cooler sites.	Henry (2001)
Lactation period	June 16-August 1. We used a 2 weeks delay for cooler sites.	Henry (2001)
Gestation activity budget	Foraging: 2 bouts of 20 min, resting in the roost: 1080 min, resting outside: 120 min	Henry (2001)
Lactation activity budget	Foraging: 3 bouts of 105min, resting in the roost: 2 bouts of 60min and 1 bouts of 1080 min, resting outside: 0 min	Henry (2001)
Foraging flight during gestation by 8.47g little brown bat	4.20 kJ h ⁻¹	Kurta et al. (1989)
Foraging flight during lactation by 8.47g little brown bat	3.90 kJ h ⁻¹	Kurta et al. (1989)
Typical diet for little brown bat	71.2% protein, 18.4% fat and 8.8% carbohydrate	Kurta et al. (1989)
Bioenergetic formulas used to quantify energy expenditure of little brown bats		
1) Calculating normothermic energy expenditure (E_{norm})		
The normothermic energy expenditure varies with ambient temperature, T_a , according to a metabolic response curve using the following equations (Hock 1951, Humphries et al. 2002, 2005, Wilcox and Willis 2016):		

when $T_a > T_{lc}$; $E_{norm} = BMR + (T_{lc} - T_a) * C_{lnorm}$
when $T_a < T_{uc}$; $E_{norm} = BMR + (T_a - T_{uc}) * C_{unorm}$
when $T_a \geq T_{lc} \leq T_{uc}$; $E_{norm} = BMR$
where BMR is the basic metabolic rate, T_{lc} is the lower critical temperature, T_{uc} is the upper critical temperature, C_{lnorm} is the thermal conductance in normothermia below the lower critical temperature, and C_{unorm} is the thermal conductance in normothermia above the upper critical temperature.
2) Quantify predicted energy expenditure during torpor depending on whether T_a was lower or higher than $T_{tor-min}$
During torpor, metabolic rate, TMR , and body temperature decline with T_a until a lower ambient set-point temperature, $T_{tor-min}$, is reached, after which torpor body temperature is defended (that is, remains constant) and consequently TMR increases. Thus, TMR varies with temperature according to (Thomas et al. 1990; Humphries et al. 2002, 2005; Wilcox and Willis 2016):
when $T_a > T_{tor-min}$; $E_{tor} = TMR_{min} * Q_{10}^{((T_a - T_{tor-min})/10)}$
when $T_a \leq T_{tor-min}$; $E_{tor} = TMR_{min} + (T_{tor-min} - T_a) * C_t$
where Q_{10} represents the change in torpor metabolism resulting from a 10 °C change in T_a , and C_t represents torpor conductance below $T_{tor-min}$.
Cooling phase = 67.2% of active arousal
3) Calculating predicted energetic cost for active arousal
The energetic cost of arousals E_{ar} is a simple function of the required increase in body temperature from T_{tor} to normothermic levels, T_{norm} , and the specific heat capacity S of the bat's tissues (Humphries et al. 2002, 2005).
$E_{ar} = (T_{norm} - T_{tor}) * S$
4) Conversion from mass-specific Vo_2 into SI (energy expenditure; Campbell et al. 2000; Wilcox et Willis 2016)
Heat Production = $(17.71P + 20.93C + 19.55L) * \text{mass-specific } Vo_2$

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Chapter 6 – Discussion

Through this thesis, I examined new insights on participatory science as well as research and conservation tools. I contributed to knowledge that will have practical uses in the management of rare and threatened animals and benefits to conservation strategies at global and local scales. In my second chapter, I focused on participatory science, that has become a popular tool to collect additional data and for monitoring trends across larger scales, especially for rare, threatened, or cryptic species. As studies on participatory science contributions generally tackle peer-reviewed publications only, I explored a wider spectrum of participatory science's contributions for the monitoring and conservation of rare or threatened species, including peer-reviewed publications, grey literature, and conservation measures. The number of participatory science projects studying rare and threatened species increased substantially after 2010, with most projects located in North America. I believed there is a great potential to expand participatory science outside of North America, Oceania, and Europe, where most rare and threatened animals are located (Pocock et al. 2017), as underlined by the negative spatial relationship between the number of threatened and data-deficient species and the number of peer-reviewed studies that show evidence in conservation (Christie et al. 2021).

As I predicted, participatory science projects contributed more to the grey literature and conservation measures than to peer-reviewed papers. Still, almost half of the projects included in my survey produced at least one peer-reviewed paper. Surveyed projects mostly generated knowledge on trends and distributions, but also on habitat selection, population dynamics, behavior, effect of threats or conservation measures on the species, and more. Several projects provided data to other organizations that then wrote management and mitigation plans or improved

policies. Data for certain species were used to evaluate threatened or endangered status at a regional, national, or international level. Data were also used to identify and establish protected or at-risk areas, such as protected breeding grounds and road mortality hotspots. Other projects contributed directly with conservation measures such as habitat restoration or protection, control of invasive species, captive breeding programs, and awareness campaigns. These statistics reinforce the usefulness of participatory science to provide concrete contributions to science and conservation.

Predictors of scientific contribution success included longevity, data quality, and collaboration type. Finding an effect of longevity is perhaps not surprising, but still valuable to convince funders for long-term support, as funding cycles often operate on short periods (Brightsmith et al., 2008). Moreover, to improve the scientific contributions of participatory science, project managers should ensure good data collection and management by integrating factors included in our data quality index or those included in Kosmala et al. (2016). Project managers should also include a diversity of stakeholders at all stages of the project to ensure best practices that link scientific research to conservation actions. Although I focused on a specific subset of participatory science projects and that a multilingual survey would have broadened the scope of my results, I believe this work still represents an informative examination of this type of project and could be expanded to other subsets of participatory science projects.

I tested in my third chapter the usefulness of data collected through a participatory science project, the Neighbourhood Bat Watch, to learn about summer trends and threats of several bat species. Using data on colony location, persistence, and counts, I assessed the impact of WNS and maternity colony exclusions from buildings on bat populations. Most of the colonies registered

though the Neighbourhood Bat Watch were found by participants, but their participation in counts required additional efforts from project managers. Data collection on counts and species identification of bats occupying maternity roosts by participants would benefit all stakeholders and may increase in the future with increased education and communication efforts, as well as the arrival of low-cost ultrasound recorders (Lundberg et al. 2021). The Neighbourhood Bat Watch demonstrates how data collection by professionals and participatory scientists can be integrated within the same program and co-inform each other. The structure of this project could be used to monitor other species that use artificial structures such as chimney swift (*Chaetura pelagica*) or species often occur in urban areas, such as squirrels (*Sciurus spp.*) or raccoons (*Procyon lotor*).

Data from the Neighbourhood Bat Watch participatory science project allowed to document a steep decline in *Myotis spp.* colony size during the first three years after WNS onset. This trend is similar to those found from hibernaculum counts and transect acoustic surveys in Quebec. (Équipe de rétablissement des chauves-souris du Québec 2019; Faure-Lacroix et al. 2020) and elsewhere in North America (Cheng et al. 2021). Such declining trends in colony size is based only on maternity colonies using buildings as roost, and therefore, living mainly in urban or semi-urban settings. Ideally, population trends for maternity colonies using natural structures (i.e. trees) as roosts should also be investigated to cover all habitats used by the population, and also to monitor trends for other WNS-impacted species that only use natural structures as roosts (e.g., *Perimyotis subflavus*). However, natural maternity roosts are more difficult to locate than those in anthropogenic structures.

Unlike what was found in Faure et al. 2020, evidence that big brown bat maternity colonies benefited from the decrease in *Myotis spp.* was weak. This difference may be explained by the

discrepancy in data collection periods, with my data being mostly collected several years after theirs and only after the arrival of WNS onset. Other increasing threats unrelated to WNS, such as habitat loss and agricultural pesticides, could also outdo the competitive release from *Myotis spp.* (Thomas 1995; Jones et al. 2009; Clark 1988). Another explanation may be that WNS negatively affects big brown bat females more than males (Barclay 2012; Simonis et al. 2021). Therefore, an overall increase in big brown populations would not be detected with maternity colony surveys. My study documented changes in maternity colony sizes but did not investigate if the number of maternity colonies changed over time in the different regions. Unfortunately, the number of colonies is biased by the registration of colonies by participants, which is rather influenced by the project advertisements and human demography than the presence of maternity colonies. Therefore, I cannot exclude the possibility of a decline or an increase in the number of colonies offsetting the trends in big brown bat colony size found in my study.

More than one third of all the colonies recorded on the Neighbourhood Bat Watch website from 1997-2020 have since been excluded. Exclusion rates are not often mentioned in the literature. The rate I found is substantial and highlights the need to further investigate the impact of exclusion on population dynamics of bats using buildings as roosts. Answering the following questions will be essential to effectively conserve those species: Where do bats go after the exclusion? Is the alternative roost and its surrounding habitat of equivalent quality than the previous one? How well do females survive and reproduce following an exclusion? With increased urbanization and a concomitant increase in modern wildlife proof dwellings, exclusions will likely become an important source of concern for species using buildings. Causes and consequences of the spatial variation of exclusions should be explored in future research. The higher probability of

exclusion in the north and in houses provides indications on where to focus research, education efforts, and mitigation measures. Project manager interventions likely helped to reduce exclusion rates. Sadly, I was not able to track down how many exclusions were avoided nor how safer were exclusions through communications with participants. This could be evaluated in future studies, along with participant perceptions of bats and the conservation of threatened species.

Although almost half of the colonies were excluded with compensation (e.g., with bat boxes added), these alternative roosts were rarely colonized in the long term. Improving bat box designs and settings was therefore essential to improve bat conservation. The use of bat boxes by bats can allow them to better survive and reproduce after an exclusion, but it also allows researchers to keep track of these excluded colonies. In my study occurring in a northern temperate environment, erecting bat boxes facing east, mounted on buildings while using a model based on passive solar architecture (such as the Ncube PH1 model) was the best set up tested. This set up increased the time in the optimal temperature range of target species, which, according to energetic modeling, saved energy when using the Ncube PH1 compared to the Classic 4-chamber. As gestating females use 2 % of their energy budget to create new tissues and lactating females 32% as milk (Kurta et al. 1989), the energy savings I estimated are likely biologically meaningful. As these bioenergetic models showed the theoretical value of my bat box designed with energy-saving concepts, the next step should be to test its colonization success and its functionality for bats on a larger scale.

Results from orientation and structure tests may not be surprising, but few investigators have explicitly examined the link between the orientation or the mounting type and nest or roost internal temperatures (Hooge et al. 1999; Wiebe 2001; Ardia et al. 2006; Mering and Chambers et

al. 2014). This is an essential component to understand what drives colonization rate of artificial structures such as bat boxes and its impact on the physiology of its occupants. Design is one of the most important characteristics determining attraction of bats or birds to artificial structures. Design refinement improves the frequency use of nest and bat boxes (Summers and Taylor 1996; Goldingay et al. 2015; Rueegger 2016). The improved thermal performance of my best model, the Ncube PH1, is likely attributed to innovative and unique features such as a passive heating zone, insulation, a reduced entrance, and an additional cool chamber. It is thanks to the integration of knowledge related to biology/ecology (bat scientists) and material properties and thermodynamics (architects and engineers) that I was able to propose a versatile passive heating design well adapted to a wide range of northern temperate environments. This successful integration of multiple knowledge brings back the value of a transdisciplinary approach highlighted in my second chapter on participatory science contributions. Artificial structure optimization using human architecture concepts such as the Ncube PH1, shows a great potential as a conservation tool for bats and potentially for other taxa like birds or other hollow-dependent mammals.

Although the Ncube PH1 is more expensive to build than the commonly used classic 4-Chamber model, I still consider that such investment is justifiable if it improves colonization rate of bat boxes in northern temperate environments. In this case, provincial government could implement incentives to promote this model. Assuring an abundance of natural roosting sites remains desirable for bat conservation (Griffiths et al. 2017). However, this improved conservation tool could be applied as a compensation measure to roost exclusion or habitat enhancement when the optimal roosting habitat is no longer available. The participatory science project the Neighbourhood Bat Watch offers a good opportunity to test this model where colonies are

excluded from buildings or where other bat box models are used, such as in the north, where natural roost availability is limited due to smaller tree sizes than in the south. A network of bat boxes registered through the Neighbourhood Bat Watch could also allow to test other important and understudied aspects of bat boxes, such as the impact of bats on the internal temperature and relative humidity of bat boxes, the presence of ectoparasites in occupied bat boxes, and the effect of mimicking designs on colonization success of bat boxes.

Another contribution of my thesis to research and conservation tools is through the PIT tagging of females at maternity colonies. I underlined for the first time the possibility to infer individual reproductive status and parturition dates from PIT tag detections, without the need to recapture individuals. As shown in at least two different regions, I was able to estimate reproductive status, parturition date, and time away from the roost during gestation for the majority of adult female bats through PIT tag detection patterns. Although PIT tagging technologies are not new to biologists (Gibbons and Andrews, 2004), evaluating individual reproductive success and parturition dates have always been challenging for researchers studying elusive species such as bats (e.g., Henry 2001; Stapelfeldt et al 2022).

This non-invasive recapture method is valuable for improving estimates of population parameters, reducing stress to organisms and stress-induced bias, as well as reducing the behavioural response bats can have to capture and that response's impact on detection probability (Ellison et al. 2007; Rigby et al. 2012). Coupling information currently available from PIT tag detections, such as apparent survival, fidelity, abundance, and time away from the roost, with estimation of reproductive status and parturition date could provide a better understanding of population dynamics and help to improve population management decisions. This information can

also be useful in several other fields in bat research (e.g., behavioral or physiological studies). I see a great potential in this method, which could be further improved by automatized data cleaning method to deal with a high number tagged individuals or with an alternative process to assess reproductive status and parturition dates, such as a breakpoint method, to deal with imperfect detections.

Using one site as a case study, I also demonstrated that early individual arrival date and warm spring mean temperature led to early parturition date while long night, warm temperature, and heavy rainfall at night increased time away from the roost of gestating females. These findings highlight the importance of warm temperature for reproductive females. As such, providing warm roosts close the optimal temperature range of bats that can buffer against temperature fluctuations, as mentioned in my fifth chapter on bat boxes, is likely highly beneficial for reproductive females, especially in spring when weather conditions are colder than in the summer.

I predicted that foraging efficiency should be reduced by low temperatures, precipitation, and strong winds (Rydell 1989; Grindal et al. 1992; Burles et al. 2009). Surprisingly, I found that low temperature decreases time away from the roost, but that high rainfall increases time away from the roost. Time away from the roost may not be a good predictor of foraging bouts and more work investigating time foraging and time resting away from the maternity roost is required to explain patterns observed in my study. A larger study including PIT tag bats at more roosts and evaluating reproductive success, survival, fidelity rates, and real foraging bouts would be highly valuable to understand individual and local variations as well as the multiple threats hindering *Myotis* population persistence and recovery. However, few maternity roosts are currently suitable

to the implementation of PIT tagging systems and host a colony big enough to make researchers' time and efforts worthwhile.

This thesis focused mostly on threatened or rare species (chapter 2), and particularly on endangered *Myotis* bats (chapter 3, 4, and 5). Still, we used the big brown bat, a now rather common species in Quebec, as a point of comparison in chapter 3. We suggest that future studies should not neglect common species, such as the big brown bat. Preserving the continued abundance of common bats species, in an otherwise declining group of mammals, is consistent with an ecosystem approach to conservation focusing on functional diversity (Agosta 2002). In addition, widespread, abundant bats, such as big brown bats, provide a wealth of research opportunities from which researchers may be able to draw some general conclusions about bat conservation as a whole (Agosta 2002). Those species also allow testing of new methods and tools on a larger sample size before their use on threatened species. Moreover, other threats than the WNS and maternity colony exclusions, not covered in my thesis, are likely to contribute to the declines of many species altogether and deserve to be investigated (e.g., wind facilities, Arnett and Baerwald 2013; climate variation, Faure-Lacroix et al. 2020; contaminant exposure, Cable et al. 2021).

