ROOSTING ECOLOGY OF TWO BATS (*MYOTIS YUMANENSIS* AND *M. LUCIFUGUS*): A COMPARISON OF MATERNITY COLONIES IN BAT BOXES AND BUILDING ROOSTS.

by

SUSAN DULC

BSc University of Victoria, 1998

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Thesis Examining Committee:

Karl W. Larsen (PhD), Thesis Supervisor
Professor, Department of Natural Resource Sciences

Cori L. Lausen (PhD), Thesis Co-Supervisor
Adjunct Faculty, Department of Natural Resource Sciences, Director of Bat Conservation,
Wildlife Conservation Society Canada

Leigh Anne Isaac (PhD), Committee Member
Adjunct Faculty, Department of Natural Resource Sciences, Small Mammal and
Herpetofauna Specialist, BC Ministry of Environment

Mark J. Paetkau (PhD), Committee Member
Associate Teaching Professor, Thompson Rivers University,
Department of Physical Sciences and Engineering

Joy M. O'Keefe (PhD), External Examiner
Assistant Professor, University of Illinois, Department of Natural Resources and
Environmental Sciences

Abstract

Human-caused habitat loss is a primary threat to the persistence of many wildlife species. Providing artificial refugia is one strategy to conserve or recover populations and is often used as compensation or mitigation for deliberate habitat modifications. If artificial refugia fail to meet the ecological function(s) of the natural habitats they are intended to replace they may, at best, be an example of misplaced conservation or, at worst, acting as ecological traps. Determining the efficacy of artificial refugia as a conservation strategy requires testing to assess how closely they mimic natural (or naturalized) habitats and confirm the benefits to the target taxa.

Bat boxes, widely regarded as a conservation tool, have been infrequently evaluated for their efficacy as artificial refugia, despite their widespread use as enhancement or replacement for lost roosts. The suitability of microclimates within bat boxes and the risk of overheating is a legitimate and growing concern. Further, mere occupancy of a box is often taken as a sign of "success" with scant attention paid to fitness outcomes for bats occupying these small structures. In 2019 and 2021, I studied roost microclimates and used surrogate measures to estimate reproductive success of mixed (*Myotis lucifugus* and *M. yumanensis*) maternity colonies occupying three roost types: buildings, bat "condos" and small four-chambered bat boxes in two regions of southern British Columbia, Canada. Temperatures > 44 °C were recorded in bat boxes in both study years and maximum relative humidity of 100% RH was frequent; building roosts seldom (< 2%, only in 2021) reached these temperature or humidity extremes and the condo never did. Heat stress indices were up to 1.5 times higher in bat boxes than in building or condo roosts. Unexpectedly, extreme heat stress values occurred three times more frequently in the temperate Kootenay region bat boxes than in the hotter, drier Okanagan region. Bat boxes remained occupied through the majority of these microclimate extremes. Vapor pressure deficits were 1.5 – 4 times lower (i.e., reduced evaporative cooling potential) in the Kootenay region than in the Okanagan. These microclimate results suggest that heat stress is far more common in boxes than other roost types but that the severity of consequences may vary regionally. Pregnancy rates in buildings and the bat condo were 1.75 times higher than in bat boxes in 2019 and 1.3 times higher in 2021; pregnancy rates were higher overall in 2021 likely due to warmer, drier weather relative to 2019. Juvenile bats in buildings and the bat condo were more developmentally advanced (i.e., had greater mass, longer forearms or more epiphyseal cartilage fusion) than those in bat boxes; this was more frequently observed in 2019 than in 2021. These results suggest gestation and juvenile development in box-roosting bats can lag behind building-roosting bats; the magnitude of effects may have been mitigated in 2021 by interannual weather variation. This research has informed a North American best management practices document for bat box use (Wildlife Conservation Society Canada, Canadian Wildlife Health Cooperative, US Fish and Wildlife Service Conservation and Recovery Working Group).

Keywords: bat boxes, ecological trap, heat stress, maternity, microclimate, *Myotis lucifugus*, *Myotis yumanensis*, overheating, reproductive success, vapour pressure deficit.

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CHAPTER 1. INTRODUCTION

ARTIFICIAL HABITATS

Biodiversity loss is widely recognized as a global crisis; of the 138,374 species assessed by the International Union for the Conservation of Nature (IUCN 2021), 28% are at risk of extinction, with the primary threat to most species is anthropogenic habitat loss (IUCN 2021). Due to the extent of human modification to ecosystems, impacts to wildlife and their habitats are ongoing and likely to be compounded by the acute and chronic effects of climate change (Kerr & Packer, 1998; Buckley & Huey, 2016; Marrot, Garant & Charmantier, 2017). In isolation, protection of remaining natural habitats may not be sufficient to ensure the persistence or recovery of imperiled species (Françoso *et al.*, 2015; Pimm, Jenkins & Li, 2018).

Conservation and population recovery efforts, including offset (compensation) or mitigation measures for industrial damage (Maron *et al.*, 2012), increasingly require active interventions, such as the creation or provision of artificial habitat or refugia. Indeed, for some species creation of artificial refugia are necessary when natural refugia are lacking or degraded (Croak, Webb & Shine, 2013). While artificial refugia may be created unintentionally - e.g., debris piles as snake hibernacula (Zappalorti & Reinert, 1994); discarded containers used by ants (Kolenda *et al.*, 2020); dock pilings used by benthic invertebrates (Cannizzo & Griffen, 2019) - more often the provision of artificial refugia is a purposeful exercise in species conservation or habitat enhancement.

There are numerous examples of artificial refugia created for conservation purposes. Aquatic examples include artificial reefs (e.g., (Simpson *et al.*, 2019; Komyakova, Chamberlain & Swearer, 2021), in-stream shelters for hellbenders (*Cryptobranchus alleganiensis*, Button *et al.*, 2020), man-made ponds or restored wetlands (Dervo, Museth & Skurdal, 2018; Anderson & Rooney, 2019; Kačergytė *et al.*, 2021), and coarse woody debris to improve fish habitat in rivers (e.g., (Guo *et al.*, 2020). The construction of a tower for Mexican free-tailed bats (*Tadarida brasilensis*) in Texas provides an early example of artificial refugia in a terrestrial environment (Storer 1924). However, the most easily recognizable refugia in terrestrial applications are nest boxes for passerines (Dale *et al.*,

2021) and other bird species (e.g., Barn owl *Tyto alba*, Bank *et al.*, 2019); Northern pygmy owl *Glaucidium gnoma*,(Baroni *et al.*, 2020). Artificial breeding chambers have been provided for ground-nesting seabirds (Bolton *et al.*, 2004; Lei, Green & Pichegru, 2014), burrowing owl *Athene cunicularia* (Menzel, 2018)(Collins and Landry 1977; Barclay 2008; Balin *et al.*, 2022) and bees (Rahimi, Barghjelveh & Dong, 2021)(Rahimi, Barghjelveh & Dong, 2021)(Rahimi, Barghjelveh & Dong, 2021). Artificial refuges have been used extensively for arboreal marsupials in Australia (Rowland, Briscoe & Handasyde, 2017), and have been built for Northern quolls *Dasyurus hallucatus* (Cowan *et al.*, 2020) black bear *Ursus americanus* (Davis, 2014), fisher *Pekania pennanti* (Davis, 2020), squirrels (Gryz, Jaworski & Krauze-Gryz, 2021) and snakes (Howarth *et al*., in press).

Artificial refugia may confer benefits to the animals that choose to settle or seek shelter within them. Animals may experience decreased risk of predation (Streich *et al.*, 2017) , decreased competition for limited resources (Bolton *et al.*, 2004), protection from weather extremes (Cowan *et al.*, 2020) and possibly greater reproductive success (Cannizzo & Griffen, 2019). Reproductive success is improved for some synanthropic species living in human structures (compared to conspecifics living in natural habitats) such as stone marten, *Martes fonia*, (Herr *et al.*, 2010) and common swifts (Schaub, Meffert & Kerth, 2016). Buildings in particular can provide artificial refugia to some species of bats. Lausen and Barclay (2006) found that big brown bats, *Eptesicus fuscus,* raising young in buildings had greater fitness than those in nearby natural rock crevice refuges.

The provision of artificial refugia also may impart unintended or negative consequences. Research has shown that artificial refugia can benefit invasive species to the detriment of native target species (e.g., (Aguilera, Arias & Manzur, 2019; Drossart & Gérard, 2020; O'Shaughnessy *et al.*, 2020). Bulger *et al.* (2019) suggest that artificial habitats may not confer equal benefits to sympatric target taxa (i.e., the effectiveness of artificial habitats may be species-specific, even in species with overlapping ranges and similar life histories). In summary, employing artificial refugia in offset or mitigation plans can result in poor conservation outcomes if the intended goals are not met. There is the added danger that, lacking empirical evidence to the contrary, artificial habitats could be acting as ecological traps (Hale and Swearer 2016) for the animals that choose to use them.

Robertson and Hutto (2006) summarize the conditions for an ecological trap to occur as follows:

i. the preference for a lower quality resource must be equal to or greater than the preference for a higher quality resource,
ii. the fitness (a reasonable surrogate measure or index thereof) of the organism must be tied to the resource; and,
iii. the fitness of the organism choosing the lower quality resource must be reduced relative to organisms choosing higher quality resources.

The formation and impacts of ecological traps have been studied in numerous taxa: birds (e.g., (Flaspohler, Temple & Rosenfield, 2001; Sherley *et al.*, 2017), insects (e.g., (Grether *et al.*, 2014; Dervo *et al.*, 2018), reptiles (e.g., (Hawlena *et al.*, 2010; Rotem *et al.*, 2013)), amphibians (e.g., (Brand & Snodgrass, 2010; Sievers *et al.*, 2018) and mammals (e.g.,(Lamb *et al.*, 2017; Hopkins *et al.*, 2021; Noonan *et al.*, 2022). Life history traits and behavioural plasticity may influence a species' susceptibility to ecological traps (Hale, Treml & Swearer, 2015). For example, species that aggregate for all or a portion of their life cycle (e.g., communal roosting; (Grether *et al.*, 2014), or those that exhibit habitat fidelity (Faille *et al.*, 2010; Ekroos *et al.*, 2012; Reynolds *et al.*, 2015) may be at increased risk of susceptibility to an ecological trap. For example, species that aggregate for all or a portion of their life cycle (e.g., communal roosting; (Grether *et al.*, 2014), or those that exhibit habitat fidelity (Faille *et al.*, 2010; Ekroos *et al.*, 2012; Reynolds *et al.*, 2015) may be at increased risk of susceptibility to an ecological trap.

Ecological traps have implications for the conservation or management of wildlife and overall ecosystem health. It is important for those providing or maintaining artificial habitats (e.g., resource managers, researchers, members of the public) to recognize, or consider the potential for, an ecological trap for several reasons. First, any misalignment in artificial habitat quality and preference may lead to population decline and ultimately decreased ecosystem function. Second, conservation resources (e.g., funding, equipment, materials, personnel) are often limiting, and thus creation of artificial habitats for wildlife management should focus on the most effective and efficient use of resources. Finally, meeting conservation objectives, at a local and global scale, will be required to protect biodiversity and support ecosystem resilience in the face of climate change.

BAT CONSERVATION AND BAT BOXES

Bats are a critical component of many healthy, functioning ecosystems and confer numerous benefits to human economies and well-being (Kunz *et al.*, 2011; Frank 2024). In their predation on nocturnal insects, bats consume agricultural and forestry pests (Kunz *et al.*, 2011). Agricultural pest consumption by bats has been estimated to be worth one billion USD to the corn industry alone (Maine & Boyles, 2015) and Frank (2024) found infant mortality rates increased in countries where farmers used more pesticides to compensate for lost natural pest control after bat population declines.

Unfortunately, bats are facing numerous threats to their populations. Logging, particularly of mature forests, and agriculture are the two most pervasive threats to roosting and foraging habitat (Frick, Kingston & Flanders, 2020). White-nose syndrome (WNS) is an introduced fungal disease that has caused catastrophic population declines in eastern North America (Frick *et al.*, 2010a; Cheng *et al.*, 2021) and has been moving westward. Climate change, wind energy development, pesticide use, and direct persecution are additional threats (Frick *et al.*, 2020). Resource managers and conservation groups need to employ a variety of strategies to mitigate these threats and achieve effective conservation of bats.

Installation of bat boxes as surrogates for natural roosting habitats has been widely assumed to be a conservation or habitat enhancement tool that assists bat populations (Rueegger, 2016). Provision of bat boxes frequently is used as a mitigation measure to compensate for roosting habitat lost due to industrial activity or eviction of bats from human residences (Brittingham and Williams 2000). Bat boxes, intended to mimic natural cavity roost features and providing one to several separate roosting chambers, come in a variety of design styles, sizes and construction materials. The two most recommended types in North America are the “rocket box” (Fig. 1.1a) and the Bat Conservation International (BCI) “maternity” box (Fig. 1.1b) (Tuttle, Kiser & Kiser, 2013; Holroyd *et al.*, 2023).