Chapter 7 – Final Conclusion and Summary

We are currently living through the Sixth Great Extinction, with rates of species loss far exceeding background. Indeed, humans have used nature and animals for their advantage since the early days of humanity and have caused unprecedented environmental damage as a result. But, with great power comes great responsibility. As one of the smartest species on earth and being endowed with consciousness, humans have the responsibility to actively manage and conserve other species. Significant technological advances over the past decades have changed the way we live and interact with the world, such that we now have the knowledge and technical support required to create new tools and collaborations that make a difference in modern conservation efforts.

Throughout this thesis, I explored ways to contribute to the conservation of wildlife, more specifically, the conservation of threatened hibernating female bats. I hope that providing evidence of participatory science contributions to science and conservation of rare and threatened species will convince those sceptical about the value of participatory science and promote its use. Some participants have knowledge that is often inaccessible using traditional research methods, while others need to reconnect with nature. I believe participatory science provides an opportunity to get the best of all while democratizing science. The Neighbourhood Bat Watch project is a good example of the usefulness of participatory science, in this case, to raise awareness about bats and to identify threats and its impacts on bat populations. Using the Neighbourhood Bat Watch database, I provided trends for declining bat species and information on where colony exclusions happened. As two endangered *Myotis* species commonly use buildings as maternity roosts, special efforts should be made to promote public awareness, mitigate human-bat conflict, and better understand causes and consequences of colony exclusions from buildings.

Contributing to the conservation of bats, I used existing tools in new ways to improve our knowledge about bat reproductive success and bat box efficiency in a northern temperate climate. In the face of WNS-associated massive mortalities, assessing reproductive success and its constraints can help biologists understand how climatic variability may jeopardize bat conservation efforts while my improved bat box model can serve as an alternative roost for bats excluded from dwellings or to enhance high quality habitats where roost availability is limited. Conservation and management for WNS-affected bats have long been focused on improving survival during hibernation, but active-season habitat management including foraging and roosting habitat may also hold the key for successful reproduction and recovery of remnant post-WNS populations (Wilcox and Willis 2016; Fuller et al. 2020).

My thesis provides the theoretical and practical foundations to improve the management of threatened female bats and their summer habitat. But its impact goes beyond the conservation of bats. My work supports the implementation of participatory science projects and provides, with the Neighbourhood Bat Watch, a project structure that can be applied to other species that use anthropic structures. The integration of human architecture concepts into bat boxes can also be applied to other taxa like birds or other hollow-dependent mammals. Finally, my work suggests that PIT tag detection patterns may be used in ways more various than one can think to infer activities of bats, and possibly, several other elusive species. With the ongoing work of passionate and dedicated biologists who increase knowledge on wildlife, create new tools, and instigate conservation actions across the globe, I hope humans succeed in protecting this imperfect yet beautiful world.

Supplementary Materials

Supplementary materials for chapter 2

Table S2.1. Full list of key words used to search for participatory science project focusing on rare or threatened species.

<i>Language</i>		<i>Key words used for web searches</i>
English	Species terms	rare, threatened, endangered, bat, chiropter*
	Project type terms	"citizen science", "citizen-based", "public particip*", particip*, volunteer*
	Establishment goal terms	program, project, monitor*, watch
	Location terms	Australia*, Oceania*, Asia*, Europe*, Russia*, Africa*, America*, worldwide, internation*
Spanish	Species terms	rara*, raro*, amenazad*, peligro, especie, fauna
	Project type terms	“ciencia ciudadana”, particip*, participativo, voluntari*
	Establishment goal terms	(programa or proyecto), observa*, monitor*
	Location terms	Mexico, Ecuador, Peru, “Costa Rica”, España, Colombia, Cuba, Guatemala, Venezuela, Argentina, Panama, Uruguay, Paraguay, Honduras, “Puerto Rico”, Bolivia, Salvador
French	Species terms	rare*, menacé*, vulnerable*, Tortuga*, anfibio, ballena*, tiburón*, mamifere, ave*, murcielago, insecto
	Project type terms	“science citoyenne”, “science participative”, (volontaire ou bénévole)
	Establishment goal terms	projet, programme, suivi
Chinese	Species terms	(受威胁的 or 濒危的), “物种 的”
	Project type terms	“公民科学”, 参与*, 志愿*
	Establishment goal terms	(方案 or 项目 or 监控)

When searching projects, each species term above was searched individually with each project and/or establishment goal and/or location terms. The first 100 links returned were screened to assess if the project fitted the predefined inclusion criteria.

Major participatory science directories included in web searches

scistarter.com, citizenscience.gov (USA), zooniverse.org, volunteer.gov, inaturalist.org, scientificamerican.com, biocollect.ala.org.au, and CitSci.org.

Note that “bat” and “chiropter*” have been included in key words in the English web search since the study primary aimed to compare bat to other taxa projects. Since the preliminary analysis of bat only projects provided similar results than other taxa projects, we decided to include bat projects in the overall analysis.

Table S2.2. Predictors of success type and category.

<i>Predictors</i>	<i>Type</i>	<i>Category</i>
Longevity (year)	continual	1945–2019
Location	categorical	North America, Central/South America, Africa, Europe, Russia, Asia, Oceania, Arctic/Antarctica, worldwide
Focal taxa	categorical	Mammal, bird, herps (amphibian and reptile), fish, invertebrate (arthropoda, mollusca), mixed
Scale of data collection	categorical	Local, regional, national, international
Collaboration type	categorical	Intradisciplinary (working within a single discipline. For example, biology), multidisciplinary (people from different disciplines working together, each drawing on their disciplinary knowledge in an additive manner. For example, studying bats from the morphology and disease-carrying point of view), interdisciplinary (integration of knowledge and methods from different disciplines using a synthesis of approaches with stronger level of cooperation), transdisciplinary (Creating a unity of intellectual frameworks beyond the disciplinary perspectives to form a new holistic approach),
Organisation type	categorical	Citizen-driven, non-profit, academic, governmental, industrial, mixed of two, mixed (3 organizations or more)
Methodological complexity	categorical	Systematic/elaborated monitoring, mixed, mass participation/simple
Data quality index	continual	Ranging from 0 to 1

Table S2.3. Location Tukey pairwise comparison test with 95% family-wise confidence level. Since Tukey's test is a post-hoc test, we first fitted a general linear regression model with a quasi-Poisson distribution and performed an ANOVA on the data. The glm included the frequency of new projects as y variable and the location and the polynomial function of the year to consider the non-linearity as x variables.

<i>Location pairwise comparisons</i>				
<i>comparisons</i>	<i>diff</i>	<i>lwr</i>	<i>upr</i>	<i>p adj</i>
America-Africa	-1.216e-1	-0.690	0.446	0.999
Antartic-Africa	-1.351e-1	-0.703	0.433	0.998
Asia-Africa	-2.702e-2	-0.595	0.541	1
Europe-Africa	2.972e-1	-0.271	0.865	0.789
North America-Africa	1.527	0.958	2.095	0.001e-18*
Oceania-Africa	5.000e-1	-0.068	1.068	0.136
South America-Africa	-1.351e-1	-0.703	0.433	0.998
Worldwide-Africa	4.054e-2	-0.527	0.609	0.999
Antarctic-America	-1.351e-2	-0.581	0.554	1
Asia-America	9.459e-2	-0.473	0.663	0.999
Europe-America	4.189e-1	-0.149	0.987	0.347
North America-America	1.648	1.08	2.217	0.000 e-16*
Oceania-America	6.216e-1	0.053	1.19	0.020*
South America-America	-1.351e-2	-0.581	0.554	1
Worldwide-America	1.621e-1	-0.406	0.73	0.993
Asia-Antarctic	1.081e-1	-0.460	0.676	0.999
Europe-Antarctic	4.324e-1	-0.136	1	0.303
North America-Antarctic	1.662	1.093	2.23	0.000 e-16*
Oceania-Antarctic	6.351e-1	0.066	1.203	0.016*
South America-Antarctic	2.942e-15	-0.568	0.568	1
Worldwide-Antarctic	1.756e-1	-0.392	0.744	0.989
Europe-Asia	3.243e-1	-0.244	0.892	0.698
North America-Asia	1.554	0.985	2.122	0.000 e-16*
Oceania-Asia	5.270e-1	-0.041	1.095	0.094
South America-Asia	-1.081e-1	-0.676	0.46	0.999
Worldwide-Asia	6.756e-2	-0.501	0.636	0.999
North America-Europe	1.229	0.661	1.798	0.000 e-16*
Oceania-Europe	2.027e-1	-0.365	0.771	0.972
South America-Europe	-4.324e-1	-1.001	0.136	0.303
Worldwide-Europe	-2.567e-1	-0.825	0.311	0.895
Oceania-North America	-1.027	-1.595	-0.458	1.000 e-6*
South America-North America	-1.662	-2.230	-1.093	0.000 e-16*

Worldwide-North America	-1.486	-2.054	-0.918	0.000 e-16*
South America-Oceania	-6.351e-1	-1.203	-0.066	0.016*
Worldwide-Oceania	-4.594e-1	-1.027	0.109	0.226
Worldwide-South America	1.756e-1	-0.392	0.744	0.989

Table S2.4. Predictors of success included in each of the scientific contribution global model.

<i>Predictors of success</i>	<i>Scientific paper</i>	<i>Grey literature</i>	<i>Conservation measure</i>	<i>Data quality index</i>
Longevity	x	x	x	x
Location	x	x	x	x
Scale of data collection	NA	NA	x	NA
Taxa	x	x	x	NA
Collaboration type	x	x	x	NA
Organisation type	x	x	x	x
Data quality index	x	x	x	NA
Methodological complexity	NA	NA	NA	x

Table S2.5. Full model selection of predictors of success on scientific paper publications ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). Δ AICc is the difference between AICc for the current model and the minimum of AICc among all the models. w_i = Akaike weights.

<i>Models</i>	<i>AICc</i>	<i>Δ AICc</i>	<i>w_i</i>
log(longevity) + $\sqrt{(1-\text{quality index})}$	287.5	0.00	0.689
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location	290.8	3.26	0.135
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration	291.5	3.98	0.094
log(longevity) + $\sqrt{(1-\text{quality index})}$ + organisation	294.4	6.91	0.022
log(longevity)	294.7	7.19	0.019
log(longevity) + location	295.7	8.21	0.011
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + collaboration	296.3	8.75	0.009
log(longevity) + $\sqrt{(1-\text{quality index})}$ + taxa	296.4	8.85	0.008
log(longevity) + collaboration	297.4	9.91	0.005
log(longevity) + $\sqrt{(1-\text{quality index})}$ + taxa + collaboration	299.8	12.33	0.001

log(longevity) + location + collaboration	299.9	12.42	0.001
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + collaboration + organisation	300.1	12.55	0.001
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + taxa	301.0	13.51	0.001
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + organisation	301.1	13.61	0.001
log(longevity) + taxa	302.1	14.57	0.000
log(longevity) + organisation	303.1	15.59	0.000
log(longevity) + location + organisation	304.0	16.49	0.000
log(longevity) + collaboration + taxa	304.3	16.82	0.000
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + collaboration + taxa	304.6	17.07	0.000
$\sqrt[3]{1-\text{quality index}}$	305.2	17.73	0.000
log(longevity) + location + taxa	305.5	18.04	0.000
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + taxa	305.9	18.36	0.000
log(longevity) + location + collaboration	307.9	20.36	0.000
log(longevity) + collaboration + organisation	308.0	20.54	0.000
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + collaboration + organisation	308.1	20.64	0.000
$\sqrt[3]{1-\text{quality index}}$ + taxa	309.4	21.88	0.000
$\sqrt[3]{1-\text{quality index}}$ + collaboration	310.0	22.50	0.000
$\sqrt[3]{1-\text{quality index}}$ + organisation	310.3	22.84	0.000
log(longevity) + location + collaboration + organisation	310.4	22.89	0.000
$\sqrt[3]{1-\text{quality index}}$ + location	311.3	23.80	0.000
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + organisation + taxa	312.2	24.67	0.000
log(longevity) + organisation + taxa	312.8	25.34	0.000
null model	313.4	25.91	0.000
$\sqrt[3]{1-\text{quality index}}$ + collaboration + taxa	314.4	26.85	0.000
log(longevity) + $\sqrt[3]{1-\text{quality index}}$ + location + organisation + taxa	314.4	26.86	0.000
$\sqrt[3]{1-\text{quality index}}$ + organisation	315.4	27.93	0.000
$\sqrt[3]{1-\text{quality index}}$ + organisation + taxa	316.9	29.43	0.000
$\sqrt[3]{1-\text{quality index}}$ + location + taxa	316.9	29.43	0.000
location	316.9	29.43	0.000
taxa	317.0	29.48	0.000
log(longevity) + location + organisation + taxa	317.2	29.66	0.000

$\sqrt{(1-\text{quality index})}$ + location + collaboration	317.2	29.66	0.000
collaboration	317.5	29.97	0.000
$\sqrt{(1-\text{quality index})}$ + location + organisation	318.0	30.46	0.000
organisation	318.8	31.31	0.000
log(longevity) + collaboration + organisation + taxa	319.2	31.73	0.000
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + collaboration + organisation + taxa	320.5	33.01	0.000
location + organisation	320.9	33.43	0.000
collaboration + taxa	321.1	33.63	0.000
location + taxa	321.6	34.10	0.000
location + collaboration	321.6	34.12	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + taxa	322.3	34.85	0.000
$\sqrt{(1-\text{quality index})}$ + collaboration + organisation + taxa	323.1	35.59	0.000
collaboration + organisation	323.5	35.99	0.000
log(longevity) + location + collaboration + organisation + taxa	323.7	36.22	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + organisation	323.8	36.27	0.000
organisation + taxa	324.9	37.42	0.000
location + collaboration + organisation	325.3	37.83	0.000
$\sqrt{(1-\text{quality index})}$ + location + organisation + taxa	325.8	38.34	0.000
location + collaboration + taxa	326.0	38.50	0.000
location + taxa	328.0	40.52	0.000
collaboration + organisation + taxa	331.5	43.99	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + organisation + taxa	332.7	45.24	0.000
location + collaboration + organisation + taxa	334.6	47.10	0.000

Table S2.6. Full predictor coefficient values, standard errors, t-values, p-values, and confidence intervals of the best model for scientific paper predictors of success.

<i>Predictors</i>	<i>Value</i>	<i>Std. Error</i>	<i>t value</i>	<i>p value</i>	<i>CI upper</i>	<i>CI lower</i>
log(longevity)	1.040	0.245	4.242	2.21e-5	0.573	1.538
$\sqrt{(1-\text{quality index})}$	-3.905	1.344	-2.904	3.67e-3	-6.669	-1.369
sc paper: int 1	0.368	0.861	0.427	6.69e-1	Na	Na
sc paper: int 2-5	0.944	0.861	1.096	2.73e-1	Na	Na
sc paper: int 6-10	2.095	0.877	2.386	1.69e-2	Na	Na
sc paper: int >10	2.653	0.896	2.959	3.08e-3	Na	Na

Table S2.7. Full model selection of predictors of success on grey literature publications ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). Δ AICc is the difference between AICc for the current model and the minimum of AICc among all the models. w_i = Akaike weights.

<i>Models</i>	<i>AIC_c</i>	Δ <i>AIC_c</i>	<i>w_i</i>
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration	331.7	0.00	0.584
log(longevity) + $\sqrt{(1-\text{quality index})}$	333.9	2.15	0.199
log(longevity) + collaboration	334.5	2.76	0.147
log(longevity)	337.1	5.41	0.039
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration + taxa	340.0	8.28	0.009
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + collaboration	340.5	8.73	0.007
log(longevity) + location + collaboration	340.7	8.93	0.007
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location	342.8	11.11	0.002
log(longevity) + $\sqrt{(1-\text{quality index})}$ + taxa	343.5	11.80	0.002
log(longevity) + location	344.0	12.27	0.001
log(longevity) + collaboration + taxa	344.2	12.45	0.001
$\sqrt{(1-\text{quality index})}$ + collaboration	346.1	14.33	0.000
log(longevity) + taxa	347.5	15.73	0.000
$\sqrt{(1-\text{quality index})}$	348.1	16.35	0.000
$\sqrt{(1-\text{quality index})}$ + collaboration + taxa	348.4	16.72	0.000
collaboration	350.1	18.35	0.000
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + collaboration + taxa	350.6	18.91	0.000
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration + organisation	351.6	19.89	0.000
log(longevity) + location + collaboration + taxa	352.0	20.28	0.000
null model	352.9	21.14	0.000
$\sqrt{(1-\text{quality index})}$ + taxa	353.0	21.31	0.000
log(longevity) + $\sqrt{(1-\text{quality index})}$ + organisation	353.3	21.59	0.000
log(longevity) + collaboration + organisation	353.4	21.63	0.000
log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + organisation + taxa	354.3	22.53	0.000
collaboration + taxa	354.5	22.82	0.000
log(longevity) + organisation	355.2	23.46	0.000
log(longevity) + location + taxa	356.1	24.36	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration	356.8	25.07	0.000

location + collaboration	358.0	26.24	0.000
taxa	358.8	27.08	0.000
$\sqrt{(1-\text{quality index})}$ + location	358.9	27.18	0.000
$\log(\text{longevity}) + \sqrt{(1-\text{quality index})}$ + collaboration + organisation + taxa	360.0	28.29	0.000
$\log(\text{longevity}) + \text{location} + \text{collaboration} + \text{organisation}$	361.4	29.63	0.000
location	361.4	29.64	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + taxa	361.5	29.76	0.000
$\log(\text{longevity}) + \sqrt{(1-\text{quality index})}$ + collaboration + organisation	362.9	31.17	0.000
$\sqrt{(1-\text{quality index})}$ + collaboration + organisation	363.7	31.93	0.000
location + collaboration + taxa	364.1	32.35	0.000
$\log(\text{longevity}) + \sqrt{(1-\text{quality index})}$ + organisation + taxa	364.1	32.42	0.000
$\log(\text{longevity}) + \text{location} + \text{organisation}$	364.3	32.56	0.000
$\log(\text{longevity}) + \text{collaboration} + \text{organisation} + \text{taxa}$	364.4	32.66	0.000
$\sqrt{(1-\text{quality index})}$ + location + organisation	365.1	33.40	0.000
$\sqrt{(1-\text{quality index})}$ + organisation	365.5	33.74	0.000
$\sqrt{(1-\text{quality index})}$ + collaboration + organisation + taxa	365.5	33.77	0.000
$\sqrt{(1-\text{quality index})}$ + location + taxa	366.2	34.49	0.000
$\log(\text{longevity}) + \text{organisation} + \text{taxa}$	366.8	35.09	0.000
collaboration + organisation	367.2	35.47	0.000
organisation	369.1	37.34	0.000
location + taxa	369.2	37.46	0.000
$\sqrt{(1-\text{quality index})}$ + organisation + taxa	371.7	39.96	0.000
collaboration + organisation + taxa	372.5	40.74	0.000
location + collaboration + organisation + taxa	375.0	43.30	0.000
$\log(\text{longevity}) + \sqrt{(1-\text{quality index})}$ + location + collaboration + organisation + taxa	375.5	43.78	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + organisation	375.6	43.83	0.000
$\log(\text{longevity}) + \text{location} + \text{collaboration} + \text{organisation} + \text{taxa}$	375.7	44.01	0.000
organisation + taxa	376.2	44.50	0.000
$\sqrt{(1-\text{quality index})}$ + location + organisation	377.9	46.18	0.000
location + organisation	378.5	46.74	0.000
$\log(\text{longevity}) + \text{location} + \text{organisation} + \text{taxa}$	379.1	47.33	0.000

log(longevity) + $\sqrt{(1-\text{quality index})}$ + location + organisation + taxa	379.2	47.44	0.000
$\sqrt{(1-\text{quality index})}$ + location + collaboration + organisation + taxa	382.1	50.39	0.000
location + collaboration + organisation + taxa	383.3	51.61	0.000
$\sqrt{(1-\text{quality index})}$ + location + organisation + taxa	387.6	55.84	0.000
location + organisation + taxa	388.2	56.52	0.000

Table S2.8. Full predictor coefficient values, standard errors, t-values, p-values, and confidence intervals of the best model for grey literature predictors of success.

<i>Predictors</i>	<i>Value</i>	<i>Std. Error</i>	<i>t value</i>	<i>p value</i>	<i>CI upper</i>	<i>CI lower</i>
log(longevity)	0.9660	0.245	3.935	8.31e-5	0.495	1.461
$\sqrt{(1-\text{quality index})}$	-2.782	1.259	-2.208	0.027	-5.324	-0.366
collab:						
intradisciplinary	-1.012	0.418	-2.417	0.015	-1.846	-0.191
collab:						
multidisciplinary	-0.527	0.461	-1.143	0.252	-1.441	0.374
collab:						
transdisciplinary	0.838	0.762	1.098	0.271	-0.673	2.359
grey lit: int 1	-0.875	0.906	-0.966	0.333	Na	Na
grey lit: int 2-5	-0.270	0.898	-0.301	0.763	Na	Na
grey lit: int 6-10	1.233	0.917	1.343	0.179	Na	Na
grey lit: int >10	1.728	0.931	1.855	0.063	Na	Na

Table S2.9. Full model selection of predictors of success on conservation measures ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). ΔiAICc is the difference between AICc for the current model and the minimum of AICc among all the models. w_i = Akaike weights.

<i>Models</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>w_i</i>
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration + taxa	318.2	0.00	0.183
log(longevity) + collaboration + taxa	318.8	0.52	0.141
log(longevity) + $\sqrt{(1-\text{quality index})}$ + taxa	319.0	0.78	0.124
log(longevity) + collaboration	319.8	1.52	0.085
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration	319.9	1.69	0.079
log(longevity) + collaboration + taxa + scale	320.4	2.13	0.063
log(longevity) + $\sqrt{(1-\text{quality index})}$ + collaboration + taxa + scale	320.5	2.22	0.060

log(longevity) + $\sqrt[3]{(1-\text{quality index})}$	320.5	2.27	0.059
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + taxa + scale	321.4	3.13	0.038
log(longevity) + taxa	321.5	3.28	0.036
log(longevity)	322.0	3.80	0.027
log(longevity) + collaboration + scale	322.3	4.08	0.024
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + scale	323.2	4.96	0.015
log(longevity) + taxa + scale	323.2	4.96	0.015
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + scale	323.9	5.70	0.011
log(longevity) + collaboration + location	324.0	5.81	0.010
log(longevity) + scale	324.7	6.45	0.007
log(longevity) + location	325.5	7.30	0.005
log(longevity) + collaboration + location + taxa	326.2	8.01	0.003
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + location	326.3	8.12	0.003
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + location	326.9	8.69	0.002
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + organisation	327.7	9.44	0.002
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + location + taxa	328.2	9.94	0.001
log(longevity) + location + taxa	328.7	10.48	0.001
log(longevity) + collaboration + organisation	328.8	10.59	0.001
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + organisation + taxa	328.9	10.71	0.001
location + taxa	329.3	11.04	0.001
log(longevity) + collaboration + location + scale	330.3	12.06	0.000
organisation	331.2	12.96	0.000
$\sqrt[3]{(1-\text{quality index})}$ + taxa	331.5	13.22	0.000
log(longevity) + location + scale	331.7	13.49	0.000
log(longevity) + collaboration + location + taxa + scale	331.8	13.58	0.000
location + scale	332.7	14.48	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration + taxa	332.9	14.65	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + organisation + taxa	333.1	14.86	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + location + scale	333.2	14.96	0.000
$\sqrt[3]{(1-\text{quality index})}$	333.6	15.36	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + location + taxa + scale	333.7	15.51	0.000
log(longevity) + collaboration + organisation + taxa	334.3	16.03	0.000
log(longevity) + location + taxa + scale	334.4	16.20	0.000

log(longevity) + organisation	334.5	16.26	0.000
log(longevity) + collaboration + organisation + scale	334.5	16.30	0.000
$\sqrt[3]{(1-\text{quality index})}$ + taxa + scale	334.6	16.41	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + organisation + scale	334.8	16.58	0.000
taxa	334.8	16.58	0.000
collaboration + taxa	334.9	16.64	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + location + taxa + scale	334.9	16.67	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration	335.4	17.13	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration + taxa + scale	336.2	17.94	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + organisation + taxa + scale	336.5	18.28	0.000
	336.5	18.28	0.000
collaboration	337.0	18.77	0.000
log(longevity) + collaboration + location + organisation	337.1	18.92	0.000
taxa + scale	337.3	19.12	0.000
collaboration + taxa + scale	337.5	19.27	0.000
$\sqrt[3]{(1-\text{quality index})}$ + scale	337.9	19.63	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + organisation + scale	337.9	19.69	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + location + organisation	339.1	20.84	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration + scale	339.8	21.53	0.000
log(longevity) + organisation + scale	339.8	21.58	0.000
log(longevity) + organisation + taxa	339.9	21.65	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + organisation + taxa + scale	340.0	21.72	0.000
scale	340.2	21.92	0.000
log(longevity) + collaboration + organisation + taxa + scale	340.2	21.99	0.000
collaboration + scale	340.8	22.53	0.000
log(longevity) + location + organisation	341.6	23.37	0.000
log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + location + organisation	342.3	24.09	0.000
$\sqrt[3]{(1-\text{quality index})}$ + location	343.1	24.87	0.000
collaboration + location	343.1	24.88	0.000
location	343.3	25.08	0.000
$\sqrt[3]{(1-\text{quality index})}$ + location + taxa	343.5	25.29	0.000
collaboration + location + taxa	343.5	25.30	0.000

log(longevity) + $\sqrt[3]{(1-\text{quality index})}$ + collaboration + location + organisation + taxa	343.6	25.37	0.000
location + taxa	343.9	25.65	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration + location	344.1	25.87	0.000
$\sqrt[3]{(1-\text{quality index})}$ + collaboration + location + taxa	344.5	26.27	0.000

Table S2.10. Full predictor coefficient values, standard errors, t-values, p-values, and confidence intervals of the best model for conservation measures predictors of success.

<i>Predictors</i>	<i>Value</i>	<i>Std. Error</i>	<i>t value</i>	<i>p value</i>	<i>CI upper</i>	<i>CI lower</i>
log(longevity)	1.035	0.246	4.204	2.62e-5	0.565	1.535
collab:						
intradisciplinary	-0.309	0.415	-0.745	4.56e-1	-1.127	0.504
collab:						
multidisciplinary	0.230	0.476	0.482	6.29e-1	-0.709	1.167
collab:						
transdisciplinary	2.040	0.800	2.548	1.08e-2	0.502	3.692
cons mes: int 1	1.666	0.614	2.711	6.70e-3	Na	Na
cons mes: int 2-5	2.458	0.634	3.875	1.06e-4	Na	Na
cons mes: int 6-10	3.952	0.697	5.666	1.45e-8	Na	Na
cons mes: int >10	4.410	0.722	6.106	1.01e-9	Na	Na

Data quality analysis results

Table S2.11. Top-5 of model selection of predictors of success on data quality index ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). $\Delta AICc$ is the difference between AICc for the current model and the minimum of AICc among all the models. ω_i = Akaike weights. Data quality index was assessed from the survey by attributing a score based on the following criteria: protocol freely available, support and training, data entry, metadata, verifiability, validation and data standardization (See appendix S3).

<i>Models</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>w_i</i>
1. method complexity + organisation + location	-142.5	0.00	0.472
2. method complexity + organisation + location + longevity	-141.0	1.46	0.227
3. method complexity + organisation	-140.1	2.37	0.145
4. method complexity + organisation + location	-138.2	4.27	0.056
5. method complexity + organisation + location + collaboration	-136.7	5.85	0.025

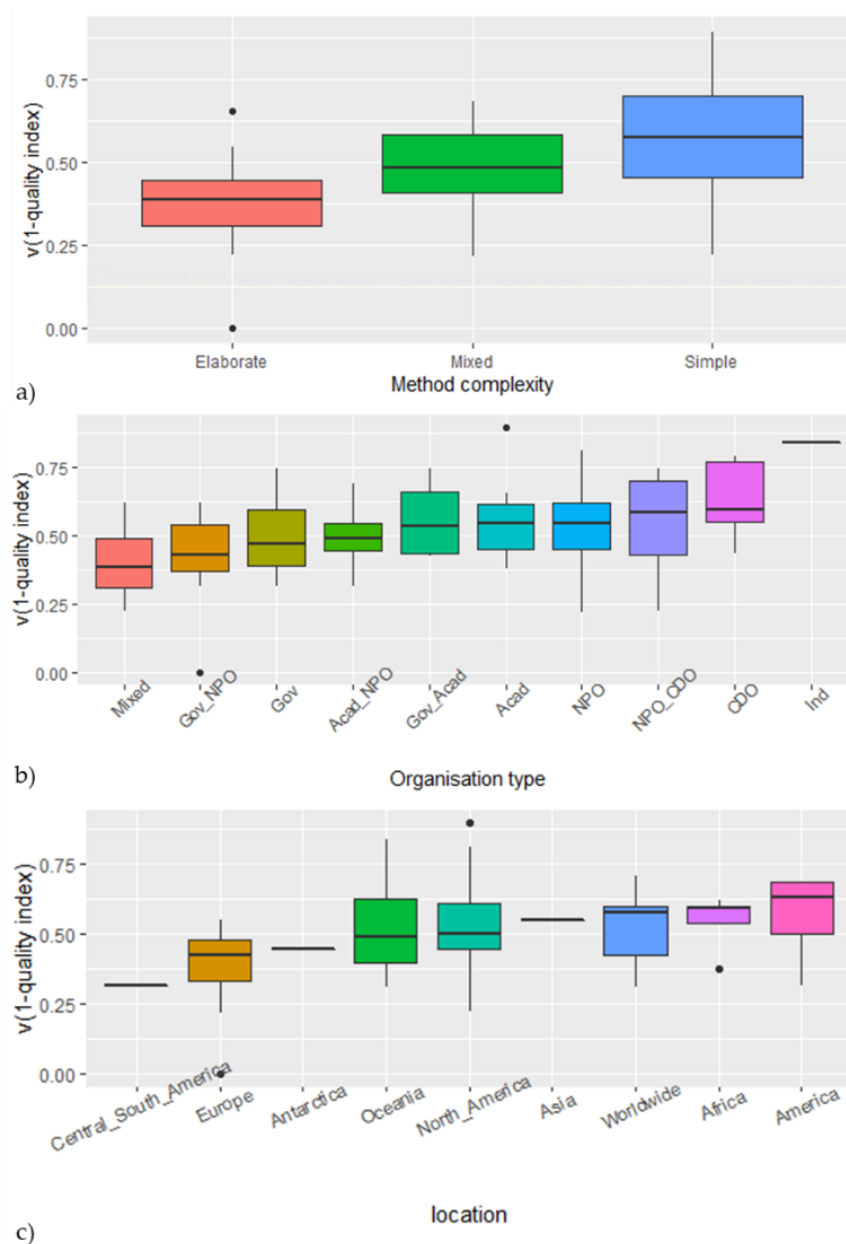


Figure S2.1. $\sqrt{(1-\text{quality index})}$ as used in the linear model in function of a) methodology complexity, b) organisation type, and c) location. Data quality index was assessed from the survey by attributing a score based on the following criteria: protocol freely available, support and training, data entry, metadata, verifiability, validation and data standardization (See appendix S3). Low $\sqrt{(1-\text{quality index})}$ means high data quality and high $\sqrt{(1-\text{quality index})}$ means low data quality, as assessed by our scoring system, In panel b), Gov means governmental organization, NPO means Non-profit organization, Acad means Academic organization, CDO means citizen-driven organization, Ind means Industrial organization, and mixed means more than two organizations as the main leader of the project.