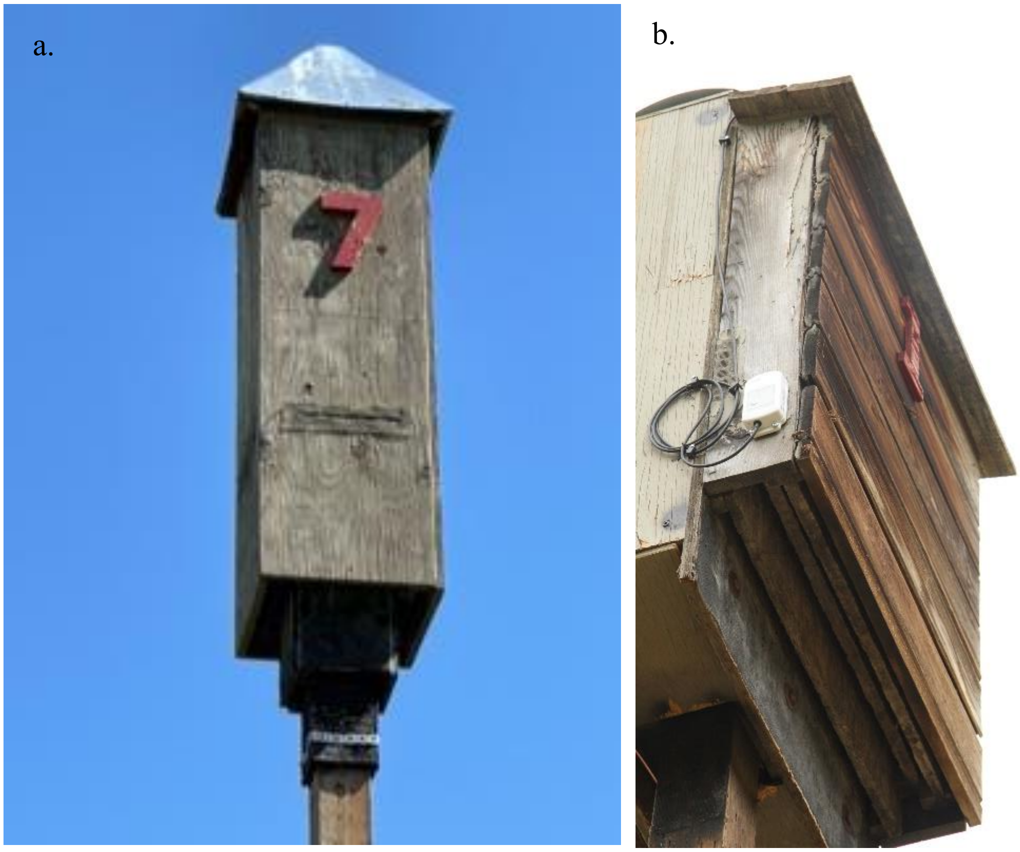

Figure 1.1. Two styles of bat boxes commonly used in North America: (a) the rocket box and (b) the four-chambered maternity box. Photos: S. Dulc

Not all bat species however will roost in artificial habitats such as a bat box. Of the ~1489 bat species globally, between 59 (Mering & Chambers, 2014) and 71 (Rueegger 2016) species will use artificial roosts and only 31 species have been documented using bat boxes to raise young (Rueegger 2016).) Of the 17 bat species that occur within British Columbia (BC), seven may use bat boxes, though only two (*Myotis lucifugus* and *Myotis yumanensis*) have been commonly documented occupying bat boxes during the maternity season (bcbats.ca). The physiological and behavioural underpinnings of roost selection can provide clues as to why some bat species might roost in a box or other artificial habitat.

THERMOREGULATION AND HABITAT SELECTION

Thermoregulation - the physiological or behavioural maintenance of homeostatic core body temperature - plays a significant role in roosting (natural or artificial) habitat selection for bats. Like all endotherms, bats have a thermoneutral zone (TNZ) – an ambient temperature range within which an individual at rest (i.e., not digesting food) is able to maintain a constant body temperature with the least amount of energy expended. The TNZ has an upper and lower critical limit and is species-specific and relative to body size and reproductive state; an animal may have a different TNZ in the summer versus the winter due to seasonal variation (Zhao *et al.*, 2014; McKechnie, Noakes & Smit, 2015; Noakes, Wolf & McKechnie, 2016). Thermoregulation in bats can be heterothermic, not requiring a mammalian core body temperature be defended; instead, bats can employ torpor to slow metabolic reactions. The metabolic rates of bats in relation to the TNZ have important implications for organismal energetic balance.

Temperatures outside of the TNZ will impact an individuals' energetic balance. Energetic balance is especially precarious for bats, given the relatively large, exposed surface area of wing and tail membranes, an inability to carry excess fat stores and energetic costs associated with flight; aerial foraging requires energetic expenditures nearly double that of terrestrially foraging mammals (Kurta *et al.*, 1989). Roost temperatures (Tr) exceeding the critical upper limit of the TNZ may require energy expenditures in activities that dissipate heat (e.g., wing-fanning, panting, wetting fur with saliva or urine), while temperatures below the lower TNZ limit require bats to raise their metabolism to generate and maintain body heat

(Reeder & Cowles, 1951), or adopt a heterothermic approach, not defending a core body temperature and instead reducing metabolic rates (Barclay *et al*., 2001).

When Tr is below the TNZ lower limit, bats can use torpor (the deliberate reduction in body temperature and metabolic rate) to reduce energetic costs associated with maintaining body temperature (Barclay, Lausen & Hollis, 2001). There are, however, physiological and potential fitness consequences involved with using torpor (Lausen & Barclay, 2006; Dzal & Brigham, 2013). While torpor reduces energetic demands, it may inhibit spermatogenesis in males (Dietz & Kalko, 2006), can delay fetal development and parturition in pregnant females (Racey & Swift, 1985) and reduce milk production in lactating females (Wilde, Knight & Racey, 1999).

Achieving energetic balance without the trade-offs brought about by using torpor is particularly important during the maternity season. Fetal development and lactation require the largest amount of energy of any phenological stage in placental mammals (Kurta *et al.*, 1989; Speakman, 2008). In temperate regions, growing seasons are relatively short and dictate food availability. For temperate zone insectivorous bats, the timeline for raising young who will themselves be able to acquire sufficient energy stores to overwinter is similarly condensed and dependent on favourable conditions. The conditions within a roost when bats are present - specifically microclimate characteristics such as temperature and humidity – will have implications to a bats' energetic balance.

By selecting roosting habitats with microclimates that are buffered from ambient conditions, significant energy savings for both mother and offspring can be realized (Lausen & Barclay, 2002). Roost microclimates that provide passive thermal benefits allow bats to utilize energy that would otherwise be necessary to maintain body temperature for reproduction and growth. Thus, roost selection for suitable microclimates is a key behavioural strategy benefitting an individual's overall energy balance, and potentially fitness, in the maternity season.

Some species use the additional behavioural adaptation of communal roosting as a means to achieve a balance between energy savings and fitness (Kerth, Weissmann & König, 2001; Sedgeley, 2001; Lausen & Barclay, 2002; Kerth, 2008). Sociality and group size can exert a significant influence on temperature (and humidity) within a roost structure (Willis &

Brigham, 2007). This social thermoregulation is energetically beneficial to young left behind in the roost while adult females forage. Communal roosting can also confer energy savings during periods of inclement weather (and low prey availability). By roosting communally in spring (early gestation) and summer (when young are most dependent), colonial bat species can optimize the energetic (and fitness) benefits during the most energy intensive period in their phenology.

To be effective as replacement habitat, bat boxes must provide the same or greater energetic (and thus fitness) benefits as the refugia they are intended to replace. Bat boxes that provide appropriate microclimates (temperature and humidity) could, in theory, be suitable replacement habitats. If, however, the cues used to select bat boxes as roosting habitat are misleading, or conditions change, bats using boxes could be "trapped" by their choice of roosting habitat.

PROJECT BACKGROUND

Recent literature suggests that the study of the efficacy and implications of providing artificial habitats is increasing but still in its infancy (Cowan *et al.*, 2021). While some wildlife species appear to benefit from anthropogenic structures (e.g., Lausen and Barclay 2006 and others), the true fitness consequences of providing artificial refugia remain uncertain for many species, including bats. There are gaps in our understanding of the influence of bat boxes on local bat populations, and the efficacy of these small structures in bat conservation. It is unclear if bat boxes provide suitable replacement roosting habitat or benefit to bats.

There are mounting concerns that some bat boxes may increasingly be functioning as ecological traps, especially as the frequency of extreme heat events increases with climate change (Flaquer *et al.*, 2014; Crawford & O'Keefe, 2021). Published accounts of bat mortalities at bat boxes during "heat waves" to date have come from Spain (Flaquer *et al.*, 2014), the United States (Crawford & O'Keefe, 2021), Australia (Griffiths, Rhodes & Parsons, 2021) and BC (Lausen *et al.*, 2022b). If bats experience elevated mortality rates (e.g., (Flaquer *et al.*, 2014) or decreased reproductive success (e.g., (Brittingham & Williams, 2000) due to box microclimate characteristics, those bat boxes may be functioning as ecological traps. In this case, provision of bat boxes as artificial habitat will be counterproductive to conservation and enhancement goals. Comparisons of roost microclimates versus ambient conditions, along with measures of reproductive success or documented mortalities, are required to assess the efficacy of bat boxes as artificial habitat.

I studied two synanthropic bat species known to use anthropogenic structures during the maternity season (*Myotis lucifugus* and *Myotis yumanensis* - hereafter Little Brown and Yuma, respectively). Both Little Brown and Yuma are known to use buildings and bat boxes to raise young and, where their ranges overlap, can often be found roosting together in the same structures (Parkinson, 1979; Luszcz *et al.*, 2016). Although the reproductive benefits of roosting in buildings has been studied in bats (Lausen & Barclay, 2006; Johnson *et al.*, 2019; Slough & Jung, 2020), I am unaware of published research on how the use of bat boxes affects the reproductive success of occupants. To address this issue, I compared bat boxes to building roosts in order to investigate if bat boxes might fulfill the criteria for an ecological trap. To do this, I set the following research objectives:

1. Characterize the microclimates available to maternity colonies in each roost structure.
2. Compare pregnancy rates to infer reproductive success in various roost structure types.
3. Assess morphometrics of juvenile bats roosting in different roost structure types.
4. Use my results to infer the efficacy of bat boxes as an enhancement or mitigation tool for my focal taxa.
5. Integrate findings from my research into the collaborative creation of a Best Management Practices (BMP) guidance document for the use of bat boxes.

For biophysical context, an overview of my study area is provided below. In Chapter 2, I characterize and compare the microclimates available in buildings and bat box roosts relative to ambient conditions of temperature and humidity. I provide results of a comparison of relative pregnancy rates and juvenile development from each roost structure type in Chapter 3. In Chapter 4, I summarize the management implications of my results and provide key best management practice recommendations on the use of bat boxes for mitigation or enhancement. I also suggest the limitations of my results and propose future research needs.

STUDY AREA

My research was conducted in two regions of southern British Columbia (BC); the central Kootenay of south-eastern BC (49.05 °N latitude, -116.30 °W longitude; 530 - 600 m elevation) and the Okanagan region of south-central BC (49.30 °N latitude, -119.26 °W longitude; 340 - 370 m elevation) (Fig. 1.2). The Kootenay region is well known for the 400 km^2 Kootenay Lake, mountainous terrain, glacier carved valleys, and a plethora of relict mines and rocky outcrops. In the Kootenay River floodplain, forested mountains, parkland, wetlands, and lakeshore are relatively undeveloped; land use types vary from agriculture to low density urban and rural residential areas (Fig. 1.3). Nearby parks and protected areas include the 7,000-hectare wetland complex of the Creston Valley Wildlife Management Area (CVWMA). In the BC biogeoclimatic ecosystem classification (BEC) system (Meidinger and Pojar 1991), upper elevation habitats are in the Engelmann Spruce - Sub-Alpine Fir (ESSF) BEC zone and valley bottom habitats are within the Interior Cedar – Hemlock (ICH) BEC zone. Warm, dry summers and cool, wet winters typify the climate in the ICH. Average high and low temperatures are 27 °C and 12 °C in summer, and 12 °C and -5 °C in winter, respectively. The annual precipitation ranges from 450-670 mm, with June and December being the wettest months of the year (ECCC 2022).

The semi-arid Okanagan region of south-central BC, along the shores of the 351 km^2 Okanagan Lake is the northern extent of the Great Basin Desert ecosystem. The majority of valley bottom and shoreline areas have been developed for urban, residential, recreational or agricultural (orchards and vineyards) use (Fig. 1.4). Undeveloped habitats upslope are a mix of grassland and relatively open pine and fir forests. In the B.C. ecosystem classification (Meidinger and Pojar 1991), the Okanagan study area is within the very dry hot subzones of Ponderosa Pine (PP xh1) and Interior Douglas Fir (IDF xh1) BEC zones. Hot, dry summers and cold, snowy winters typify the climate within the PP and IDF. Average high and low temperatures are 29 °C and 15 °C in summer, and 0 °C and -5 °C in winter, respectively. The annual precipitation ranges from 280-670 mm, with June and December being the wettest months of the year (ECCC 2022). A comparison of 30-year climate norms (1981-2010) with mean monthly temperature and cumulative precipitation during my study for both the Kootenay and Okanagan are provided in Figure 1.5 and 1.6.