Table S2.12. Tukey pairwise comparison test with 95% family-wise confidence level for the methodology complexity. Since Tukey's test is a post-hoc test, we first fitted the best linear regression model (lm) and performed ANOVA on the data.

<i>Pairwise comparisons</i>	<i>diff</i>	<i>lwr</i>	<i>upr</i>	<i>p adj</i>
Mixed-Elaborate	0.095	0.016	0.173	0.013
Simple-Elaborate	0.182	0.106	0.257	3.00e-7
Simple-Mixed	0.086	0.030	0.143	0.001

Table S2.13. Tukey pairwise comparison test with 95% family-wise confidence level for the organization type. Since Tukey's test is a post-hoc test, we first fitted the best linear regression model (lm) and performed ANOVA on the data. Gov means governmental organization, NPO means Non-profit organization, Acad means Academic organization, CDO means citizen-driven organization, Ind means Industrial organization, and mixed means more than 2 organization as the main leader of the project.

<i>Pairwise comparisons</i>	<i>diff</i>	<i>lwr</i>	<i>upr</i>	<i>p adj</i>
Mixed-Gov_NPO	0.020	-0.147	0.189	0.999
Acad_NPO-Gov_NPO	0.081	-0.115	0.277	0.943
Gov-Gov_NPO	0.090	-0.069	0.251	0.711
NPO_CDO-Gov_NPO	0.106	-0.098	0.312	0.801
Gov_Acad-Gov_NPO	0.109	-0.123	0.342	0.879
Acad-Gov_NPO	0.127	-0.039	0.293	0.297
NPO-Gov_NPO	0.149	0.002	0.296	0.044*
CDO-Gov_NPO	0.194	-0.021	0.411	0.116
Ind-Gov_NPO	0.380	-0.022	0.783	0.081
Acad_NPO-Mixed	0.060	-0.115	0.236	0.982
Gov-Mixed	0.070	-0.063	0.203	0.796
NPO_CDO-Mixed	0.086	-0.099	0.271	0.888
Gov_Acad-Mixed	0.088	-0.126	0.304	0.943
Acad-Mixed	0.106	-0.035	0.247	0.317
NPO-Mixed	0.128	0.010	0.246	0.021*
CDO-Mixed	0.174	-0.024	0.372	0.136
Ind-Mixed	0.359	-0.033	0.753	0.103
Gov-Acad_NPO	0.009	-0.158	0.177	1.000
NPO_CDO-Acad_NPO	0.025	-0.185	0.237	0.999
Gov_Acad-Acad_NPO	0.028	-0.209	0.266	0.999
Acad-Acad_NPO	0.046	-0.128	0.219	0.997
NPO-Acad_NPO	0.068	-0.087	0.223	0.918
CDO-Acad_NPO	0.113	-0.108	0.336	0.817

Ind-Acad_NPO	0.299	−0.106	0.705	0.345
NPO_CDO-Gov	0.016	−0.162	0.193	0.999
Gov_Acad-Gov	0.018	−0.190	0.227	0.999
Acad-Gov	0.036	−0.095	0.167	0.996
NPO-Gov	0.058	−0.047	0.164	0.742
CDO-Gov	0.104	−0.087	0.295	0.757
Ind-Gov	0.289	−0.100	0.679	0.334
Gov_Acad-NPO_CDO	0.002	−0.242	0.248	1.000
Acad-NPO_CDO	0.020	−0.163	0.203	0.999
NPO-NPO_CDO	0.042	−0.123	0.208	0.998
CDO-NPO_CDO	0.088	−0.142	0.318	0.964
Ind-NPO_CDO	0.273	−0.136	0.684	0.492
Acad-Gov_Acad	0.017	−0.196	0.231	0.999
NPO-Gov_Acad	0.039	−0.159	0.239	0.999
CDO-Gov_Acad	0.085	−0.169	0.340	0.985
Ind-Gov_Acad	0.270	−0.154	0.695	0.556
NPO-Acad	0.022	−0.092	0.137	0.999
CDO-Acad	0.067	−0.128	0.264	0.981
Ind-Acad	0.253	−0.139	0.645	0.538
CDO-NPO	0.045	−0.134	0.225	0.998
Ind-NPO	0.231	−0.153	0.615	0.638
Ind-CDO	0.185	−0.231	0.601	0.910

Table S2.14. Tukey pairwise comparison test with 95% family-wise confidence level for the location. Since Tukey's test is a post-hoc test, we first fitted the best linear regression model (lm) and performed ANOVA on the data*.

<i>Pairwise comparisons</i>	<i>diff</i>	<i>lwr</i>	<i>upr</i>	<i>p adj</i>
Europe- Central_South_America	0.058	−0.331	0.449	0.999
Antarctica- Central_South_America	0.130	−0.395	0.657	0.996
Oceania- Central_South_America	0.197	−0.183	0.578	0.777
Worldwide- Central_South_America	0.208	−0.186	0.603	0.761
North_America- Central_South_America	0.218	−0.156	0.593	0.651
Africa- Central_South_America	0.228	−0.187	0.644	0.720

Asia-Central_South_America	0.231	−0.295	0.758	0.897
America-Central_South_America	0.247	−0.159	0.655	0.596
Antarctica-Europe	0.072	−0.318	0.462	0.999
Oceania-Europe	0.138	−0.003	0.280	0.060.
Worldwide-Europe	0.149	−0.027	0.326	0.166
North_America-Europe	0.159	0.033	0.285	0.003*
Africa-Europe	0.169	−0.050	0.389	0.273
Asia-Europe	0.172	−0.217	0.563	0.893
America-Europe	0.189	−0.014	0.393	0.091
Oceania-Antarctica	0.066	−0.314	0.447	0.999
Worldwide-Antarctica	0.077	−0.317	0.472	0.999
North_America-Antarctica	0.087	−0.287	0.462	0.998
Africa-Antarctica	0.097	−0.318	0.513	0.998
Asia-Antarctica	0.100	−0.426	0.627	0.999
America-Antarctica	0.116	−0.290	0.524	0.991
Worldwide-Oceania	0.010	−0.142	0.164	0.999
North_America-Oceania	0.020	−0.070	0.112	0.998
Africa-Oceania	0.030	−0.171	0.233	0.999
Asia-Oceania	0.033	−0.346	0.414	0.999
America-Oceania	0.050	−0.134	0.234	0.994
North_America-Worldwide	0.010	−0.129	0.149	0.999
Africa-Worldwide	0.020	−0.207	0.248	0.999
Asia-Worldwide	0.023	−0.371	0.418	1.000
America-Worldwide	0.039	−0.172	0.251	0.999
Africa-North_America	0.009	−0.181	0.201	1.000
Asia-North_America	0.013	−0.362	0.388	1.000
America-North_America	0.029	−0.143	0.202	0.999
Asia-Africa	0.003	−0.413	0.419	1.000
America-Africa	0.019	−0.230	0.269	0.999
America-Asia	0.016	−0.391	0.424	1.000

* We also tried to test the influence of predictors on database size, but different projects had different meaningful unit to evaluate the database size (i.e. number of sites, count, and observations). As the subsample created by those three divisions was too low for the global model to converge, we were unable to evaluate the influence of predictors on the database size.

Survey:
**Scientific contributions of citizen science projects focusing on rare
and threatened species.**

1. Project name:

2. How many years have you been (or were) managing this program?

- ☐ < 1 year
- ☐ 1-2 years
- ☐ 2-5 years
- ☐ ≥ 5 years

3. What is your highest level of educational attainment?

- ☐ High school
- ☐ Professional studies
- ☐ Collegial
- ☐ University (undergrad)
- ☐ University (Master)
- ☐ University (PhD)
- ☐ University (postdoc)

4. What year was your program founded?

5. Is it still running? If not, mention the year the program ended.

- ☐ Yes
- ☐ No: Ending year: _____

6. What is the largest scale at which your project is (was) operating?

- ☐ Local
- ☐ Regional
- ☐ National
- ☐ International

7. Location of data collection? More than one choice is possible.

- ☐ North America: is it in a specific country or region? _____
- ☐ South America: is it in a specific country or region? _____
- ☐ Central America: is it in a specific country or region? _____
- ☐ Europe: is it in a specific country or region? _____
- ☐ Russia: is it in a specific region? _____
- ☐ Asia: is it in a specific country or region? _____
- ☐ Africa: is it in a specific country or region? _____
- ☐ Worldwide

8. What is (was) the focal taxon for your project? More than one choice is possible.

- ☐ Non-flying mammal
- ☐ Flying mammal
- ☐ Bird
- ☐ Reptile
- ☐ Amphibian
- ☐ Marine mammal
- ☐ Fish
- ☐ Insect

9. What is (was) the type of data collected? More than one choice is possible.

- ☐ Locations where the species has been observed
- ☐ Locations where the species reproduces
- ☐ Counts of individuals
- ☐ Counts of colonies or group of individuals
- ☐ Absence as well as presence of individuals
- ☐ Indirect presence (i.e. call, pellet, footprint, etc.)
- ☐ Other: _____

10. What is (was) the main goal(s) of the project? More than one choice is possible.

- ☐ Advancement of scientific knowledge (Distribution, ecology, population dynamics, etc.)
- ☐ Conservation
- ☐ Dissemination of results to the general public
- ☐ Public education and engagement

11. Protocol and participant training.

a) Is (Was) a written protocol freely available?

- ☐ Yes
- ☐ No

Comments:

b) Did you use one or more rounds of pilot testing of the protocol before officially collecting data through this protocol.

- ☐ Yes
- ☐ No

Comments:

c) Is (Was) personal training/support freely available (i.e. data collection, organism identification, use of equipment)? More than one choice is possible.

- ☐ In-person support (i.e. training or workshop)
- ☐ Hard copy support (i.e. pamphlets or guide)
- ☐ Electronic support (i.e. webpages or downloadable materials)
- ☐ None

Comments:

d) How systematic are (were) the task procedures and data entry (e.g. for online data entry, do fields enforce type (e.g. counts are integers), and for categorical variables, users select from lists rather than entering free-form text)?

- ☐ Systematic (only check boxes and/or items selected from lists except for comments)
- ☐ Semi-systematic (a mix of check boxes, lists, enforce type and free-form text)
- ☐ Non-systematic (only free-form text)

Comments:

e) Does (Did) the project record relevant metadata? More than one choice is possible.

- ☐ Environmental conditions (temperature, precipitation, time of day, etc.)
- ☐ Equipment or device settings (such as mobile device operating system version)
- ☐ Characteristics of the volunteers themselves (such as the level of education or training)
- ☐ None
- ☐ Other: _____

12. Is (Was) there a collection feature allowing for data verifiability? More than one choice is possible.

- ☐ Submission of photos
- ☐ Submission of audio
- ☐ Submission of specimens
- ☐ Expert present at the time of collection
- ☐ None
- ☐ Other: _____

13. Is (Was) there data validation by a professional after the participant data entry?

- ☐ Yes
- ☐ No

Comments:

14. Is (was) collection effort standardized or accounted for in data analysis? I.e., were data standardized for inter-individual variation, effort, time, or distance?

- ☐ All (all data collection methods were standardized)
- ☐ Some (only a portion of data collection methods were standardized)
- ☐ None
- ☐ Not applicable (no data analysis yet)

Comments:

15. Database size.

a) What is (was) the total numbers of;

Sites? _____

And/or

Counts? _____

And/or

Observations? _____

And/or

Other? Please, describe: _____

b) What is (was) the mean number of new entries per year of;

Sites? _____

And/or

Counts? _____

And/or

Observations? _____

And/or

Other? Please, describe: _____

16. Was (Were) peer-reviewed publications produced using the project data?

- ☐ None that I am aware of
- ☐ 1

- ☐ 2-5
- ☐ 6-10
- ☐ >10

If the answer is yes, please, include the full title(s) and/or the link(s) of the paper(s) if possible.

17. Was (were) grey literature(s) (i.e. government reports, conference proceedings, conference abstracts, book chapters, theses, or magazine articles) produced using the project data?

- ☐ None that I am aware of
- ☐ 1
- ☐ 2-5
- ☐ 6-10
- ☐ >10

If the answer is yes, please, include the full title(s) and/or the link(s) of the paper(s) if possible.

18. Do (Did) conservation measures (e.g. conservation initiatives, management decisions, or policy actions) result from the project data?

- ☐ None that I am aware of
- ☐ 1
- ☐ 2-5
- ☐ 6-10
- ☐ >10

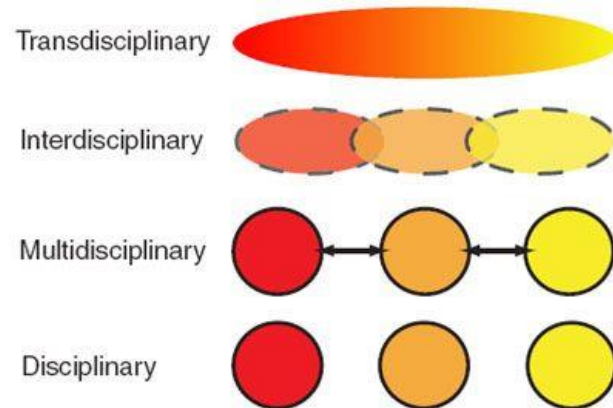
If the answer is yes, please, describe the measure(s).

19. What type of organizations runs (ran) the project? More than one choice is possible.

- ☐ Governmental. Name the organization: _____
- ☐ Academic. Name the organization: _____
- ☐ Industrial. Name the organization: _____
- ☐ Non-profit Organization. Name the organization: _____
- ☐ Citizen-driven organization. Name the organization: _____

20. What is (was) the disciplinary type? if your disciplinary type has changed over time, please checked your latest type and mention when and what was your previous type in the comments.

- ☐ **Intradisciplinary**
Working within a single discipline (i.e. biology).
- ☐ **Multidisciplinary**
People from different disciplines working together, each drawing on their disciplinary knowledge in an additive manner (i.e. studying bats from the morphology and disease-carrying point of view).
- ☐ **Interdisciplinary**
Integration of knowledge and methods from different disciplines using a synthesis of approaches with stronger level of cooperation.
- ☐ **Transdisciplinary**
Creating a unity of intellectual frameworks beyond the disciplinary perspectives to form a new holistic approach.



© Photo from nature.com

Comments:

21. What is (was) your governance structure? if your structure has changed over time, please checked your latest type and mention when and what was your previous structure in the comments.

Definitions based on Conrad & Hilchey, 2010.

- ☐ **Consultative/functional**
Most often government led, community run; government recognizes problem and uses community-based monitoring group to monitor. Traditionally referred to as top-down.

- ☐ Collaborative/multi-party

Often governed by a board or group representing as many facets of the community as possible: private landowners, the general public, businesses, government, universities, etc. i.e. watershed.

- ☐ Transformative

Community led, run, and funded. Governed from the “bottom-up”. Also called community-based, grassroots, or advocacy groups. Community focuses on an issue with the hopes of initiating government action. Often focuses on specific local issues with no private sector or government support.

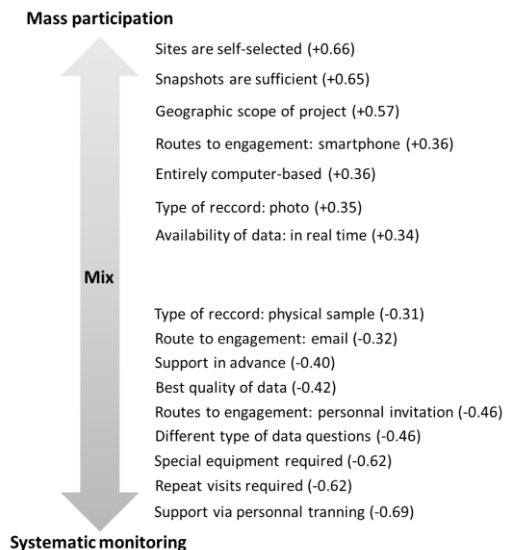
Comments:

22. What is (was) the methodological approach of the project? If you check more than one choice because your project has many components, please explain it in the comments.

Figure based on Pocock & al. 2017 (table 1, axis 1).

- ☐ Mass participation
Tended to be projects in which anyone can get involved anywhere.
- ☐ Mixed
- ☐ Systematic
Tended to require participation at pre-defined sites that are visited repeatedly and to require particular equipment e.g. binoculars or tape measures.

Comments:



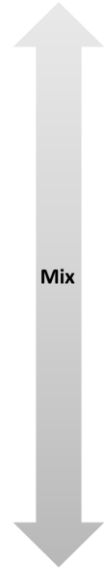
23. What is (was) the methodological complexity of the project? If you check more than one choice because your project has many components, please explain it in the comments.

Gradient based on Pocock & al. 2017 (table 1, axis 2).

- ☐ **Elaborate**
Tended to have complex protocols coupled with comprehensive supporting material and yield comparatively rich datasets.
- ☐ **Mixed**
- ☐ **Simple**
Tended to have little or no structured protocol, although they may require expertise such as species identification, and produced big datasets with simple structures.

Comments:

Elaborate



Mix

Simple

Best quality of data (+0.58)
Support via supporting material (+0.52)
Different types of data questions (+0.51)
Background context (+0.48)
Route to engagement: website (+0.47)
Targetted at school children (+0.44)
Availability of data: to view (+0.42)
Registration required (+0.36)
Support via online media (+0.34)
Availability of data: in real time (-0.40)
Type of record: score (+0.31)

24. If you win the pre-paid card price, can we mention your name and organization as winner in the participation thank you email?

- ☐ **Yes**
- ☐ **No**

Supplementary materials for chapter 3

Table S3.1. Administrative regions of Quebec with its population in 2020, area, and land cover classes. Data from: <https://statistique.quebec.ca/en/vitrine/region>.

Administrative regions	Population in 2020 (inhab.)	Total Area (km ²)	Land cover classes (%)				Last update of land cover classes
			Artificial	Agricultural	Forest and wetlands	Water plan	
1. Bas-Saint-Laurent	197 897	28 396	1.14	8.00	69.04	21.82	2004
2. Saguenay-Lac-Saint-Jean	278 971	94 463	0.54	1.60	87.95	9.92	2008
3. Capitale-Nationale	757 065	20 966	2.80	3.90	82.37	10.93	2002
4. Mauricie	274 013	39 902	0.93	2.55	85.52	11.00	2008
5. Estrie	333 704	10 505	3.57	16.17	77.40	2.86	2007
6. Montréal	2 069 849	625	71.77	1.44	6.55	20.24	2007
7. Outaouais	401 388	34 048	0.92	3.56	85.24	10.29	2003
8. Abitibi-Témiscamingue	147 897	64 573	0.51	2.27	86.18	11.04	2005
9. Côte-Nord	905 29	93 833	0.44	0.06	49.76	49.74	2013
10. Nord-du-Québec	461 78	79 286	0.35	0.03	89.22	10.40	2011
11. Gaspésie-Îles-de-la-Madelaine	906 97	77 973	0.26	0.42	25.09	74.22	2004
12. Chaudières-Appalaches	432 782	16 129	3.14	19.22	71.16	6.49	2003
13. Laval	442 648	267	56.90	16.39	19.02	7.73	2007
14. Lanaudière	524 368	13 508	3.21	9.65	78.45	8.69	2008
15. Laurentides	631 592	22 510	2.62	4.05	84.83	8.49	2005
16. Montérégie	1 603 232	11 810	9.05	53.46	31.37	6.12	2009
17. Centre-du-Québec	251 671	7 260	3.55	41.01	50.82	4.62	2006

Table S3.2. Model selection based on the Akaike information criterion corrected for small sample sizes (AICc) of factors influencing large scale maternity colony size trends in Quebec, Canada.

Model	AIC _c	Δ _i AIC _c
(Twins + I(Twins ²)) * species_id * region + reprod_period + (1 colony_id)	7665.516	0
ln(Twins+2) * species_id * region + reprod_period + (1 colony_id)	7959.779	294.263
Twins * species_id * region + reprod_period + (1 colony_id)	9346.371	1680.855
Twins * species_id + region + reprod_period + (1 colony_id)	10207.09	2541.574
year + species_id * region + reprod_period + (1 colony_id)	10427.89	2762.374
Twins * region + species_id + reprod_period + (1 colony_id)	11397.25	3731.734
Twins + species_id * region + reprod_period + (1 colony_id)	11817.17	4151.654

Supplementary materials for chapter 4

Table S4.1. Mixed effect model selection to determine arrival date and spring weather variables used in the global model of parturition date at the Domaine Joly, Quebec, Canada (n=80). Individual identification and year were included as random factors in all models. Models ranked by their corresponding Akaike's information criterion corrected for small sample. Best model is bolded. If more than one model had $\Delta AIC_c < 2$, the most parsimonious model was considered best.

Model	AIC_c	$\Delta_i AIC_c$	w_i
Arrival date + Mean temperature at night + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	332.37	0.00	0.55
Arrival date + Mean temperature + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	333.36	0.99	0.33
Arrival date + Nb of days with maximal temperature between 21-32 °C + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	337.34	4.97	0.05
Arrival date + Mean temperature at night + Total rainfall + Mean wind speed	337.88	5.51	0.03
Arrival date + Mean temperature + Total rainfall + Mean wind speed	338.77	6.40	0.02
Arrival date + Nb of hours between 21-32 °C + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	341.1128	8.74	0.01
Arrival date + Nb of hours between 21-32 °C + Total rainfall + Mean wind speed	341.29	8.92	0.01
Arrival date + Nb of days with maximal temperature between 21-32 °C + Total rainfall + Mean wind speed	342.6445	10.28	0.00
Arrival date + Nb of hours between 15-32 °C + Total rainfall + Mean wind speed	347.05	14.68	0.00
(1 arrival_date) + Nb of hours between 21-32 °C + Total rainfall + Mean wind speed	347.61	15.25	0.00
Arrival date + Nb of hours between 15-32 °C + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	348.16	15.79	0.00

Table S4.2. Top 5 of mixed effect models of parturition date on arrival date and spring weather conditions used for model selection at the Domaine Joly, Quebec, Canada (n=80). Individual identification and year were included as random factors in all models. Models ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). $\Delta_i\text{AICc}$ is the difference between AICc for the current model and the minimum of AICc among all the models. w_i = Akaike weights. Best model is bolded. If more than one model had $\Delta\text{AICc} < 2$, the most parsimonious model was considered best.

Model	AIC_c	$\Delta_i\text{AIC}_c$	w_i
Arrival date + Mean temperature at night + Mean wind speed	331.80	0	0.51
Arrival date + Mean temperature at night + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	333.37	1.57	0.23
Arrival date + Mean temperature at night	334.48	2.69	0.13
Arrival date + Mean wind speed	336.46	4.66	0.05
Arrival date + Nb of days with rainfall between 2.5-25 mm + Mean wind speed	336.86	5.06	0.04

Table S4.3. Mixed effect model selection to determine weather condition variables used in the global model of time away from the roost at the Domaine Joly, Quebec, Canada (n=687). Night length and reproductive status were included as fixed factors in all models as well as individual identification and year as random factors. Models ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). $\Delta_i\text{AICc}$ is the difference between AICc for the current model and the minimum of AICc among all the models. ω_i = Akaike weights. Best model is bolded. If more than one model had $\Delta\text{AICc} < 2$, the most parsimonious model was considered best.

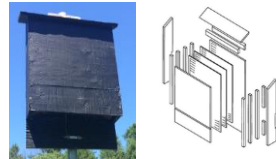


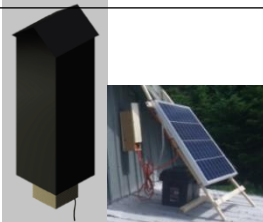
Model	AIC _c	$\Delta_i\text{AICc}$	ω_i
Reproductive status + Night length + Mean temperature + Total rainfall + Mean wind speed	6835.76	0.00	0.75
Reproductive status + Night length + Mean temperature + Mean rainfall + Mean wind speed	6838.21	2.46	0.22
Reproductive status + Night length + Minimal temperature + Mean rainfall + Mean wind speed	6843.39	7.64	0.02
Reproductive status + Night length + Minimal temperature + Total rainfall + Mean wind speed	6844.76	9.00	0.01

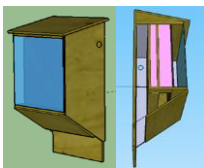
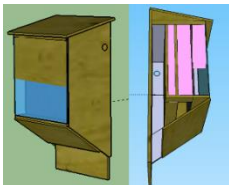


Table S4.4. Top 5 of mixed effect models of foraging bouts on night length, reproductive status, and weather conditions used for night weather variables selection at the Domaine Joly, Quebec, Canada (n=687). Individual identification and year were included as random factors in all models. Models ranked by their corresponding Akaike's information criterion corrected for small sample size (AICc). $\Delta_i\text{AICc}$ is the difference between AICc for the current model and the minimum of AICc among all the models. ω_i = Akaike weights. Best model is bolded. If more than one model had $\Delta\text{AICc} < 2$, the most parsimonious model was considered best.

Model	AIC _c	$\Delta_i\text{AICc}$	ω_i
Night length + Mean Temperature + Total rainfall	6833.90	0.00	0.31
Night length + Mean Temperature + Total rainfall + Mean wind speed	3834.00	0.12	0.14
Reproductive status + Night length + Mean Temperature + Total rainfall	6835.50	1.63	0.12
Reproductive status + Night length + Mean temperature + Total rainfall + Mean wind speed	6835.80	1.87	0.03
Mean Temperature + Total rainfall	6838.50	4.66	0.03

Supplementary materials for chapter 5

Table S5.1. Description of bat box models tested in Quebec, Canada, from 2016 to 2019. Model names refer to their shape and number of passive heating (PH) zones (1, 2 or 3 reflexives faces). An iButton was placed in the top quarter of each bat box except for the newly designed models where one iButton was placed in the main or warm chamber and a second one in the lower or cold chamber.

Model		Image(s)	Dimensions and materials	Description	Years and number of bat boxes tested on poles and buildings
Traditional					
1	Classic (4-chambers)		78x43x11 cm wood	Rectangular shape. Commonly used in North America. Developed by Bat Conservation International. Cheap and easy to build.	2016 (n _{pole} =2, n _{build} =3) 2017 (n _{pole} =10, n _{build} =16) 2018 (n _{pole} =6, n _{build} =5) 2019 (n _{pole} =6, n _{build} =5)
2	European (1-chamber)		44x29x9 cm woodcement	Rectangular shape. Chillon bat box from wildcare. Woodcement commonly used in Europe. This material has similar properties than wood, but more durable and heavier.	2016 (n _{pole} =2, n _{build} =2) 2017 (n _{pole} =2, n _{build} =2) 2018 (n _{pole} =2, n _{build} =2) 2019 (n _{pole} =2, n _{build} =2)
Rocket					
3	Insulated rocket (1-chamber)		120x34x34 cm wood and 2.5 cm thick styrofoam insulation	The rocket model has an elongated shaped that allow a vertical gradient of temperature. One big chamber evolving around a closed space in the middle used to insert a pole or a heat mat.	2016 (n _{pole} =1, n _{build} =1) 2017 (n _{build} = 1) 2018 (n _{pole} =1) 2019 (n _{build} =1)
4	Insulated heated rocket (1-chamber)		120x34x34 cm wood, 2.5 cm thick styrofoam insulation, heated mat, and a solar kit (undulator, timer, converter, battery, and solar panel)	The rocket model has an elongated shaped that allow a vertical gradient of temperature. One big chamber evolving around a closed space in the middle used to insert a pole or a heat mat. Developed by Genivar in 2011 and adapted to solar energy by Quebec MFFP in 2016. Considering the capacity limit of the battery, a timer was set to turn on the heated mat for 30 minutes three times per night: 12:00AM, 2:00AM, and 4:00AM.	2016 (n _{pole} =1, n _{build} =1) 2017 (n _{pole} =2, n _{build} =1) 2018 (n _{pole} =1, n _{build} =2) 2019 (n _{pole} =2, n _{build} =1)

Newly designed model					
5	Biclimat.0 PH1 (2-chambers)		60x30x20 cm wood, 2.5 cm thick styrofoam insulation, permabase cement board, and plexiglass	One "cold" chamber at the back. In the middle, the insulated "hot" chamber stands against a frontal passive heating zone that conducts the heat inside. The passive heating zone is made of plexiglass, an empty space (air) and a conductive material (permabase cement board).	2016 ($n_{\text{pole}}=2$, $n_{\text{build}}=2$) 2017 ($n_{\text{pole}}=2$, $n_{\text{build}}=2$) 2018 ($n=0$) 2019 ($n=0$)
6	Biclimat PH1 (2-chambers)		81x43x23 cm wood, 2.5 cm thick styrofoam insulation, permabase cement board, and plexiglass	Same as the Biclimat model but bigger dimensions and a reduction of the passive heating zone by two thirds. at Transition Énergétique Quebec.	2017 ($n_{\text{pole}}=3$, $n_{\text{build}}=4$) 2018 ($n_{\text{pole}}=3$, $n_{\text{build}}=4$) 2019 ($n=0$)
7	Rocket PH2 (1-chamber)		120x34x34 cm wood, 2.5 cm thick styrofoam insulation, plexiglass, and permabase cement board	Same as the insulated rocket model, with the addition of two passive heating zones of 25cmx25cm at the bottom facing east and west. Designed for pole.	2017 ($n_{\text{pole}}=4$) 2018 ($n_{\text{pole}}=4$) 2019 ($n_{\text{pole}}=4$)
8	Classic PH2 (3-chambers)		65x58x20 cm wood, 2.5 cm thick styrofoam insulation, clapboards, corrugated PVC panel, and permabase cement board,	Same shape as the classic model but insulated at front and the back and covered with clapboards. Reduction of the entrance to one inch wide. Two passive heating zones on each side, facing east and west, made of corrugated plexiglass to increase the contact surface, an empty space (air) and a conductive material (permabase cement board). Designed for pole.	2018 ($n_{\text{pole}}=3$) 2019 ($n_{\text{pole}}=3$)

9	Classic PH1 (3-chambers)		65x53x24 cm wood, 2.5 cm thick styrofoam insulation, plexiglass, and permabase cement board	Same as the Classic PH2 2018 but with only one passive heating zone at the front facing east. Designed for building.	2018 ($n_{\text{build}}=4$) 2019 ($n_{\text{build}}=4$)
10	Ncube.0 PH1 (3-chambers)		77x52x24 cm wood, 2.5 cm thick styrofoam insulation, plexiglass, and clay brick	Similar shape as the classic PH1 model, but fully insulated. Use of a reduced chicane entrance (2.5 x 10.2 cm). One passive heating zone at the front facing east, overlapping with the entrance preferably facing east. The passive heating zone is made of a high-core corrugated plexiglass, an empty space (air) and a conductive material (clay brick) slowly diffuse the heat inside the three chambers. Convection principle due to an opening at the top of zone. Removable insulated roof. Designed for building.	2018 ($n_{\text{pole}}=2$, $n_{\text{build}}=5$) 2019 ($n_{\text{pole}}=1$, $n_{\text{build}}=5$)
11	Ncube.0 PH3 2018 (4-chambers)		92x41x24 cm wood, 2.5 cm thick styrofoam insulation, plexiglass, and clay brick, light cement panel	Same as the Ncube PH1 2018, but with three passive heating zones facing east, south, and west overlapping with the entrance and the chambers. Conduction principle due to the fixation of the brick on a light cement panel. Removable insulated roof. Designed for pole.	2018 ($n_{\text{pole}}=2$, $n_{\text{build}}=5$) 2019 ($n_{\text{build}}=5$)
12	Ncube PH1 (3-chambers)		92x41x24 cm wood, 5 cm thick styrofoam insulation, plexiglass, and clay brick, light cement panel	Improved version Ncube PH1 2018 and Ncube PH3 2018 with thicker insulation (10.2 vs. 5 cm). Removable insulated roof. A cool zone at the bottom of the entrance had been added made of 3 wood wall and a fence where bats could safely go if overheating in the main chambers. One passive heating zone at the front facing east overlapping with the main chambers only. Heating zone using conduction principle.	2019 ($n_{\text{pole}}=4$, $n_{\text{build}}=4$)

Table S5.2. Parameter estimates, standard error (SE), t value, and the probability of observing any value equal or larger than t from generalized additive mixed model accounting for time, date, external temperature, orientation, site, and individual bat box identity for T_{int} for the mounting experiment.