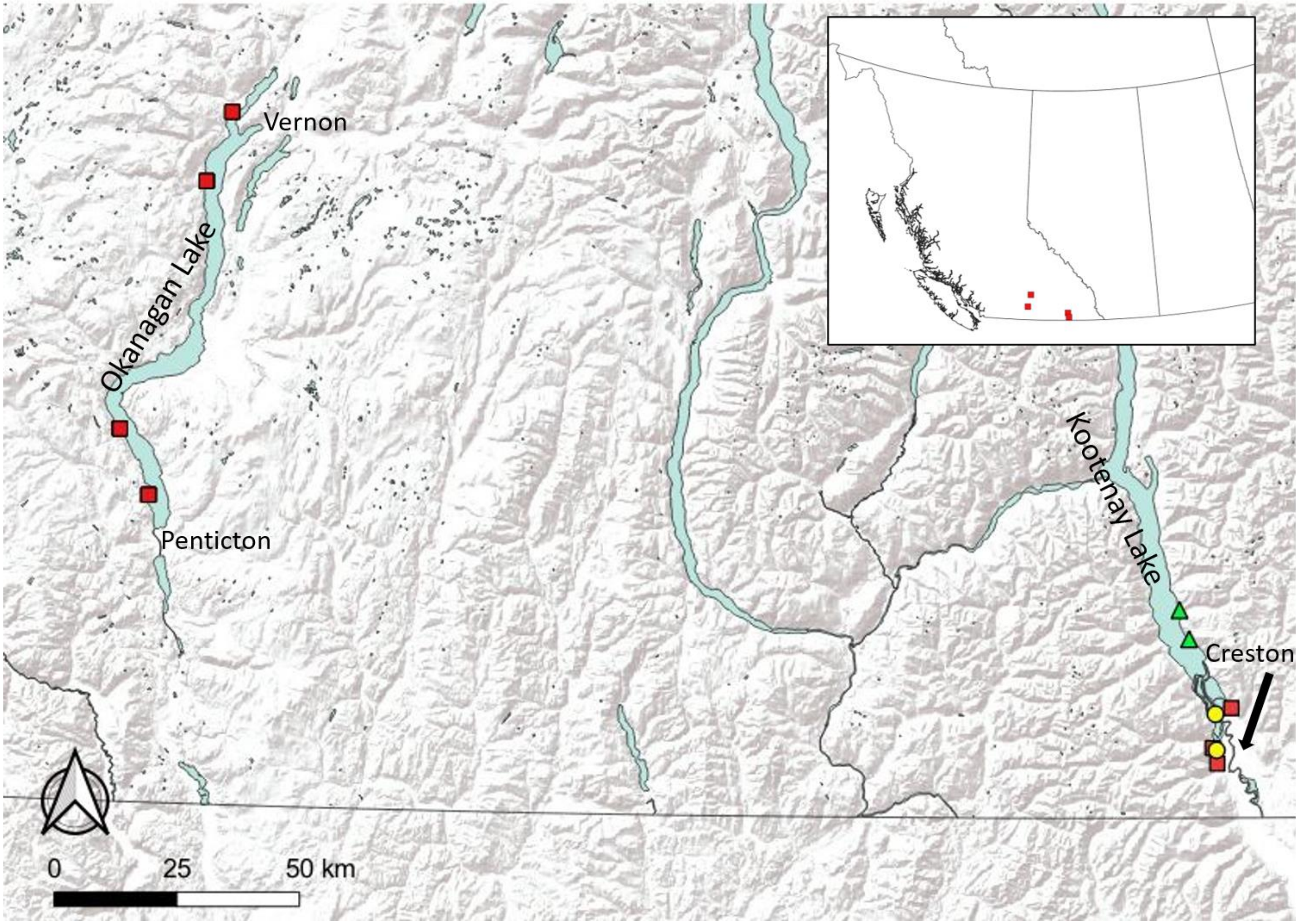

Figure 1.2. Locations of bat box (squares), building (triangles) and bat condos (circles) included in my 2019-2021 research comparing maternity roosts in the Okanagan (left) and Kootenay (right) regions of British Columbia, Canada.

Figure 1.3. View of the wetland complex (top) and forested slope (bottom) habitat types adjacent to Kootenay Lake in the Kootenay study region. Photos: S. Dulc.

Figure 1.4. View of Okanagan Lake and adjacent landscapes at Fintry Provincial Park (top) and Sun-Oka Provincial Park (bottom) in the Okanagan study region. Photos: S. Dulc.

STUDY SITE SELECTION

My study sites were chosen from a database of known Little Brown and Yuma maternity colonies documented by the Kootenay Community Bat Project (KCBP) and the BC Community Bat Project (BC Bat). The KCBP has been raising awareness and supporting local landowners in conserving bats in the Kootenay region for 17 years. As a result of their outreach program and volunteer efforts, there are numerous known bat roosts monitored yearly. Similarly, the Community Bat Projects of BC (BCCBP) is a province-wide network of community bat programs aimed at fostering awareness and assisting landowners in conservation of bats, documenting maternity roosts and coordinating annual bat counts at these roosts. I selected a total of six sites within the Kootenay region and an additional four sites (for remote data collection only) in the Okanagan area. Site details and photos are provided in Appendix A.

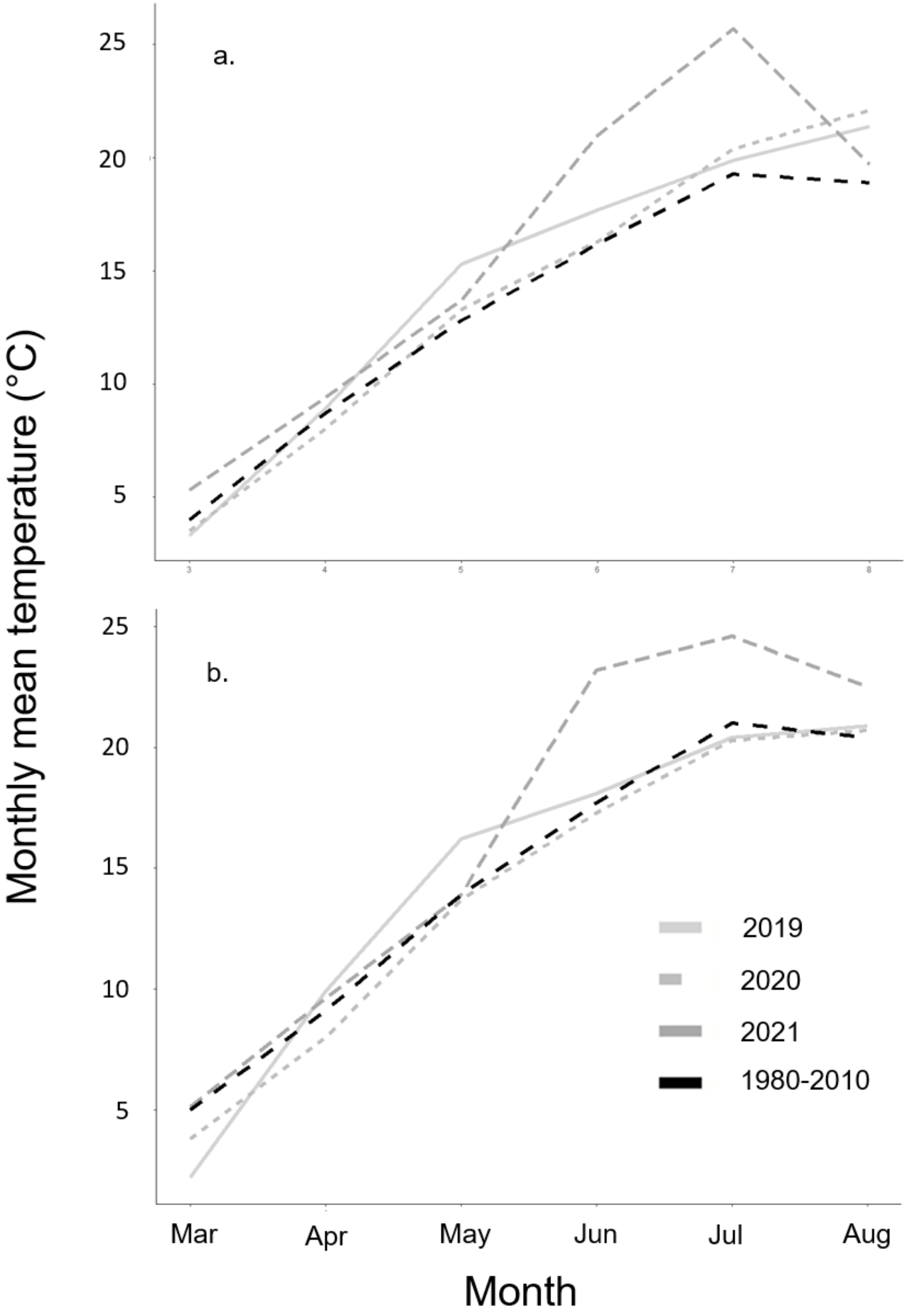

Figure 1.5. Mean monthly (March – September) temperatures in the a) Kootenay, and b) Okanagan regions of British Columbia during this study (2019 -2021) compared to Environment and Climate Change Canada 30-year climate norms (1981-2010) for Creston and Penticton, British Columbia (respectively). Data compiled from Environment and Climate Change Canada.

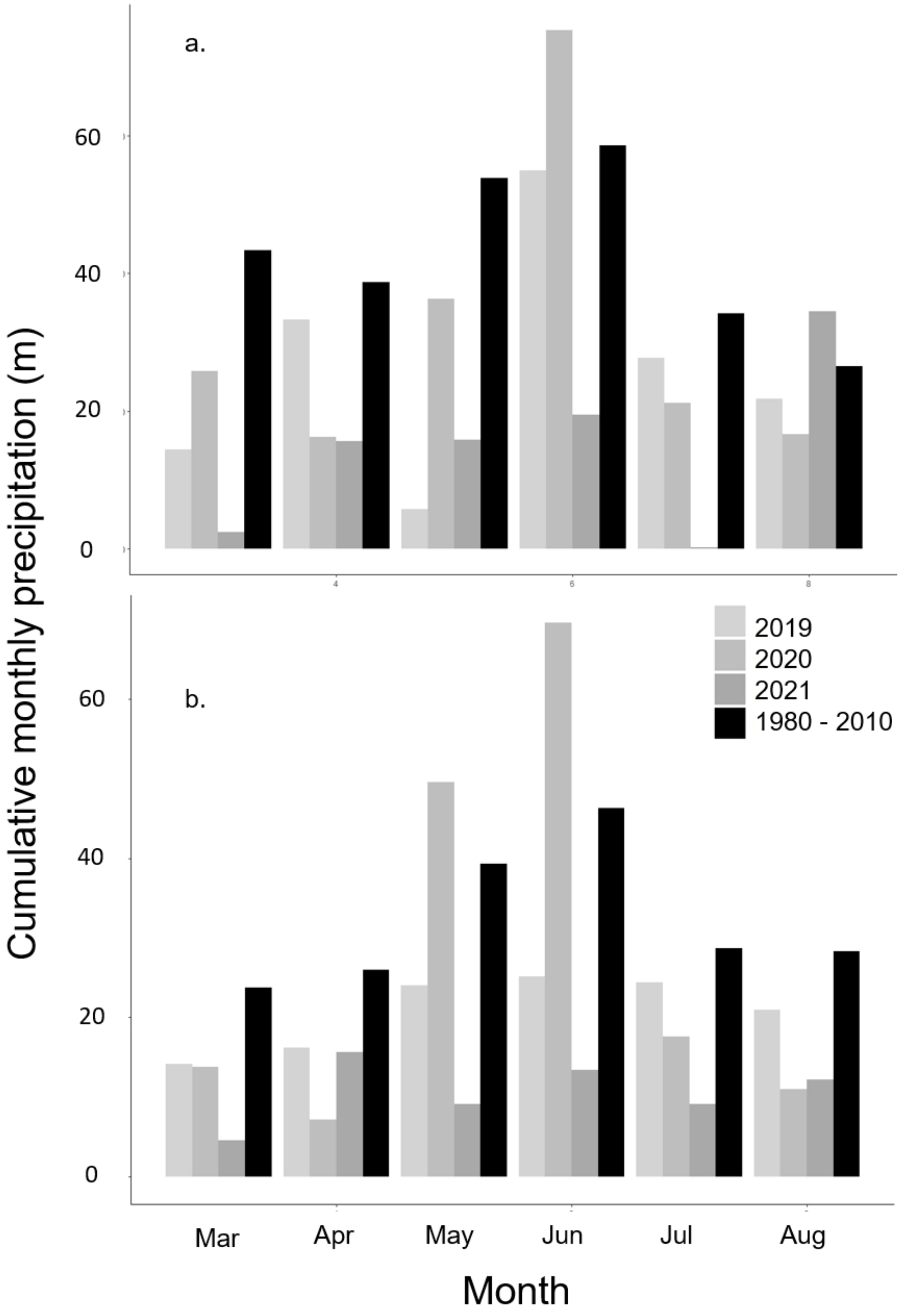

Figure 1.6. Cumulative monthly (March – September) precipitation in the a) Kootenay, and b) Okanagan regions of British Columbia during this study (2019 -2021) compared to Environment and Climate Change Canada 30-year climate norms (1981-2010) for Creston and Penticton, British Columbia (respectively). Data compiled from Environment and Climate Change Canada.

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CHAPTER 2. CHARACTERIZING AND COMPARING ROOST MICROCLIMATES IN BAT BOXES AND BUILDINGS

INTRODUCTION

Synanthropes are wildlife species that have adopted a close association with humans, despite or because of anthropogenic landscape alteration. Some urban-adapted wildlife create shelters beneath (e.g., badger burrows, Davison *et al.*, 2008)) or on (e.g., swallow mud nests, Jeong *et al.*, 2023)) human structures. Synanthropic species unable to construct or excavate their own refugia may use the interior of human structures as essential habitat that otherwise may be limited in the environment (Schaub, Meffert & Kerth, 2016; Dale *et al.*, 2021).