	Estimate	SE	t value	$\text{Pr}(> t)$
Intercept	18.110	2.039	8.882	< 2e-16 ***
Heated building	3.176	0.360	8.815	< 2e-16 ***
Non heated building	3.556	0.360	9.871	< 2e-16 ***
Pole	3.570	0.360	9.911	< 2e-16 ***

Table S5.3. Adjusted p-values of the mounting comparisons from generalized additive mixed model accounting for time, date, external temperature, orientation, site, and individuals bat box identity. Asterisks (*) represent significant T_{int} differences among mountings during the day and night. P-values have been adjusted for multiple comparisons using the R function `wald_gam`.

Mounting comparison	Heated building		Non-heated building		Pole	
	Day	Night	Day	Night	Day	Night
Heated building			0.326	0.740	0.050*	0.009**
Non-heated building	0.326	0.740			0.326	0.023*
Pole	0.050*	0.009**	0.326	0.023*		

Table S5.4. Parameter estimates, standard error (SE), t value, and the probability of observing any value equal or larger than t from generalized additive mixed model accounting for time, date, external temperature, mounting, site, and individual bat box identity for T_{int} for the orientation experiment.

	Estimate	SE	t value	Pr(> t)
Intercept	-2.041e-05	3.840e-04	-0.053	0.958
External	-3.618	0.597	-6.057	1.4e-09 ***
South	-1.178	0.598	-1.972	0.049 *
South-East	0.214	0.299	0.716	0.474
West	-0.145	0.597	-0.243	0.808
Non heated building	0.401	0.597	0.671	0.502
Pole	0.141	0.598	0.235	0.814
Year	0.011	4.454e-04	24.253	< 2e-16 ***
External:Non heated building	-0.298	0.810	-0.368	0.713
South:Non heated building	0.448	0.845	0.530	0.596
West:Non heated building	-0.509	0.845	-0.603	0.547
External:Pole	-0.037	0.81	-0.046	0.963
South:Pole	0.670	0.845	0.792	0.428
South-East:Pole	0.214	0.299	0.716	0.474

Table S5.5. Adjusted p-values of the orientation comparisons from generalized additive mixed model accounting for time, date, external temperature, mounting, site, and individual bat box identity. Asterisks (*) represent significant T_{int} differences between orientations during the day and night. P-values have been adjusted for multiple comparisons using the R function `wald_gam`.

Orientation comparison	Heated building		Non-heated building		Pole	
	Day	Night	Day	Night	Day	Night
East-South	0.046 *	0.274	0.023*	0.876	0.023 *	0.642
East-West	0.033*	0.007 **	0.014*	0.417		
South-West	0.310	0.106	0.787	0.334		
East-SouthEast					0.232	0.977
South-SouthEast					0.283	0.624

Table S5.6. Parameter estimates, standard error (SE), t value, and the probability of observing any value equal or larger than t from generalized additive mixed model accounting for time, week, year, mounting, external temperature, site, and individual bat box identity for T_{int} for the design experiment.

	Estimate	SE	t value	$\Pr(> t)$
Intercept	612.775	275.523	2.224	0.026 *
Biclimatic PH1 hot chamber	2.098	0.605	3.467	5.28 e-04 ***
Biclimatic PH1 cold chamber	0.080	1.906	0.042	0.967
Biclimatic PH1.0 cold chamber	1.110	0.740	1.500	0.134
Biclimatic PH1.0 hot chamber	2.994	0.739	4.053	5.06e-05 ***
Classic	1.080	0.508	2.110	0.035 *

Classic PH1	2.152	0.734	2.933	0.003 **
Classic PH2	3.042	0.674	4.514	6.38e-06 ***
European	0.246	0.613	0.401	0.688
External	-2.662	0.497	-5.355	8.60e-08 ***
Ncube PH1.0	2.742	0.707	3.879	1.28 e-04 ***
Ncube PH3.0	3.995	0.703	5.686	1.31e-08 ***
Ncube PH1 lower chamber	-0.270	0.747	-0.362	0.718
Ncube PH1 main chamber	3.968	0.746	5.320	1.05e-07 ***
Heated Insulated Rocket	4.540	1.012	4.485	7.32e-06 ***
Insulated Rocket	-0.293	0.695	-0.421	0.673
Rocket PH2	1.693	0.597	2.834	0.005 **
August 2	-0.485	0.064	-7.613	2.75e-14 ***
July 1	0.195	0.065	3.026	0.002 **
July 2	0.166	0.064	2.586	0.010 **
June 1	-0.171	0.076	-2.260	0.024 *
June 2	0.0149	0.067	0.223	0.823
May 2	-0.798	0.089	-8.925	< 2e-16 ***
September 1	-0.808	0.073	-11.069	< 2e-16 ***
Pole	-0.325	0.236	-1.375	0.169
Year	-0.293	0.137	-2.148	0.032 *

Table S5.7. Adjusted p-values of the bat box design comparisons from the generalized additive mixed model accounting for time, week, year, mounting, external temperature, site, and individual bat box identity. Asterisks (*) represent significant T_{int} differences between models during the day and night. P-values have been adjusted for multiple comparisons using the R function `wald_gam`.

Model comparison	Classic		European		Bilimate 2017 hot chamber		Biclimat 2017 cold chamber		Classic PH1 2018		Classic PH2 2018		Ncube PH1 2018	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Classic			0,68	0,522	0.006 **	0,909	0,288	0,328	0,403	0.039 *	0,808	0.013 *	0,959	0.013 *
European	0,68	0,522			0.009 **	0,659	0,592	0,782	0,649	0.022 *	0,614	0.010 *	0,732	0.008 **
European V2	0,303	0.077 .	0,243	0,153	0,872	0.093 .	0,144	0,191	0,178	0.008 **	0,406	0.005 **	0,363	0.005 **
Biclimat PH1.0 hot chamber	2.93e-05 ***	0,642	4.54e-05 ***	0,972	0.061 .	0,741	9.28e-06 ***	0,792	1.13e-04 ***	0.048 *	0.002 **	0.028 *	0.001 **	0.025 *
Biclimat PH1.0 cold chamber	0,444	0,698	0,331	0,917	0,278	0,792	0,168	0,74	0,224	0.055 .	0,649	0.033 *	0,566	0.029 *
Biclimat PH1 hot chamber	0.006 **	0,909	0.009 **	0,659			0.001 **	0,463	0.009 **	0.057 .	0.074 .	0.027 *	0.056 .	0.024 *
Biclimat PH1 cold chamber	0,288	0,328	0,592	0,782	0.001 **	0,463			0,993	0.012 *	0,324	0.004 **	0,42	0.004 **
Classic PH1	0,403	0.039 *	0,649	0.022 *	0.009 **	0.057 .	0,993	0.012 *			0,383	0,856	0,467	0,807
Classic PH2	0,808	0.013 *	0,614	0.010 *	0.074 .	0.027 *	0,324	0.004 **	0,383	0,856			0,882	0,946
Ncube PH1.0	0,959	0.013 *	0,732	0.008 **	0.056 .	0.024 *	0,42	0.004 **	0,467	0,807	0,363	0.005 **		
Ncube PH3.0	0,432	6.95e-04 ***	0,338	8.07e-04 ***	0,211	0.002 **	0,15	2.51e-04 ***	0,198	0,339	0,582	0.001 **	0,554	0,457
Ncube PH1 main chamber	0.022 *	0.018 *	0.021 *	0.011 *	0,869	0.030 *	0.006 **	0.005 **	0.013 *	0,82	0,809	0.005 **	0.063 .	0,992
Ncube lower chamber	0,251	0,344	0,466	0,701	0.004 **	0,449	0,771	0,88	0,799	0.019 *	0,133	0,259	0,321	0.007 **
Heated Insulated Rocket	0,951	4.79e-04 ***	0,877	2.97e-04 ***	0,147	8.09e-04 ***	0,628	1.63e-04 ***	0,645	0.056 .	0,388	2.11e-04 ***	0,932	0.079 .
Insulated Rocket	0.006 **	0.086 .	0.034 *	0.045 *	1.27e-05 ***	0,111	0,102	0.027 *	0,161	0,742	0.023 *	0.014 *	0.030 *	0,558
Rocket PH2	0,1	0.063 .	0,324	0.043 *	2.14e-04 ***	0.097 .	0,631	0.017 *	0,705	0,587	0.089 .	0.012 *	0,224	0,397
External	1.07e-13 ***	1.83e-04 ***	4.70e-07 ***	0.036 *	2.16e-16 ***	0.009 **	1.24e-05 ***	0.080 .	7.19e-04 ***	2.09e-05 ***	6.90e-04 ***	0,56	7.68e-06 ***	1.69e-06 ***

Model comparison (Continued)	Ncube PH3 2018		Ncube 2019 main chamber		Ncube 2019 lower chamber		Heated Rocket		Non Heated Rocket		Rocket PH2 2017		External	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Classic	0,432	6.95e-04 ***	0.022 *	0.018 *	0,251	0,344	0,951	4.79e-04 ***	0.006 **	0.086 .	0,1	0.063 .	1.07e-13 ***	1.83e-04 ***
European	0,338	8.07e-04 ***	0.021 *	0.011 *	0,466	0,701	0,877	2.97e-04 ***	0.034 *	0.045 *	0,324	0.043 *	4.70e-07 ***	0.036 *
European V2	0,582	0.001 **	0,809	0.005 **	0,133	0,259	0,388	2.11e-04 ***	0.023 *	0.014 *	0,089 .	0.012 *	6.90e-04 ***	0,56
Biclimat PH1.0 hot chamber	0.008 **	0.004 **	0,146	0.028 *	5.91e-05 ***	0,714	0.008 **	7.68e-04 ***	3.05e-08 ***	0.087 .	2.22e-06 ***	0.098 .	< 2e-16 ***	0.093 .
Biclimat PH1.0 cold chamber	0,957	0.004 **	0,285	0.032 *	0,154	0,669	0,588	9.04e-04 ***	0.008 **	0.099 .	0.086 .	0,112	2.36e-06 ***	0.079 .
Biclimat PH1 hot chamber	0,211	0.002 **	0,869	0.030 *	0.004 **	0,449	0,147	8.09e-04 ***	1.27e-05 ***	0,111	2.14e-04 ***	0.097 .	2.16e-16 ***	0.009 **
Biclimat PH1 cold chamber	0,15	2.51e-04 ***	0.006 **	0.005 **	0,771	0,88	0,628	1.63e-04 ***	0,102	0.027 *	0,631	0.017 *	1.24e-05 ***	0.080 .
Classic PH1	0,198	0,339	0.013 *	0,82	0,799	0.019 *	0,645	0.056 .	0,161	0,742	0,705	0,587	7.19e-04 ***	2.09e-05 ***
Classic PH2	0,641	0,396	0.086 .	0,956	0,257	0.008 **	0,845	0.070 .	0.020 *	0,604	0,145	0,415	1.23e-06 ***	1.30e-06 ***
Ncube PH1.0	0,554	0,457	0.063 .	0,992	0,321	0.007 **	0,932	0.079 .	0.030 *	0,558	0,224	0,397	7.68e-06 ***	1.69e-06 ***
Ncube PH3.0			0,207	0,467	0,122	7.79e-04 ***	0,603	0,224	0.007 **	0,197	0.056 .	0,089 .	2.23e-07 ***	1.61e-08 ***
Ncube PH1 main chamber	0,207	0,467			0.005 **	0.009 **	0,145	0.084 .	9.40e-05 ***	0,572	0.002 **	0,421	9.44e-11 ***	4.86e-06 ***
Ncube lower chamber	0,122	7.79e-04 ***	0.005 **	0.009 **			0,516	2.67e-04 ***	0,254	0.037 *	0,924	0.034 *	0.003 **	0,225
Heated Insulated Rocket	0,603	0,224	0,145	0.084 .	0,516	2.67e-04 ***			0,122	0.031 *	0,44	0.017 *	0.004 **	8.62e-07 ***
Insulated Rocket	0.007 **	0,197	9.40e-05 ***	0,572	0,254	0.037 *	0,122	0.031 *			0,228	0,853	0.091 .	7.27e-05 ***
Rocket PH2	0.056 .	0,089 .	0.002 **	0,421	0,924	0.034 *	0,44	0.017 *	0,228	0,853			1.35e-04 ***	3.66e-06 ***
External	2.23e-07 ***	1.61e-08 ***	9.44e-11 ***	4.86e-06 ***	0.003 **	0,225	0.004 **	8.62e-07 ***	0.091 .	7.27e-05 ***	1.35e-04 ***	3.66e-06 ***		