Wildlife that use buildings as refugia may come into direct conflict with humans over concerns of human health, property damage or other nuisances such as odour or noise (Voigt & Kingston, 2016). In some cases, wildlife may lose access to these human structures through eviction or exclusion (Harbusch & Racey, 2006; Johnson *et al.*, 2019). Further, as buildings deteriorate, renovation or replacement often results in loss of essential habitat for synanthropic species (Schaub *et al.*, 2016). The loss of these anthropogenic habitats particularly is detrimental to wildlife that exhibit high site fidelity and use buildings for raising young (Brigham & Fenton, 1986; Lewis, 1995).

For synanthropic bat species that readily use buildings as refugia (hereafter roosts), bat boxes often are installed in the immediate vicinity to compensate for eviction or exclusion from a building roost (Lourenço & Palmeirim, 2004; Mering & Chambers, 2014; Rueegger, 2016). In these situations, bats may use these boxes because of their strong site fidelity rather than preference for a bat box as habitat (Brigham & Fenton, 1986). And, while bat boxes may fulfill some roost requirements, the success of bats using them ultimately depends on how well the conditions support reproduction or overall survival.

The relative benefits or detriments of a particular roost structure can be gauged by comparing conditions provided within the roost. This is because roost microclimate has a direct influence on bat physiology and behaviour (Kerth, Weissmann & König, 2001; Lausen & Barclay, 2002; Willis & Brigham, 2005). Quantifying and tracking roost temperature and humidity characteristics may serve to predict the suitability of a particular structure. Roost microclimates themselves may be influenced by factors such as solar exposure (due to orientation or shading), insulation, structural properties of airflow, number of bats present, roost cavity volume, or substrate material (Rueegger, Goldingay & Law, 2018; Gorecki, Rhodes & Parsons, 2019; Fontaine *et al.*, 2021; Crawford *et al.*, 2022).

Roost microclimates are critical indicators of roosting habitat quality (Hamilton & Barclay, 1994; Sedgeley, 2001; Mering & Chambers, 2014), as appropriate microclimates can result in significant energy savings for bats (Lausen & Barclay, 2002; Willis & Brigham, 2005). Appropriate microclimates include roost temperatures that remain within the thermoneutral zone (TNZ) – the species-specific temperature range wherein resting body temperature can be maintained with minimum energy expenditure – and facilitate energy savings, particularly for reproductive females during the energetically demanding maternity season (Burnett & August, 1981). Roost temperatures that remain within the TNZ support reproduction, growth of young and the deposition of fat, benefitting survival and fitness.

Roost temperatures below the bat's lower TNZ limit require maintenance of body temperature through increased metabolism (Reeder & Cowles, 1951) or the use of torpor (Barclay, Lausen & Hollis, 2001). Depending on an individual's reproductive status, there are physiological, and potentially fitness consequences involved with using torpor (Lausen & Barclay, 2006; Dzal & Brigham, 2013). The use of torpor during gestation can delay fetal development and thus parturition (Racey & Swift, 1981), possibly to the detriment of juvenile or maternal survival (Racey & Entwhistle, 2000), and reduces milk production in lactating females (Wilde, Knight & Racey, 1999).

If roost temperatures exceed the critical upper limit of the TNZ however, energy allocation towards activities that dissipate heat (e.g., wing-fanning, panting, wetting fur with saliva or urine) may be required. Prolonged exposure to excessively high temperatures may result in deleterious consequences or mortality (Licht & Leitner, 1967; McKechnie & Wolf, 2019). Another often over-looked factor contributing to heat stress is humidity (Berman *et al.*, 2016). Evaporative cooling potential is limited when air is high in moisture content and bats -- lacking sweat glands -- rely on evaporative cooling to dissipate heat (McKechnie & Wolf, 2019). High humidity combined with high temperature within roosts will increase hyperthermia risk, and at its extreme is detrimental to bats, decreasing the overall quality of a roost.

The danger of hyperthermia and hyperthermia-caused mortality may be amplified for reproductive females (due to elevated basal metabolic rates while gestating or lactating) and young (due to generally reduced thermoregulatory ability (Welbergen *et al.*, 2008) or greater surface to volume ratio for heat absorption). This is particularly true for bats occupying boxes; owing to their small size, limited ventilation and conventional guidance on colour/placement (dark colours in full sun), bat boxes may experience higher temperatures and humidities than would occur in building or tree-cavity roosts elevating overheating risks for inhabitants (Flaquer *et al.*, 2014; Griffiths, Rhodes & Parsons, 2021). If the consequences of overheating lead to reduced fitness (through mortality or reproductive failure), bat boxes may be acting as ecological traps (Crawford & O'Keefe, 2021; Lausen *et al.*, 2022).

To compare the prevalence of overheating risks in anthropogenic roost structures, I investigated the temperature and relative humidity profiles of building roosts, bat boxes and bat condos. I sought to characterize the microclimate of these roost types relative to the thermal tolerances and reproductive phenology of two focal species, *Myotis lucifugus* and *M. yumanensis*. Because previous studies have brought into question the safety of bat boxes (e.g., Flaquier *et al.*, 2014, Griffiths *et al.*, 2021), I studied roost microclimates of these structures (both when occupied by and when vacant of bats) relative to building roosts and bat condos, structures that (to date) have not been implicated in overheating concerns for bats.

Additionally, I examined microclimate profiles to determine whether certain roost types were likely to create conditions that could lead to heat stress (based on temperatures exceeding the TNZ upper limit and high humidity), and to what extent bats stayed in roosts in these extreme conditions. While bats demonstrate season-long, daily fidelity to buildings (Lewis, 1995), there may be a higher level of roost switching associated with smaller structures ((Bartonička & Řehák, 2007; Bideguren *et al.*, 2019); but see (Lourenço & Palmeirim, 2004; Flaquer *et al.*, 2014). With climate projections indicating warmer, potentially drier summer conditions, along with an increased occurrence of extreme high temperature events in my study regions (Selkirk College 2021; (Hewer & Gough, 2018), the risk of heat stress will increase. As unprecedented heatwaves (e.g., across the Pacific Northwest in 2021) and record-breaking temperatures - 49.6 °C in British Columbia in 2021 - (White *et al.*, 2023) become increasingly common, potential heat stress events may become more frequent. Understanding microclimates in different types of bat roosts can inform management of artificial structures in a changing climate.

METHODS

My study was conducted in two regions (henceforth study "areas") ~200 km apart; the Kootenay (49.08 °N latitude, -116.5 °W longitude) and the Okanagan (49.46 °N latitude, -119.6 °W longitude) regions of British Columbia (BC), Canada (Figure 2.1) in 2019 and 2021. Average summer (June – August) high and low temperatures are 27 °C and 12 °C, respectively, in the Kootenays, and this region receives an average of 59 mm of cumulative summer precipitation. In the Okanagan, average summer high and low temperatures are 29 °C and 15 °C, respectively, and the cumulative summer precipitation is 37 mm. A more detailed description of study area habitats and historical (1980- 2010) climate data is provided in Chapter 1.

Individual study sites were located within each of the two regional study areas (Fig.2.1). Kootenay area study sites, located on private land or on the Creston Valley Wildlife Management Area (CVWMA), were near the town of Creston at the southeastern end of Kootenay Lake. Okanagan area study sites were located on private land and in provincial parks along the western shore of Okanagan Lake, east of Vernon, and as far south as Penticton. All sites are maternity colonies of *Myotis yumanensis* (Yuma) and *M. lucifugus* (Little Brown) and all bat boxes were four-chambered maternity-style boxes (as per plans given in Tuttle *et al.* (2013). Roost structure details and photos can be found in Appendix 1. All told, in the Kootenay, I studied three bat box sites (a total of six boxes) two bat condo sites (one occupied, one unoccupied) and two building roost sites. In the Okanagan, I studied four bat box sites with a total of 12 bat boxes.

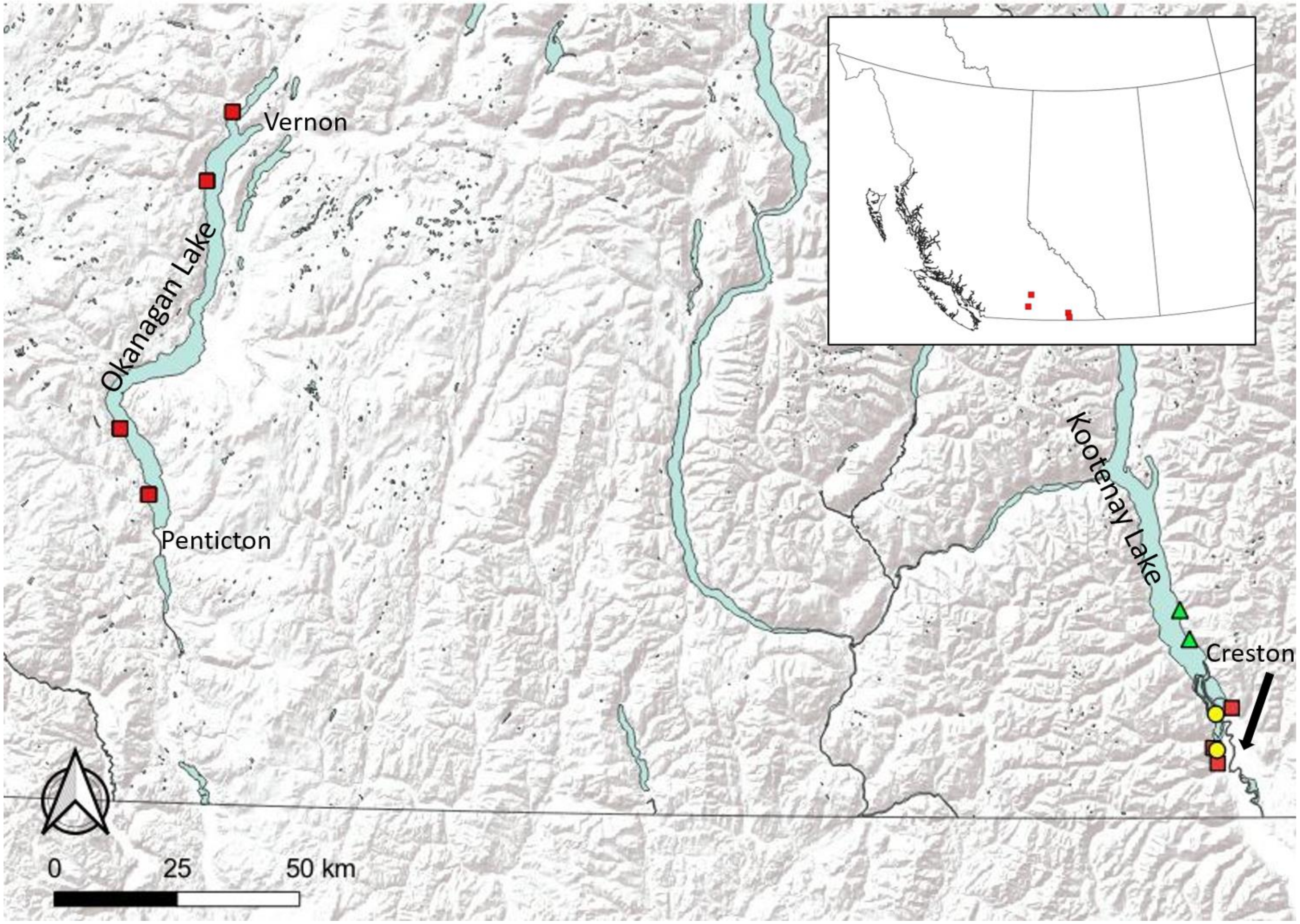

Figure 2.1. General location of bat box (squares), bat condo (circles), and building roost (triangles) sites included in the 2019 – 2021 roost microclimate study in the Kootenay (right) and Okanagan (left) regions (see inset) of southern British Columbia, Canada. Note that multiple bat boxes occurring at sites are not visible at this scale.

Starting in late March and continuing throughout the summer of each year, I visually checked boxes in both study areas to determine bat occupancy. The latest that bats were ever detected at a roost prior to winter was early November. From May to August each year, deployed Roost Loggers (Titley Scientific, Australia) within three meters of roosting bats to record acoustic activity (Kootenay and Okanagan) as evidence of occupancy. In the Kootenay, I was able to conduct occupancy checks at least weekly throughout the summer, using exit counts, capture events, guano or insect wings to confirm roost occupancy. I visually checked inside bat condos in early spring and late fall but did not access the interior (did not open hatch doors) during summer to prevent potential disturbance to bats. Due to the distance between study areas, I was only able to visually examine Okanagan roosts once in mid-summer prior to pup volancy. I conducted multiple routine surveys (to document behaviour and conduct mortality checks) at all Kootenay region roosts during seasonally extreme temperatures in 2019 and 2021; outside of extreme heat events, such surveys were prompted by landowners who observed unusual bat behaviour.

I used HOBO data loggers (MX2302A, U23-003, or U23 Pro V2; Onset Corporation, USA) to record microclimate conditions every 15 minutes (resulting in 96 measurements per day) between 31 March and 31 August in 2019 and 2021. I collected roost and local ambient temperature (T) data from two building roosts, two bat condos and a total of 18 bat boxes (six in Kootenay and 12 in Okanagan). As not all available HOBOs had relative humidity (RH) sensors, RH data were collected from two buildings, two condos and nine bat boxes in 2019; in 2021, RH data was available for two buildings, one condo and seven bat boxes. To protect all HOBO sensor probes from bat urine and prevent bats roosting against or on the probe from influencing measurements, I attached a short (~30 mm) section of a drinking straw (~10 mm diameter) onto the probe end, protruding ≤2 mm beyond the sensor.