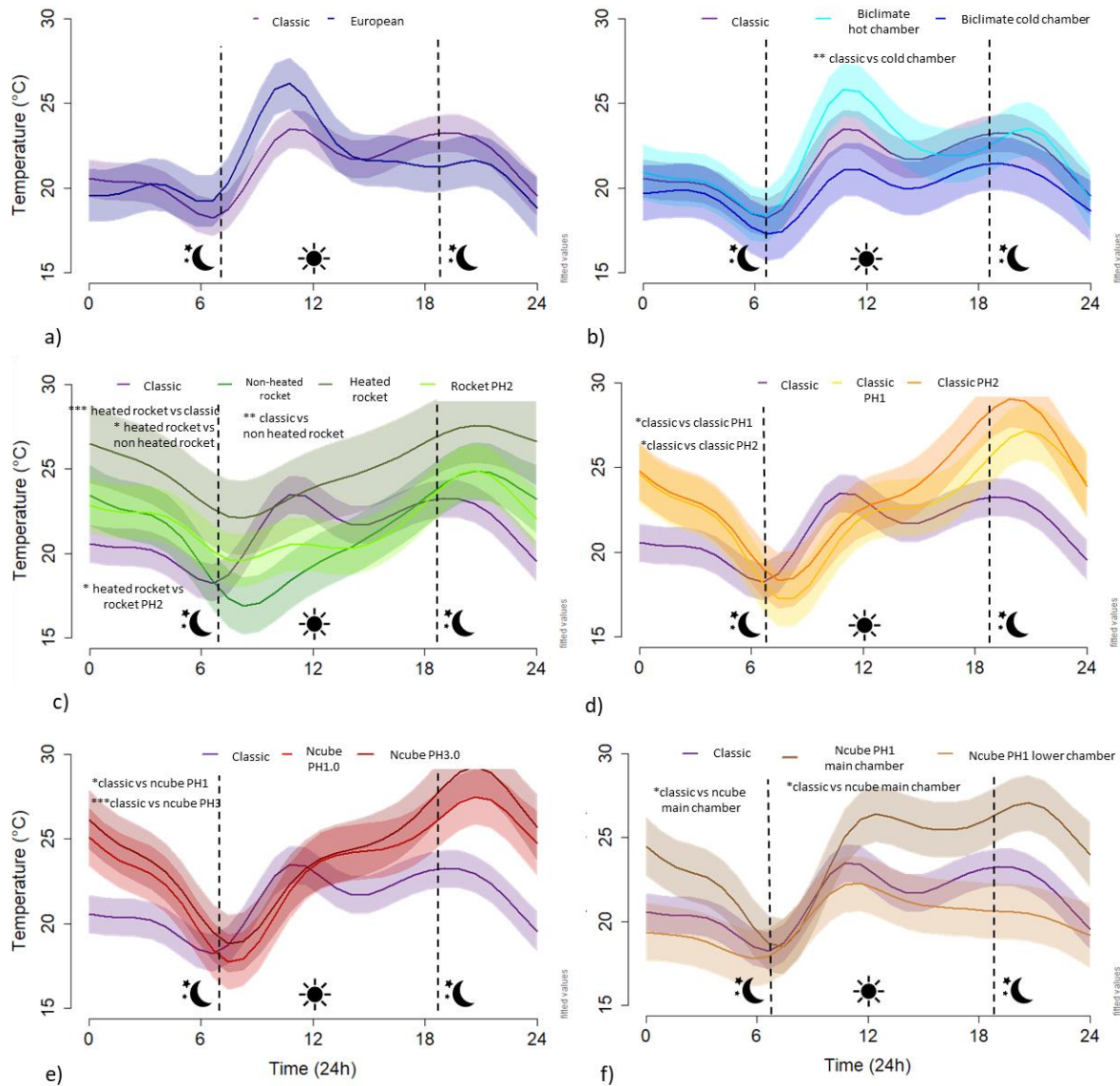
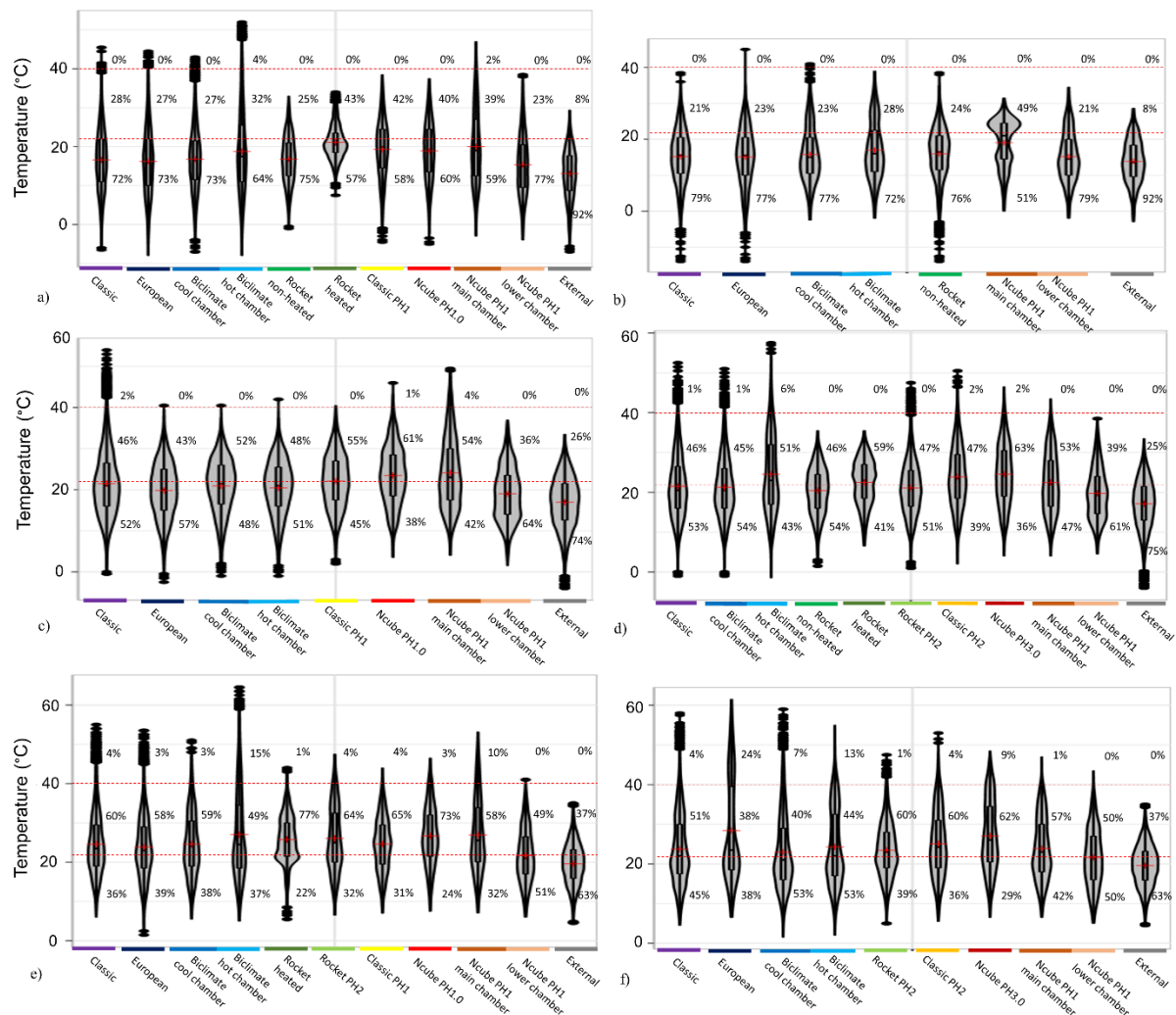


Figure S5.1. Estimated hourly patterns for different bat box designs compared with the Classic models. The estimated values are based on a generalized additive mixed model accounting for time, week, year, mounting, external temperature, site, and individual bat box identity. Values of fixed factors have been set to: week = first half of July, year = 2019, mounting = building, external temperature = 18°C. a) European, b) Biclimatic cold and hot chambers, c) Heated Rocket and Rocket PH2, d) Classic PH1 and PH2, e) Ncube PH1.0 and PH3.0, and f) Ncube PH1 main and lower chambers. The dotted vertical lines represent the separation between the day and the night. The asterisks (*) represent significant differences between models during the day and night.



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12 Figure S5.2. Variation of internal temperatures for all models from mid-May to mid-September
 13 2017-2019 per climate and mounting type in Quebec, Canada: a) cooler sites on buildings, b)
 14 cooler sites on poles, c) intermediate sites on buildings, d) intermediate sites on poles, e) warmer
 15 sites on buildings, f) warmer sites on poles. The violins represent the temperature range of each
 16 model with the minimal and maximal temperature represented by the bottom and the top of the
 17 violin respectively. The width of the violin represents the distribution of the data. The black
 18 horizontal bar represents the median and the red cross the mean value. The red dotted lines
 19 represent the extended optimal temperature range of 22-40 °C. The percentages below, in
 20 between, and over the extended optimal temperature range are represented beside each violin.

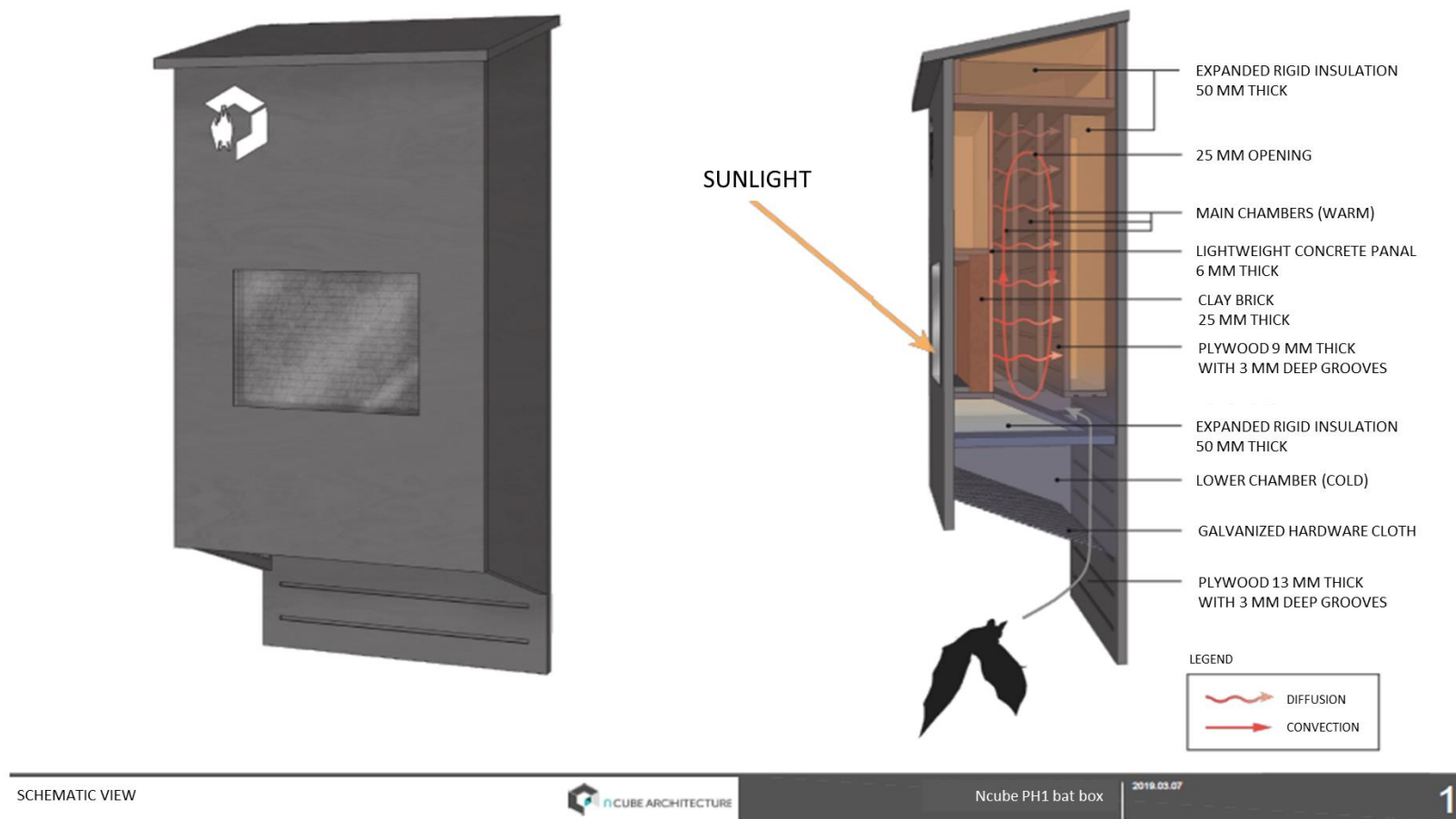
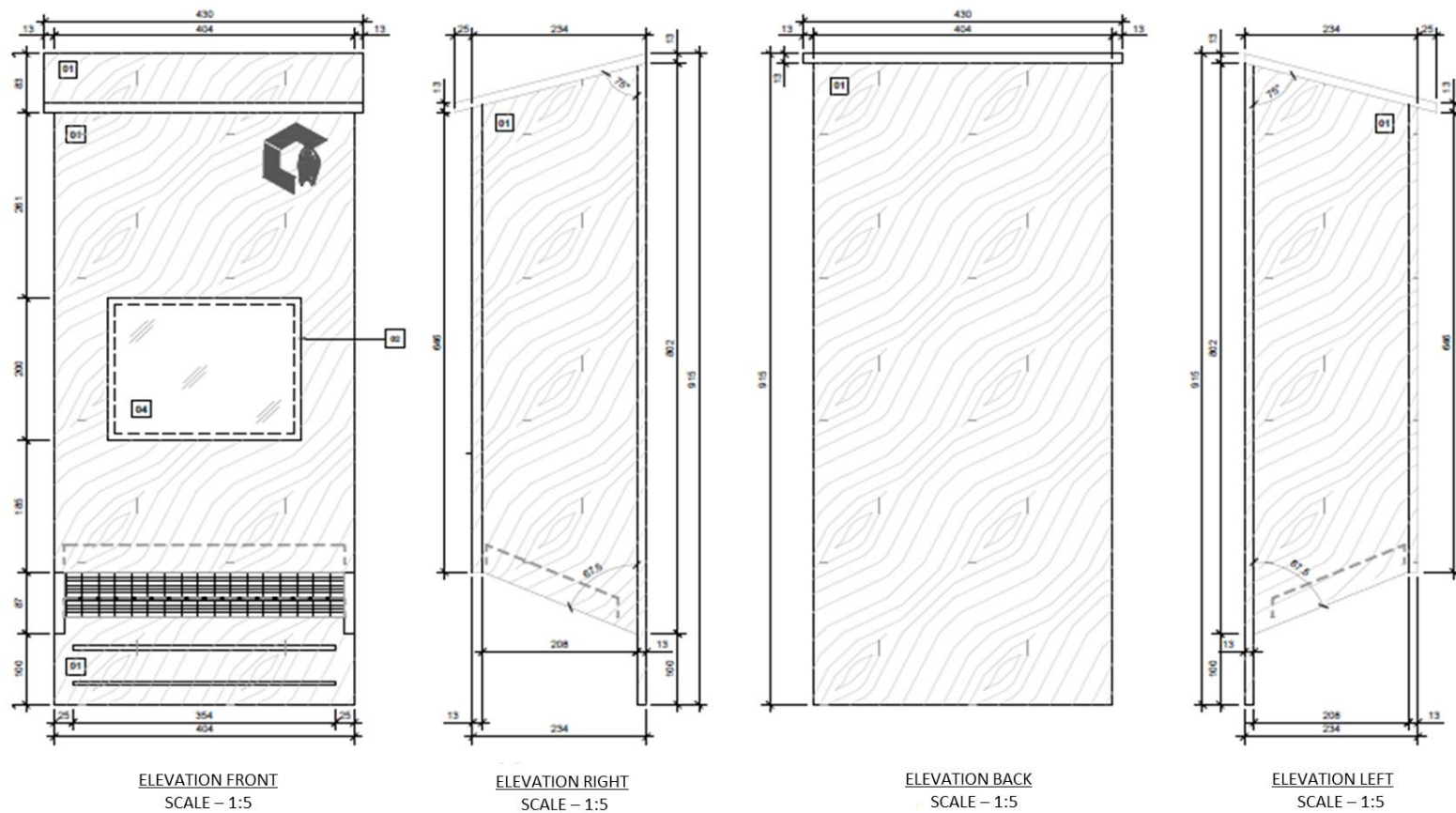


Figure S5.3. Schematic view of the Ncube PH1 2019. The improved Ncube PH1 2020 plan is available in French and English on Batwatch.ca.