For building roosts, I positioned the thermo-data logger probes (henceforth “HOBO(s)”) on roof rafters above guano accumulations (indicating roosting locations). Within these sites I varied logger locations to record in the suspected warmest and coolest positions within the roost. For bat boxes, I mounted HOBO control units on the exterior of the box and inserted the sensor probes through either a hole in the roof, side of the box or into the chamber from the box entrance so that final sensor position was within ~40 mm of the top of the box. I made all drilled holes around the cable air- and watertight with a non-toxic duct-sealer (to prevent rainwater ingress or heat loss). At the end of the monitoring season, I plugged holes with additional duct-sealer to prevent water penetration during the winter. Bat condo HOBOs were installed by CVWMA personnel within the open top ‘loft’ and in spaces between interior baffled boxes (see Appendix A and B for description/photos), not directly inside baffled chambers (bats may roost on the exterior of baffled boxes in addition to inside chambers). Ambient HOBOs were hung within a solar shield in the shade at each roost site by myself (Kootenay region site and privately-owned sites in the Okanagan) and by BC Parks staff (Okanagan provincial park sites).

DATA ANALYSIS

Due to equipment malfunctions or delays in installation, not all sites rendered a complete suite of microclimate or acoustic data for each month or year. I used Anabat Insight (Version 2.0.8-0-g4157d1f) and AnalookW (Version 4.5q) software (Titley Scientific, Australia) to analyze acoustic data; noise files were discarded and files with bat calls (≥ 2 calls) during emergence (ending 1.5 hours after sunset) and roost return (beginning 1.5 hours before sunrise) timing windows were summarized by recording night. I used acoustic summaries to categorize daily roost occupancy as either occupied (≥ 10 files with bat calls), unoccupied (< 10 files with bat calls), or unknown (ambiguous or acoustic data not recorded). Occupancy status was also confirmed when practicable by roost exit counts, visual inspection (roost interior or guano traps), or capture. I assessed microclimate data distributions; I analyzed untransformed temperature data (normally distributed) and square-root transformed relative humidity data (strongly skewed to high humidity values). I performed all calculations and statistical analyses (using a threshold $P < 0.05$ for significance) in R Version 4.3.2 (R Core Team, 2023).

I calculated roost volumes (RVOL, cubic meters) from approximate dimensions of each roost structure. I also assigned an orientation (OR) based on the cardinal direction aspect of the largest surface area for each roost; for bat boxes this was the front face. I categorized microclimate data into “DAY” (sunrise to sunset, to the nearest 15-minute increment) and “NIGHT” (sunset to sunrise, to the nearest 15-min increment) time periods (PERIOD). I considered four inter-seasonal stages (STAGE) per year (YR) for comparison, based on the relevant phenology of my focal species, following Bartonička and Řehák (2007). The four stages are:

- **Spring (Early;** 31 March – 22 May, 53 days) includes bats' emergence from hibernation, returning to roosts within their summer range, foraging and using torpor to replenish fat lost during hibernation. During this season, embryos implant and fetal development begins).
- **Pregnancy** (**PG**; 23 May – 14 June, 23 days) includes the last stage of gestation (late pregnancy) ending on the earliest known parturition date in my study areas (14 June; S. Dulc unpublished data).
- **Lactation** (**LAC**; 15 June – 12 July, 28 days) covers the neonatal and nursing phase.
- **Post-lactation** (**PL**; 13 July – 31 August, 50 days) encompasses the weaning period.

Using published thermoregulatory tolerance of my focal species (Studier & O'Farrell, 1976; Braun *et al.*, 2015), I calculated the proportion of time in each roost site that the microclimate fell within physiologically-relevant temperature categories, namely: (i) < 32 °C which was below the lower limit of the summer TNZ ($\mathbf{T_{cmin}}$), (ii) ≥ 32 °C to ≤40 °C within summer TNZ ($\mathbf{T_{nz}}$), (iii) > 40 °C to ≤ 44 °C as the upper limit of thermal tolerance (critical thermal maxima, $\mathbf{T_{cmax}}$), and (iv) temperatures greater than 44 °C ($\mathbf{T_x}$) as being lethal (Licht & Leitner, 1967; O'Farrell & Studier, 1970; Burnett & August, 1981; Flaquer *et al.*, 2014; Griffiths *et al.*, 2017; Rueegger, 2019; Noakes, McKechnie & Brigham, 2021).

I chose the Steadman Heat Index (HIs) used by the National Weather Service to compare heat stress potential between occupied roosts. Heat stress indices provide a relative level of health hazard posed (to humans) by combinations of temperature and RH (NOAA 2023) and can be calculated in numerous ways, each taking into account and emphasizing differing additional variables such as air flow and incident radiation (Sherwood, 2018; Simpson *et al.*, 2023). Vecelio *et al.* (2022) found HIs to be comparable to other heat stress indices, performing better at low activity levels than other metrics.

HIs takes into account human physiology and assumes magnitudes for several parameters (e.g., wind speed, solar exposure, metabolic output) (Rothfusz 1990) requiring only temperature and relative humidity data. Many of the assumptions within standard heat stress indices are likely not applicable to bats (as individuals or as a colony). However, in the absence of heat stress indices tailored specifically to the physiology of my focal taxa and microclimate extremes, using HIs permits relative comparison between roosts. Similarly, because different heat stress indices can provide different measures and conclusions (Simpson *et al.*, 2023), here I use an HIs only as a relative metric that can be used to compare and contrast between roosts and study sites. At high temperatures and humidities, HIs values become large - beyond survivable for even extremophiles - rendering the “perceived” temperature meaningless; thus, here I present HIs as unitless to avoid implying the biological outcomes that could be associated with such high index values. To calculate HIs, I converted my temperatures from Celsius to Fahrenheit, calculated the HIs profile for each occupied roost using the Rothfusz (1990) formula (NOAA 2023), then converted HIs values (°F) back to Celsius for roost comparisons and summary statistics. The equation for calculating HIs values follows:

$$\begin{aligned}\text{HIs} = {} & -42.379 + 2.04901523*\text{temp} + 10.14333127*\text{RH} + \\ & (-0.22475541*\text{temp}*\text{RH}) + (-6.83783\text{e-}3*\text{temp}^2) + \\ & (-5.481717\text{e-}2*\text{RH}^2) + 1.22874\text{e-}3*\text{temp}^2*\text{RH} + \\ & 8.5282\text{e-}4*\text{temp}*\text{RH}^2 + (-1.99\text{e-}6*\text{temp}^2*\text{RH}^2)\end{aligned}$$

where temp = temperature (°F) and RH = relative humidity (%).

The danger thresholds of heat stress index are not known for *M. lucifugus* or *M. yumanensis*, but I chose the HIs value of 108 (corresponding to 100% RH and 40 °C) as a heat stress threshold of interest. This was based on literature to date suggesting temperatures above 40 °C are stressful (Licht & Leitner, 1967) (but see (Henshaw & Folk, 1966)), or potentially lethal in bat boxes (Lourenço & Palmeirim, 2004; Flaquer *et al.*, 2014; Griffiths *et al.*, 2021) and observations by Rensel *et al.* (2023) that as few as 20 bats in a roost produced an RH of 100%. I thus considered maximum HIs to assess potential for bat overheating among occupied roost types during reproductive stages (pregnancy, lactation, and post-lactation) when bat colonies would likely be at their largest.

As relative humidity alone does not adequately describe the potential for evaporative water loss (Kurta, 2014) or resultant heat dissipation, I also calculated equivalent vapour pressure deficit (VPD) values for all microclimate data (in occupied roosts only) using information found in Allen *et al.* (2005) and the following equation:

$$\mathrm{VPD} = 6.11 * \exp((5417.7530 * ((1/273.16) - (1/(273.15 + \mathrm{temp})))\ )/\ (\mathrm{temp} + 273.15)) * (1 - (\mathrm{RH} / 100))$$

where temp = temperature (°C) and RH = relative humidity (%).

I tested for statistically significant ($\alpha = 0.05$) differences in microclimate means between roost types (within and between years across reproductive stages and occupancy status), with ANOVA pairwise contrasts with a Bonferroni correction through the R-package 'emmeans' (Lenth *et al.*, 2018). I investigated seven roost variables as potentially predictive (Table 2.1) for response variables: 1) roost temperature (TEMP); 2) roost relative humidity (RH); and 3) Steadman Heat Index (HIs). I used generalized linear mixed models (Table 2.2) for comparing microclimates between roosts with the package 'glmmTMB' (Brooks *et al.*, 2017) to account for the repeated measures at each site and considered ambient conditions (temperature and relative humidity) as covariates, 'SITE' and year (YR) as the random factors. Using the package 'DHARMa' (Hartig 2022), I reviewed plots of residuals from fitted models to assess dispersion, heteroscedascity or correlation assumptions. I used R package MuMIn (Bartoń 2009) to calculate AICc weights and rankings for multiple models.

RESULTS

ROOST OCCUPANCY

In 2019, 56% of bat boxes (10 out of 18) were continuously occupied. In 2021, 44% of bat boxes (8/18) were continuously occupied, and all had been continuously occupied in 2019. Both buildings and one bat condo were continuously occupied in both years (Fig. 2.2). With the exception of two acoustic recordings on 22 July 2019, and a single *Eptesicus fuscus* observed during a roost exit count on 26 June 2021, the lack of acoustic, guano or visual evidence indicated one bat condo (Condo C) was unoccupied in both years (Fig. 2.2). Several power failures and programing errors led to a higher proportion of "unknown" occupancy status classifications (33%, 6/18) in 2021 than in 2019 (17%, 3/18; Fig. 2.2).

Table 2.1. Descriptions of roost variables investigated as potentially important for predicting microclimate conditions (temperature, relative humidity and heat stress index) in maternity roost sites in the Kootenay and Okanagan study region of southeastern British Columbia, Canada in 2019 and 2021.

Parameter	Description	Possible values/categories
TYPE	Roost structure type	Box, Building, or Condo
AcOCC	Roost occupancy status based on acoustic evidence	Occupied or Vacant
OR	Roost cardinal orientation	East, West, North, Southwest, or Multiple
RVOL	Roost volume	0.04 m^3 - 165 m^3
PERIOD	Portion of 24-hour day	Day (sunrise to sunset) or Night (sunset to sunrise)
STAGE	Phenological phase relative to reproduction	EARLY (31 March – 22 May): occupation of summer range; PG (23 May – 14 June): gestation and earliest parturition; LAC (15 June – 12 July): neo-natal and nursing; OR PL (13 July – 31 August): post-lactation
REGION	Study area	Kootenay or Okanagan

Table 2.2. Generalized linear mixed-effects models used to assess variables as potentially predictive of microclimate conditions (temperature, relative humidity and heat stress index) recorded in maternity roost sites in the Kootenay and Okanagan study region of southeastern British Columbia, Canada in 2019 and 2021. Ambient conditions of temperature (Tamb), relative humidity (RHamb) and any interaction between Tamb and RHamb were fixed covariates, SITE and YEAR were random effects in all models. Abbreviations are explained in Table 2.1.

Model	Parameters
M1	TYPE
M2	AcOCC
M3	OR
M4	RVOL
M5	PERIOD
M6	STAGE
M7	REGION
M8	TYPE + AcOCC
M9	TYPE + AcOCC + OR
M10	TYPE + AcOCC + OR + PERIOD + STAGE
M11	TYPE + AcOCC + PERIOD + STAGE
M12	AcOCC + STAGE
M13	AcOCC + PERIOD
M14	AcOCC + PERIOD + STAGE
M15	AcOCC + OR + PERIOD + STAGE
M16	AcOCC + OR + PERIOD + STAGE + REGION
M17	REGION + PERIOD + STAGE
M18	OR + STAGE
M19	OR + PERIOD + STAGE

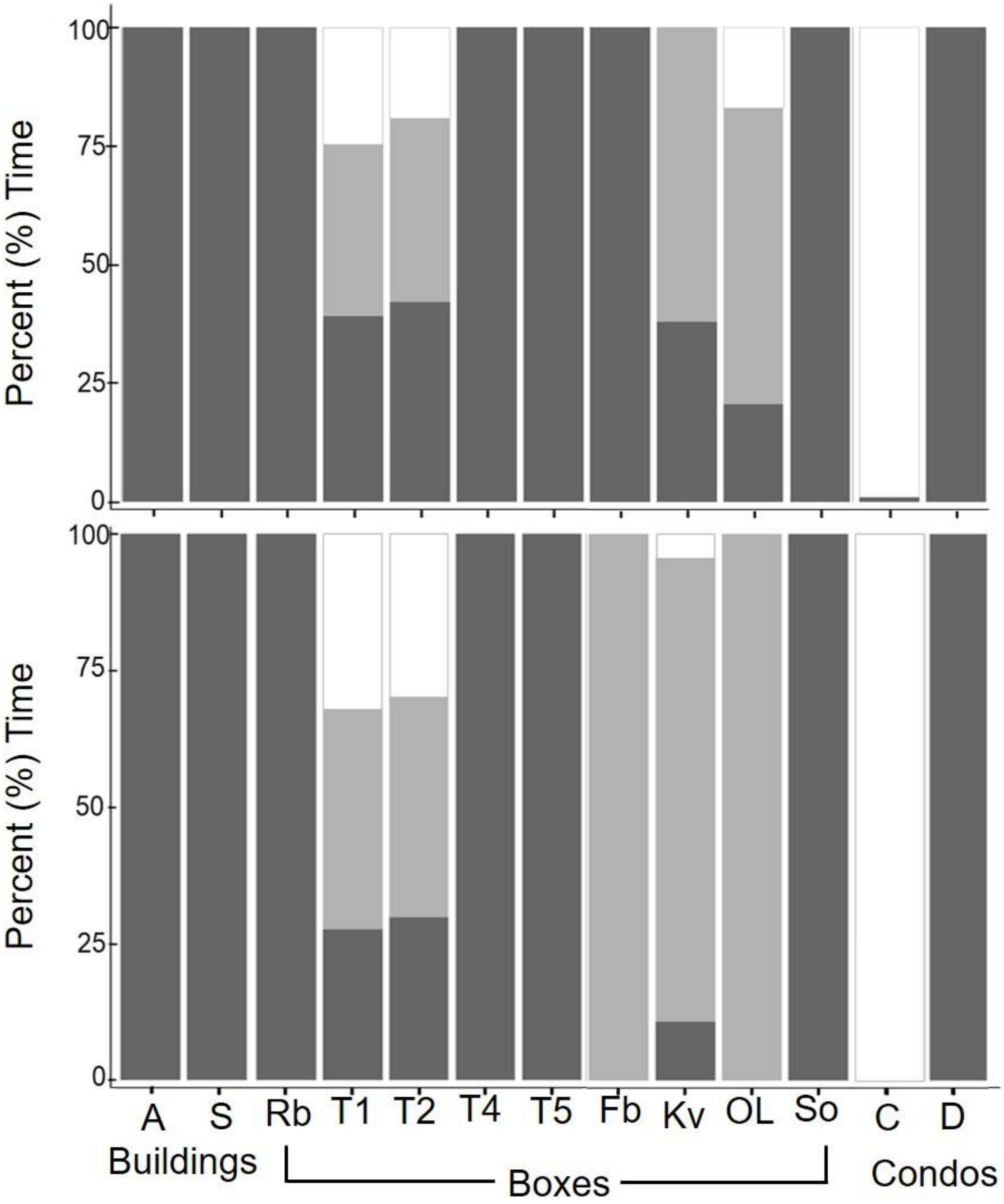

Figure 2.2. Occupancy status (occupied = dark grey, vacant = white, or unknown = light grey) based on available acoustic evidence, as a percentage of time between 22 May and 31 August, of building, bat box and bat condo roosts in southeastern British Columbia, Canada in 2019 (top) and 2021 (bottom). Unknown occupancy status was assigned if acoustic evidence was unavailable.

TEMPERATURE

I found roost temperatures in the 14 boxes, two buildings and two condos were most often (> 70% of the time) < 32 °C (**T_{cmin}**) (Fig. 2.3). Only 25% of the recorded temperatures in all roosts were within the **T_{nz}** category (32 - 40 °C), (Fig. 2.3). In 2019, 57% (n = 8) of box roosts experienced **T_{cmax}** (40 – 44 °C) and six of these boxes were continuously occupied during these temperatures (Table 2.2). **T_{cmax}** temperatures were recorded in both buildings in 2021 only. Lethal temperatures (**T_x;** > 44 °C) were not recorded in buildings in 2019, but were recorded in 29% (n = 4) of bat boxes; three were continuously occupied. In 2021, all bat box roosts and one of two buildings experienced **T_x** temperatures, albeit only 2.2% and 0.8% of the time, respectively (Table 2.3). It should be noted that HOBO sensor probes for bat boxes were placed in the tops of bat box chambers; bats lower down in the bat box may have experienced slightly cooler conditions. Similarly, in building roosts, the exact location of roosting bats relative to the HOBO sensors was typically not known as bats were observed to change microsite roosting locations within the buildings.

Of all occupied roosts, bat boxes had the lowest minimum temperatures and the highest maximum temperatures in each STAGE, in both 2019 and 2021 (Appendix C; Table C2.2 and Table C2.3). Bat boxes had the highest temperature variability relative to other roost types, across all stages in 2019 and 2021. For example, during a hot, sunny day (12 June) in 2019 (Fig. 2.4), the mean difference between roost and ambient temperature (T_{roost} – $T_{ambient}$) was highest in bat boxes ($\overline{x}$ = 10.53 ± 5.04 °C, n=96 T_{roost} minus $T_{ambient}$ datapoints/roost/day) and nearly double that in buildings ($\overline{x}$ = 5.62 ± 2.49 °C, n=96). Figure 2.5 illustrates the temperature difference (T_{roost} minus $T_{ambient}$) on a cool, cloudy day (8 June) in 2019; T_{roost} – $T_{ambient}$ was highest in bat boxes ($\overline{x}$ = 10.45 ± 2.50 °C, n=96) and again about twice that in buildings ($\overline{x}$ = 5.46 ± 2.05 °C, n=96). Bat condos had the most stable temperatures relative to other structure types even during regional heat waves, across all stages in 2019 and 2021. Summary statistics for roost temperatures by type are provided in Appendix C (Table C2.2 and Table C2.3).

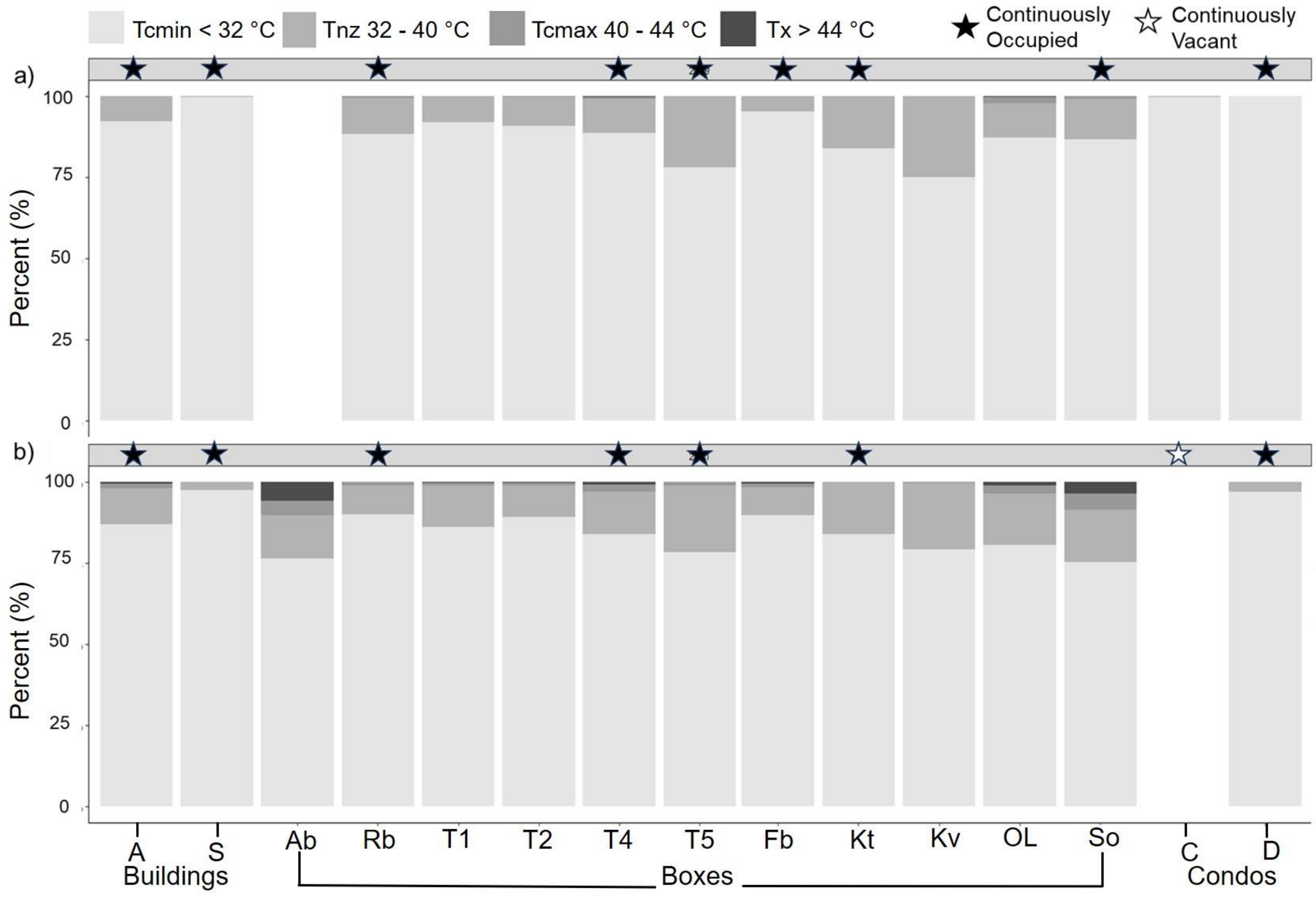

Figure 2.3. Proportion of time that roost temperatures were within each of four defined categories (see legend) between 31 March and 31 August in a) 2019 and b) 2021 in building, bat box and bat condo roosts in southeastern British Columbia, Canada. Blank bars indicate unavailable temperature data; stars above bars indicate continuous occupancy status (vacant or occupied) and bars without stars indicate discontinuous occupancy.

Table 2.3. Occupancy status proportions for building, box and condo roosts while experiencing temperatures within four categories in southeastern British Columbia (2019 - 2021). The four categories, relative to the summer thermoneutral zone for the focal taxa (Licht and Leitner 1967; O'Farrell and Studier 1970) were: T_{cmin} (< 32 °C), T_{nz} (32 - 40 °C), T_{cmax} (40 -44 °C) and T_x (> 44 °C).

Year	Temperature category	Occupied	Vacant	Unknown Occupancy	Roost types affected
2019	T_{cmin}	0.75	0.10	0.15	All roost types
	T_{nz}	0.80	0.06	0.14	All roost types
	T_{cmax}	0.68	0.13	0.19	Boxes only
	T_x	0.61	0.28	0.11	Boxes only
2021	T_{cmin}	0.62	0.04	0.34	All roost types
	T_{nz}	0.57	0.07	0.36	All roost types
	T_{cmax}	0.45	0.05	0.50	Boxes, both buildings
	T_x	0.28	0.03	0.69	Boxes, one building

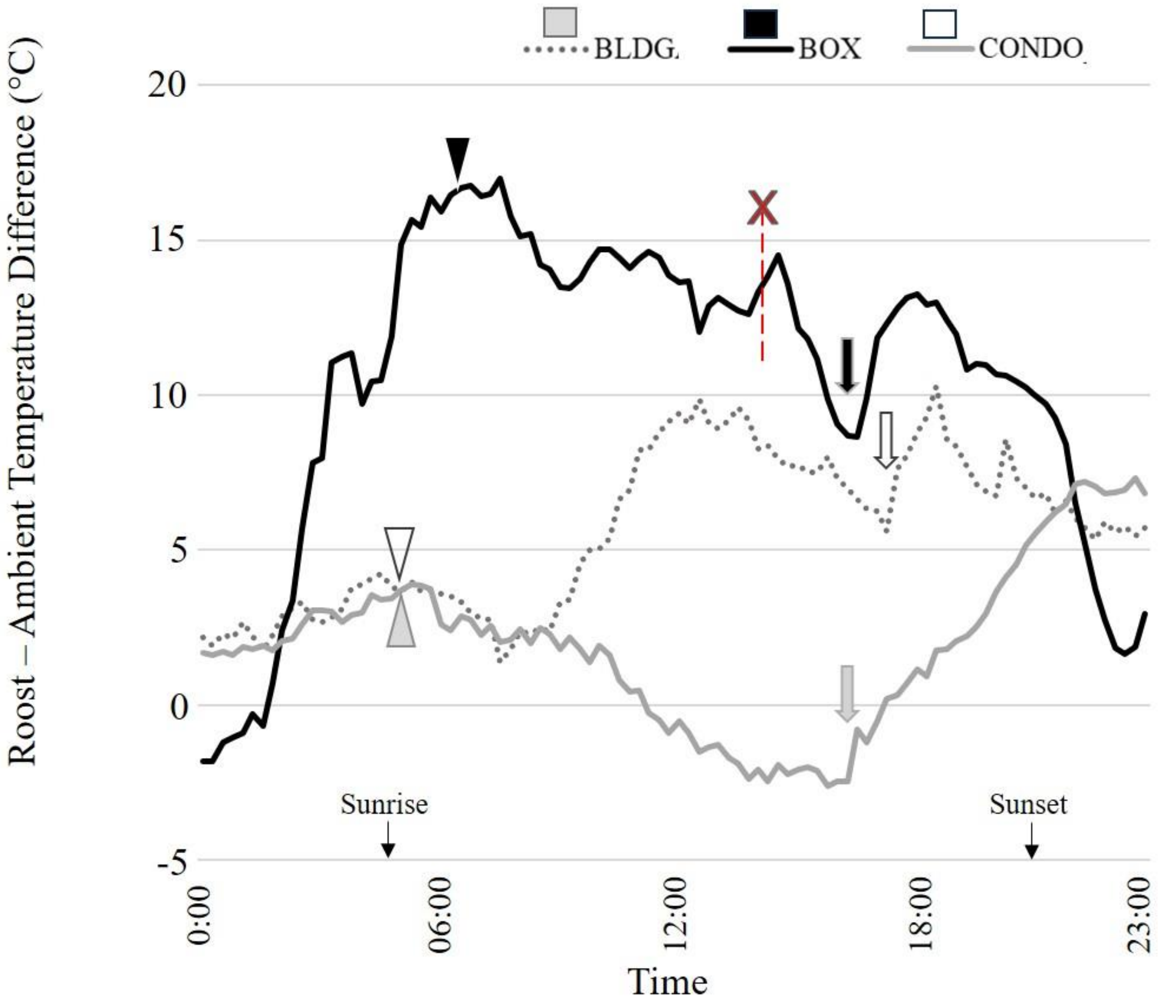

Figure 2.4.Temperature differences between occupied roosts and roost site ambient (T_{roost}-$T_{ambient}$) over a 24-hour period on 12 June 2019 (hot day) at a bat box (solid black), a building (dashed grey) and the bat condo (solid grey). The “X” and red dashed line indicates the beginning of the observed heat stress event (i.e., bats flying out of the bat box seeking shade in nearby trees; see Appendix D). Sunrise and sunset times are noted with line arrows. Time of minimum ambient temperature (triangles) and maximum ambient temperature (block arrows) are noted for each site.