ELEVATION VIEW



Ncube PH1 bat box

2019.03.07

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Figure S5.4. Design plan of the Ncube PH1 2019. Elevation view.

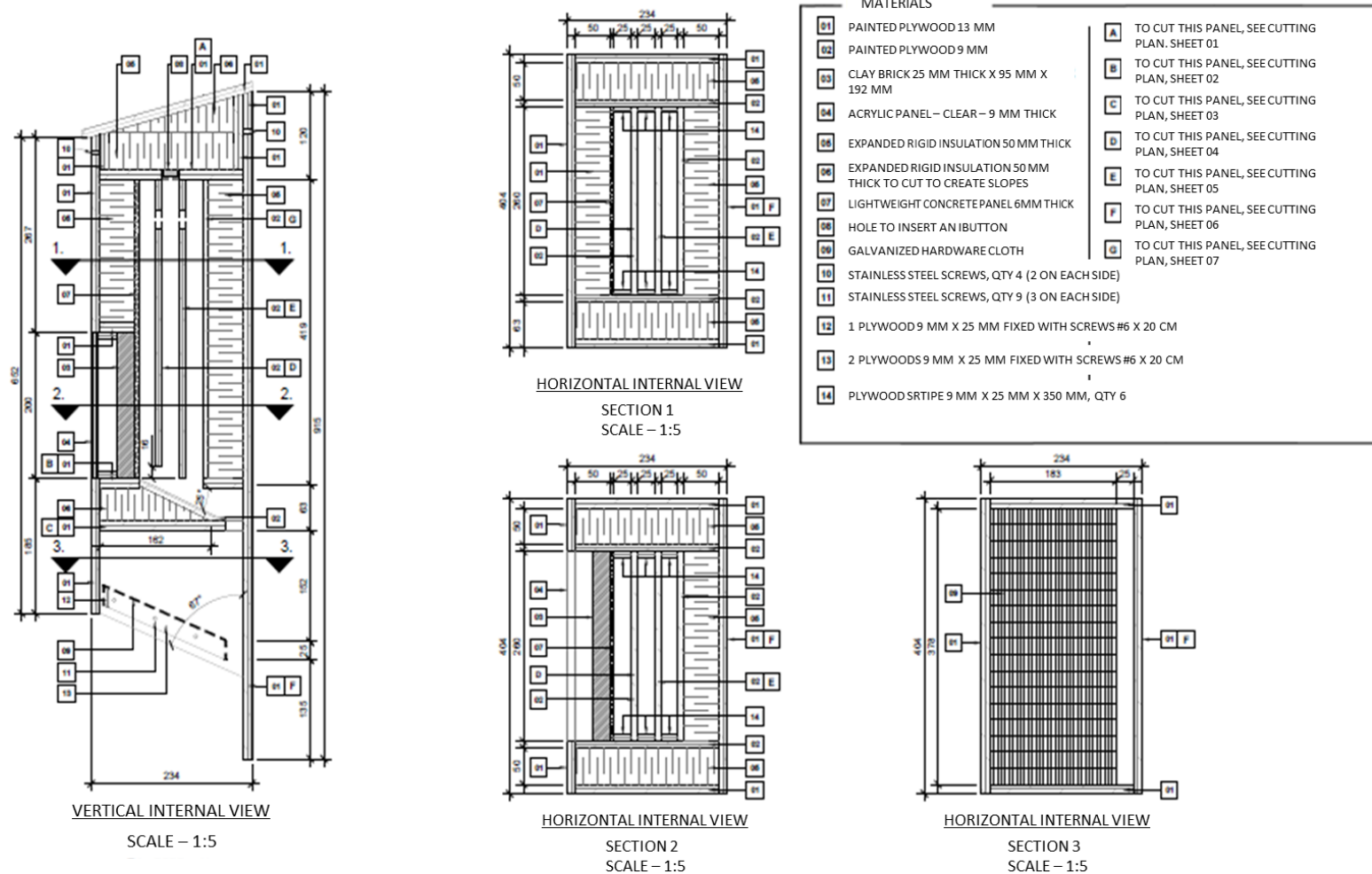


Figure S5.5. Design plan of the Ncube PH1 2019. Cutting plane view.

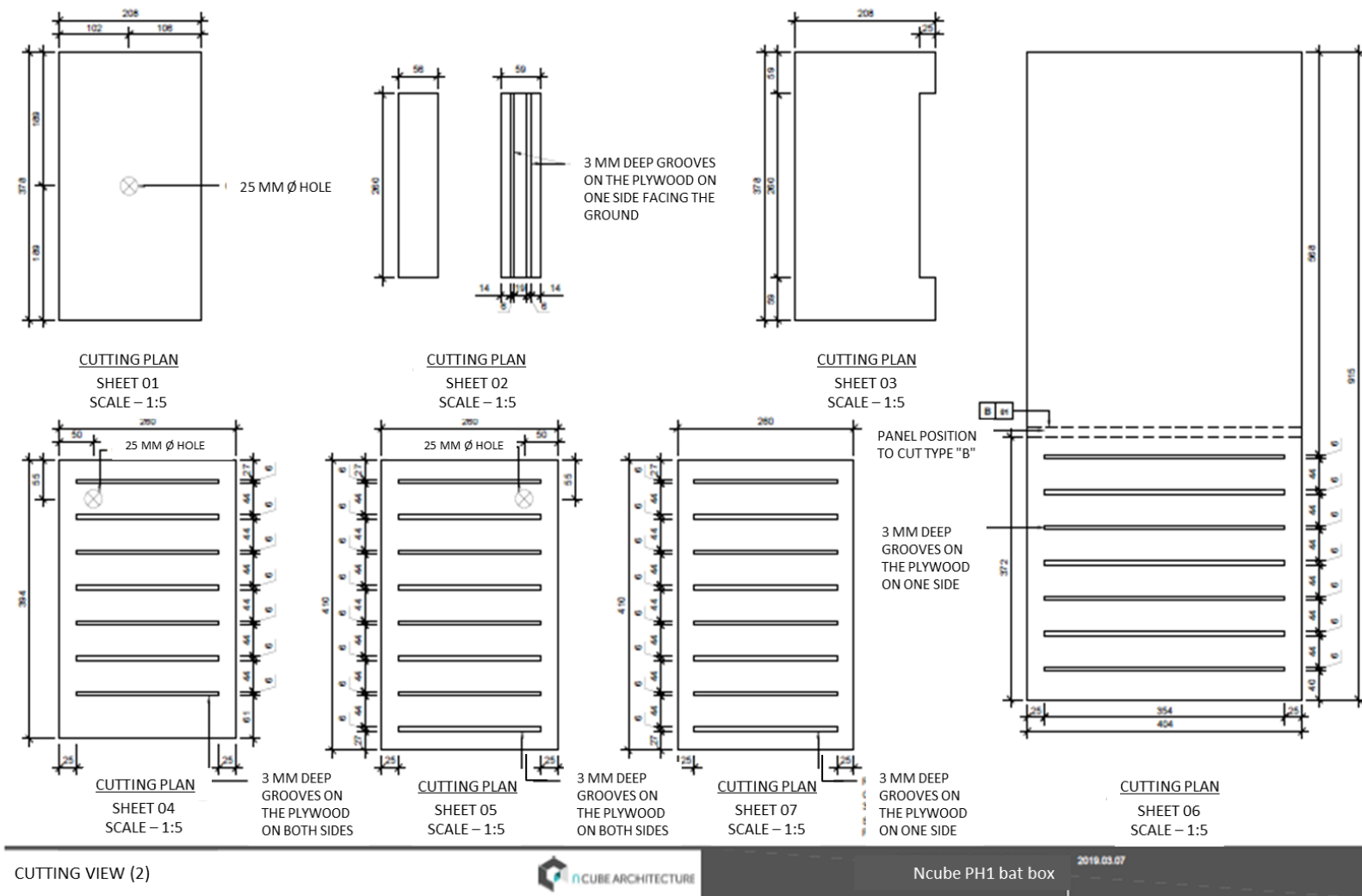


Figure S5.6. Design plan of the Ncube PH1 2019. Cutting plane view (2).

Table S5.8. Site GPS position, location, climate, meteorological station type, and distance of the meteorological station from bat boxes.

Sites	GPS location	Regional location	Köppen climate type	Type	Distance
Warmer 1	45.50393, -75.81336	Outaouais	Humid continental	Davis vantage vue In situ	< 100 m.
Warmer 2	45.41109, -73.94468	Montreal	Humid continental	Environment Canada station (Ste Anne de Bellevue)	< 1000 m.
Intermediate 1	46.71640, -71.54246	Quebec	Humid continental	Davis vantage vue In situ	< 100 m.
Intermediate 2	46.59438, -72.11343	Quebec	Humid continental	Davis vantage vue In situ	< 100 m.
Intermediate 3	46.61753, -71.84768	Centre-du-Quebec	Humid continental	Davis vantage vue In situ	< 100 m.
Cooler 1	47.32049, -71.14918	Quebec	Humid continental	Environment Canada station (Forêt Montmorency)	< 500 m.
Cooler 2	51.68861, -75.82278	Nord-du-Quebec	Subarctic	Davis vantage vue In situ	< 100 m.

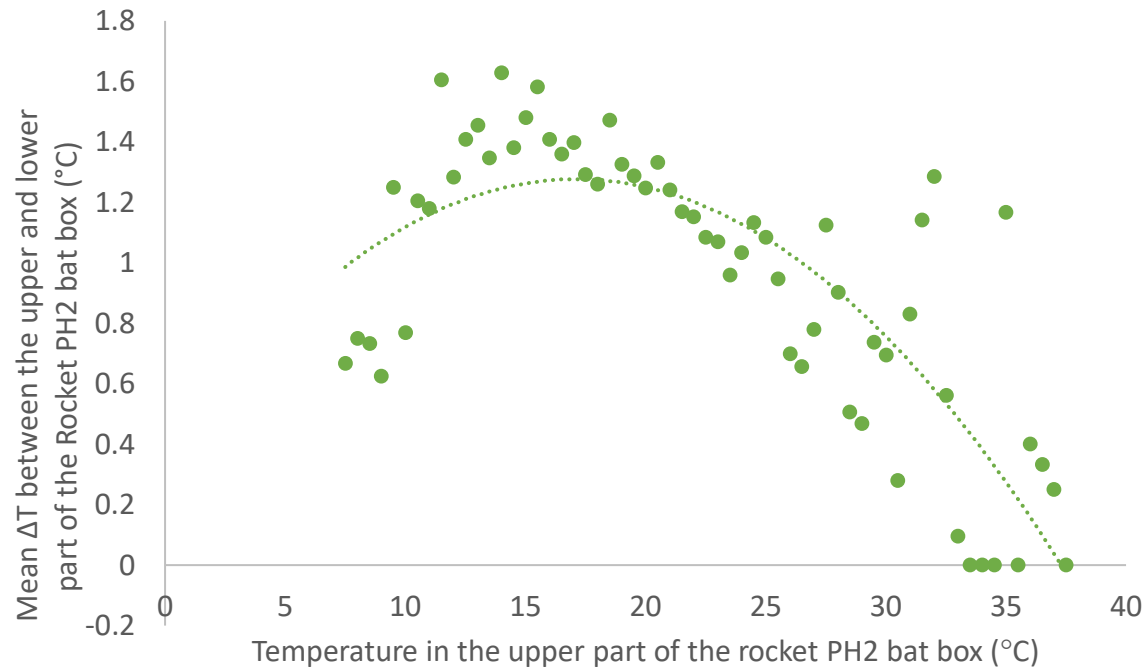


Figure S5.7. Temperature variation (°C) between the upper and lower part of the Rocket PH2 bat box on a pole from mid-May to Mid-September 2019 at site warmer 2 in Québec, Canada. The passive heating zones faced east and west. The green dotted line represents the trend curve following a polynomial function.

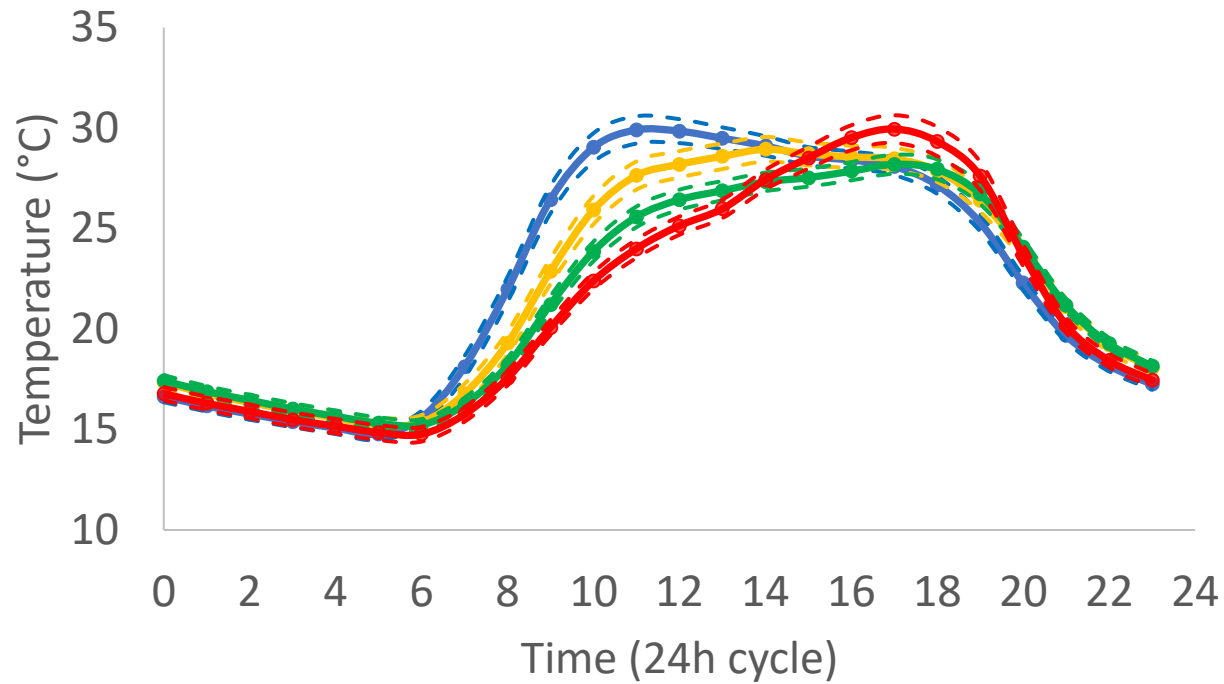


Figure S5.8. Daily mean temperature (°C) of classic 4-chambers bat boxes in the four chambers facing south from mid-May to Mid-September 2017 on poles at intermediate and warmer sites (n=2) Québec, Canada. C1 = chamber, C2 = chamber 2, C3 = chamber 3, C4 = chamber 4, from the front to the back of the bat box, and Text = external temperature.

Table S5.9. GAMM model description for the orientation, mounting and model experiments.

Treatments	Response variable (Y)	Explanatory variable (x)	Fixed factor	Random factor
Orientation	T _{int}	Orientation	Time (as smoothed term and a categorical interaction with Orientation), T _{ext} (with a categorical interaction with Orientation), Date, Mounting	Location (with a random intercept), individual bat box identity (with a random intercept)
Mounting	T _{int}	Mounting	Time (as smoothed term and a categorical interaction with Mounting), T _{ext} (with a categorical interaction with Mounting), Date, Orientation	Location (with a random intercept), individual bat box identity (with a random intercept)
Model	T _{int}	Model	Time (as smoothed term and a categorical interaction with Model), T _{ext} (with a categorical interaction with Model), Week, Mounting	Location (with a random intercept), individual bat box identity (with a random intercept)

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