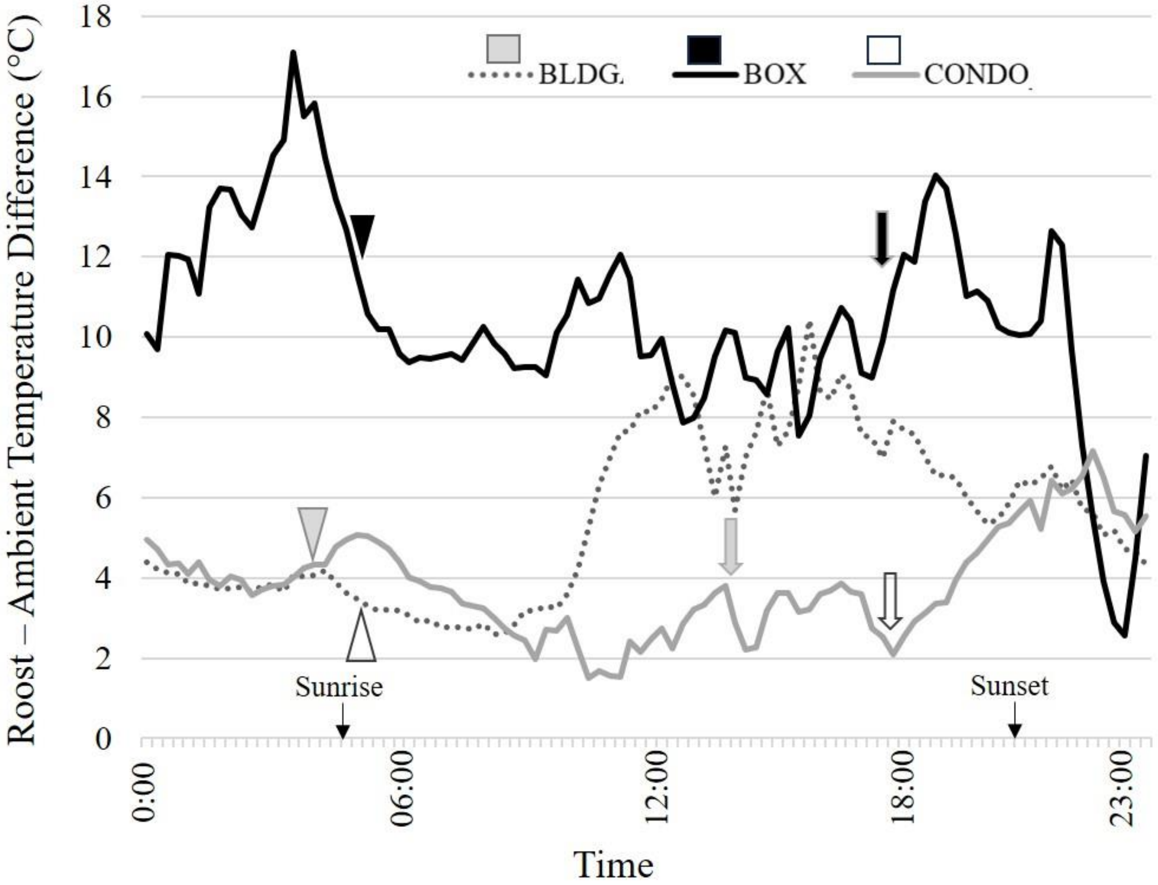

Figure 2.5. Temperature differences between occupied roosts and roost site ambient (T_{roost}-$T_{ambient}$) over a 24-hour period on 08 June 2019 (cool day) at a bat box (solid black), a building (dashed grey) and the bat condo (solid grey). Sunrise and sunset times are noted with line arrows. Time of minimum ambient temperature (triangles) and maximum ambient temperature (block arrows) are noted for each site.

RELATIVE HUMIDITY AND VAPOUR PRESSURE DEFICIT

Maximum daily readings of 100% RH were recorded in all occupied boxes in 2019 and 2021. I found that RH within all occupied boxes reached, and remained at, ≥ 90% on 4 - 66 days (2019) and on 24 – 101 days (2021). While it is possible that sensor saturation can produce erroneous readings of 100% RH (i.e., for longer than this condition is actually present), I did find that each of my sensors did reset to readings below 100% RH so appeared to be functioning correctly. RH in other occupied roost types did not exceed 88% in 2019 (Appendix 2, Table A.2.2). I found that relative humidity in vacant boxes did not exceed 80.0% in either year. In 2021, RH also reached 100%, albeit briefly, in both buildings on 66 - 70 days. High RH (≥ 90%) occurred 1.6 – 2.4 times as frequently in boxes as buildings over a 40-day (960 hours) monitoring period (Appendix 2, Table A.2.1).

Across all roost types, I found mean RH was highest in occupied boxes, in all reproductive stages, in both years (2019, $\overline{x}$ range 80 – 91.2%; 2021, $\overline{x}$ range 79.7 – 89.1%) (Appendix 2, Table A2.3). Lowest mean RH in all reproductive stages occurred in buildings in 2019 and in the condo in 2021 (Appendix 2, Table A2.3), although proximity of roosting bats to sensors within these structures was unknown. In both 2019 and 2021, occupied boxes in the Kootenay region had significantly higher mean RH across all reproductive stages (Pr(>F) <0.001, nested ANOVA, Bonferroni correction for 16 tests; REGION, df = 1; STAGE, df = 3; REGION:YR, df = 2) than those in the Okanagan (Fig. 2.5). Condos had the lowest RH variability, across all reproductive stages in 2019 (one occupied condo, one vacant condo) and 2021 (one occupied condo).

Mean VPD per reproductive stage for occupied roosts (Kootenays), ranged from 0.54 (± 0.98) kPa during lactation (box roost) to 3.26 (± 0.91) kPa during pregnancy (building roost) in 2019, and from 0.63 (± 0.639 kPa) to 3.64 (± 0.84) kPa (pregnancy and post-lactation, respectively) in 2021 (Appendix 2; Table A2.4 and A2.5). Mean VPDs (per reproductive stage) in the condo were relatively stable in both years (Fig. 2.6) and comparable to buildings in 2019 (~2-3 kPa); 2021 building VPD values were 2.5 – 5 times lower than 2019 VPD values. Mean VPD per reproductive stage was 1.5 – 4 times lower in Kootenay boxes than in Okanagan boxes in 2019 (Fig. 2.7) and 2 – 4 times lower in 2021 In both study years, occupied boxes in Kootenay had significantly lower mean VPD across all reproductive stages (Fig. 2.7) compared to those in the Okanagan ((Pr(>F) <0.001, nested ANOVA, Bonferroni correction for 16 tests; REGION, df = 1; STAGE, df = 3; REGION:YR, df = 2).

HEAT STRESS INDEX

Mean HIs (per reproductive stage) were up to 1.5 times higher in bat boxes than for building or condo roosts values in both 2019 and 2021. Mean HIs values for roosts were significantly different by region (nested ANOVA with Bonferroni correction, F(1, 262345) = 954.45, MSE = 587, Pr(>F) =2e-16): I found bat boxes in the Kootenay had mean HIs (per reproductive stage) 1.1 – 1.25 times higher than those in the Okanagan in both years (Fig. 2.8). The interaction between region and year was also significant (F(2, 262345) = 47.08, MSE = 587, Pr(>F) =2e-16). Mean HIs values for roosts were significantly different among reproductive stages (F(3, 262345) = 1240.39, MSE = 587, Pr(>F) =2e-16), with highest HIs in boxes during lactation in both years. Summary statistics for HIs values, by roost type are provided in Appendix 2 (Table A2.4 and A2.5).

HIs values exceeded my chosen threshold of 108 (unitless to avoid implying perceived temperatures) in occupied boxes in the Kootenay during all reproductive stages (PG, LAC, PL) in both study years and 2–7 times more often in 2021 as in the same stage in 2019. HIs > 108 occurred 14.8% of the time in 2019 (n = 5,732/38,784 observations) and 21.80% of the time in 2021 (n = 8456/38,783 observations) in occupied box roosts. During lactation, Kootenay boxes experienced HIs > 108 almost three times more frequently than Okanagan boxes; maximum HIs above 108 occurred only 0.07% of the time in the Okanagan and only in 2019. Building roost maximum HIs exceeded the 108 threshold 1.2% of the time (n = 65/5281 observations), but only during lactation and only in 2021 (Fig. 2.9). Maximum HIs did not exceed the threshold in the condo in either year. Overall, HIs > 108 occurred 4.5 times as often in 2021 as in 2019.

Tables 2.4 and 2.5 provide a summary of general results for all microclimate metrics measured or calculated for the three roost types studied.

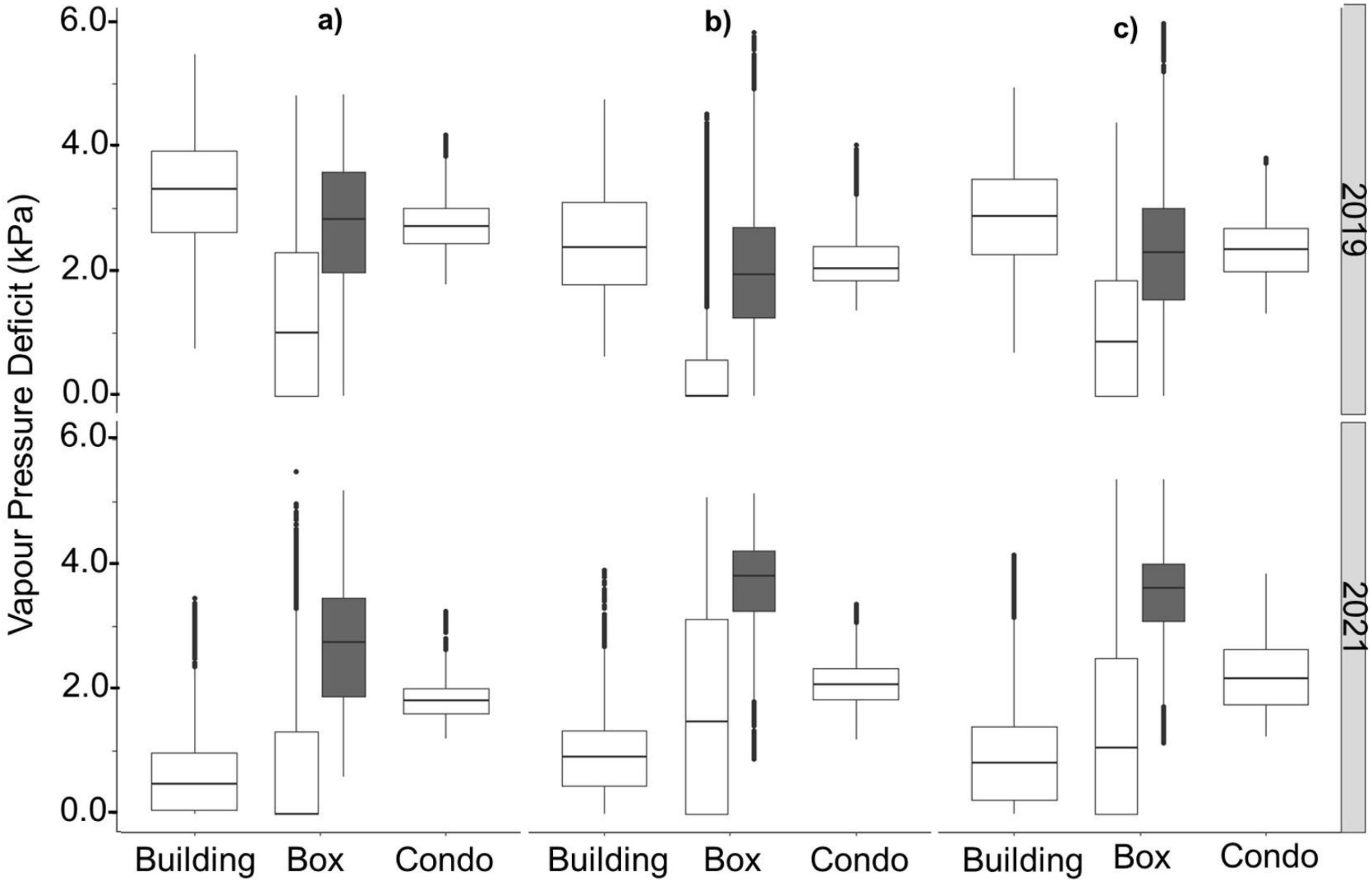

Figure 2.6. Boxplots of vapour pressure deficit in occupied building, box and condo roosts during three reproductive stages: b) PG, gestation and earliest known parturition, 23 May – 14 June; c) LAC, neo-natal and nursing, 15 June – 12 July; and d) PL, post-lactation, 13 July – 31 August in the Kootenay (white) and Okanagan (grey) study areas of southern British Columbia in 2019 (top) and 2021 (bottom). Sample size (number of roosts) for each boxplot are provided in brackets. Boxplots denote median, Q1 and Q3, whiskers show minimum and maximum values, and outliers (as points).

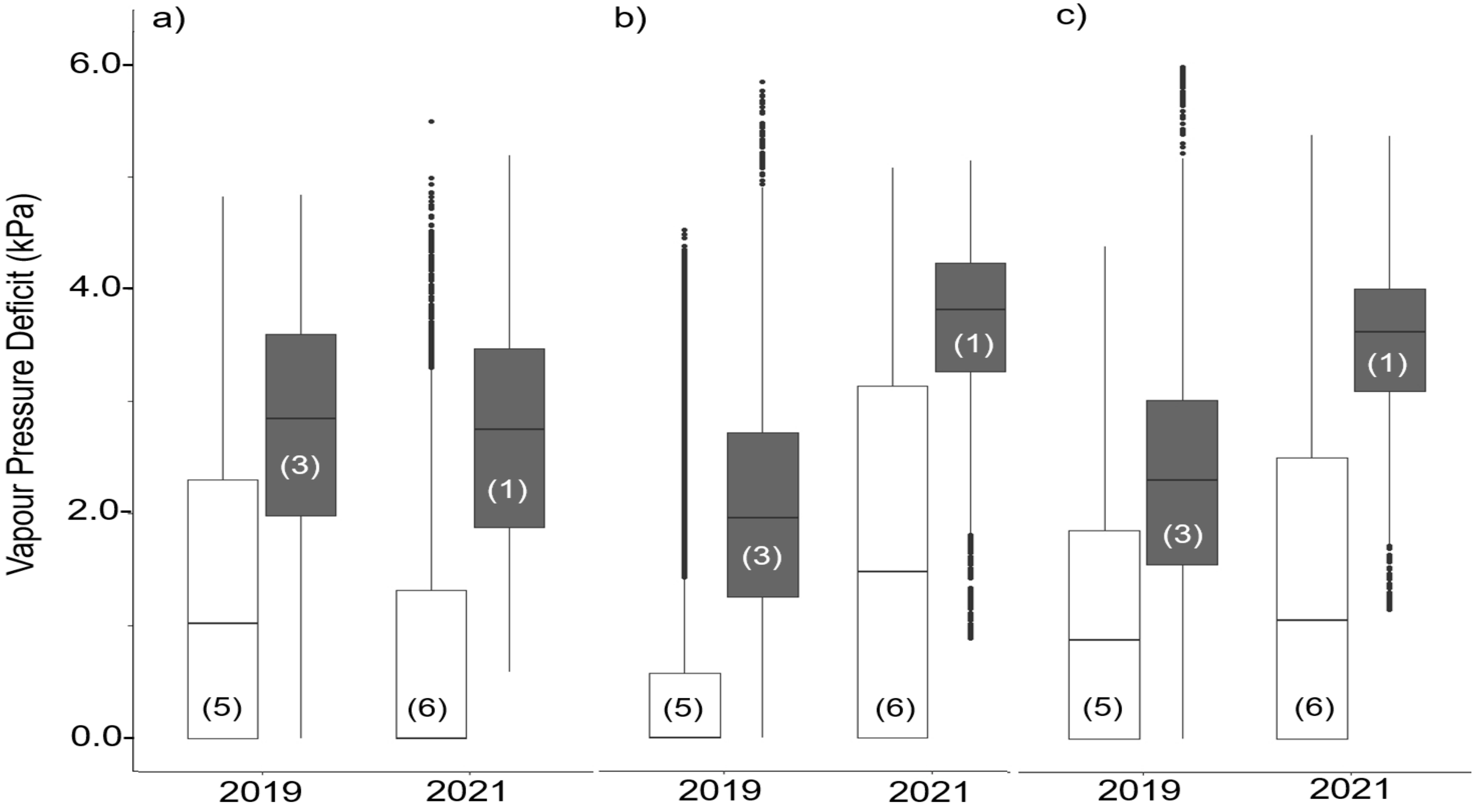

Figure 2.7. Boxplots of vapour pressure deficit in occupied bat box roosts during three reproductive stages: a) PG, gestation and earliest known parturition, 23 May – 14 June; b) LAC, neo-natal and nursing, 15 June – 12 July; and c) PL, post-lactation, 13 July – 31 August in the Kootenay (white) and Okanagan (grey) study areas of southern British Columbia in 2019 and 2021. Sample size (number of roosts) for each boxplot are provided in brackets. Boxplots denote median, Q1 and Q3, whiskers show minimum and maximum values, and outliers (as points).

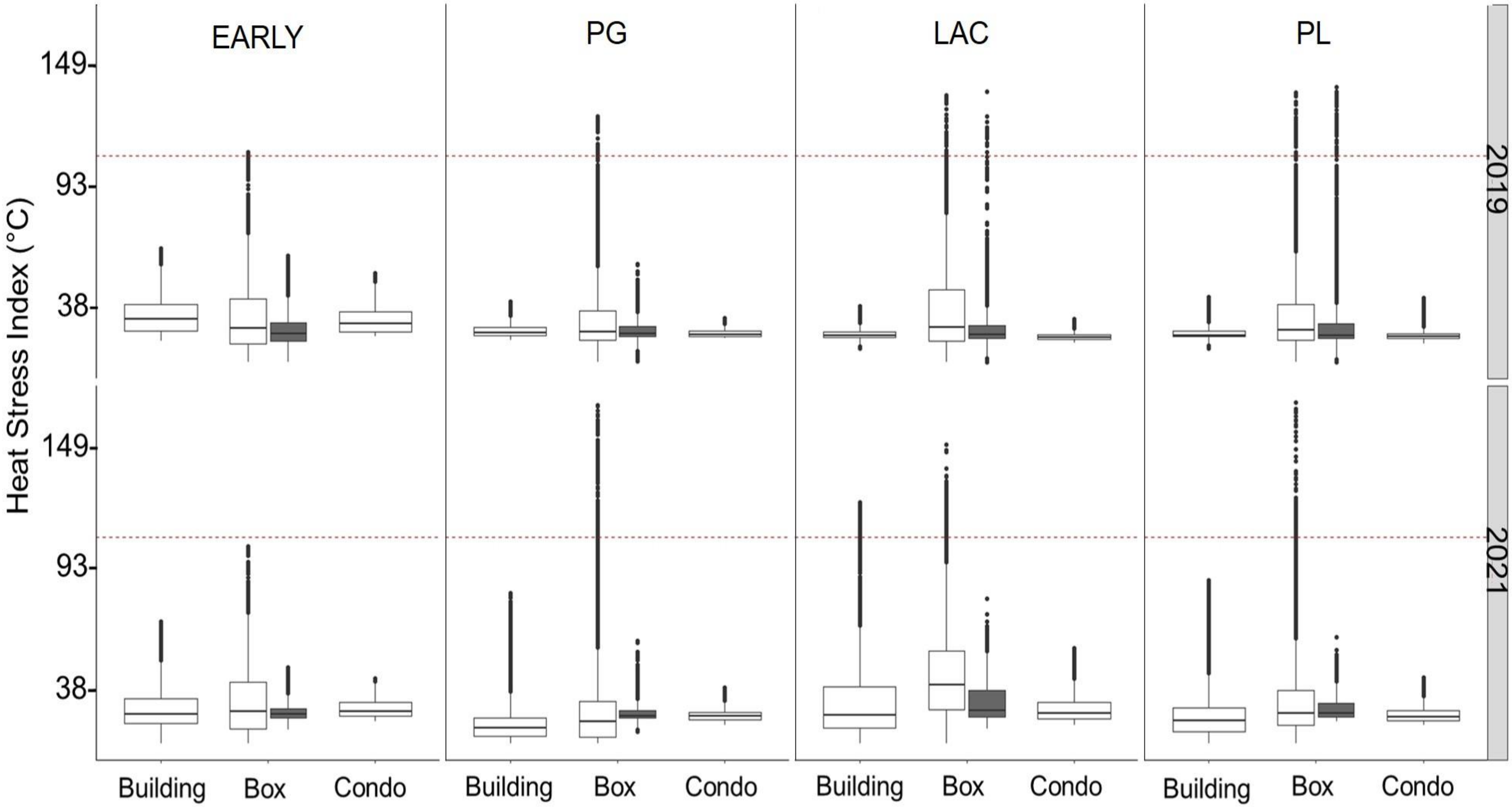

Figure 2.8. Mean heat stress indices (HIs) for occupied roosts, by type, in the Kootenay (white) and Okanagan (grey) study regions of British Columbia during a) EARLY season, occupation of summer range, 31 March – 22 May and three reproductive stages: b) PG, gestation and earliest known parturition, 23 May – 14 June; c) LAC, neo-natal and nursing, 15 June – 12 July; and d) PL, post-lactation, 13 July – 31 August, in 2019 (top) and 2021 (bottom). The dashed line represents the presumed heat stress danger threshold corresponding to 40 °C and 100% relative humidity. Boxplots denote median, Q1 and Q3, whiskers show minimum and maximum values, and outliers (as points).

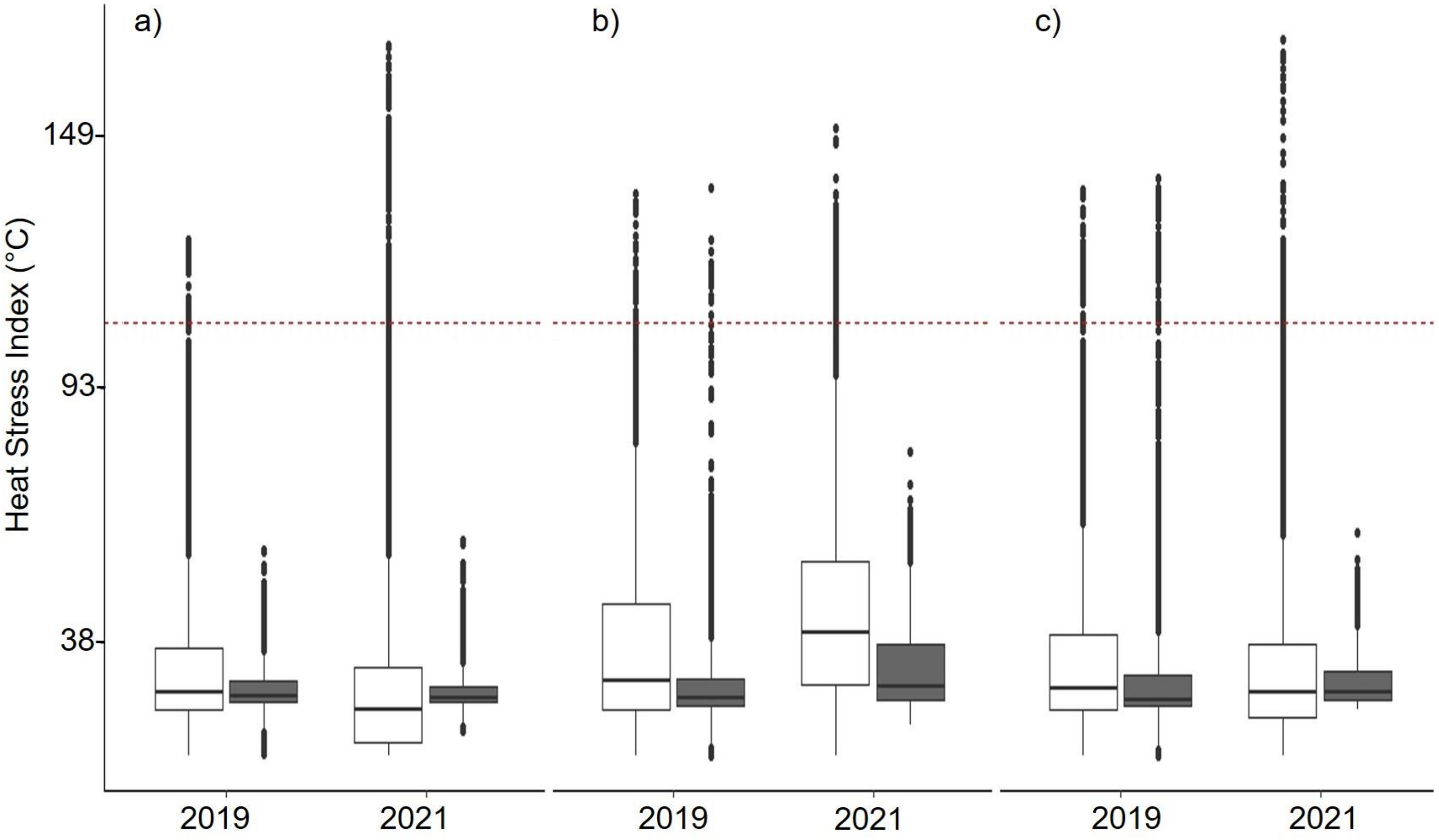

Figure 2.9. Mean heat stress indices (HIs) for occupied box roosts in the Kootenay and Okanagan study regions of British Columbia during three reproductive stages: a) PG, gestation and earliest known parturition, 23 May – 14 June; b) LAC, neo-natal and nursing, 15 June – 12 July; and c) PL, post-lactation, 13 July – 31 August, in 2019 and 2021). The dashed line represents the presumed heat stress danger threshold corresponding to 40 °C and 100% relative humidity.

Table 2.4. Proportion of time roost microclimates were within the thermoneutral zone (Tnz Temps) and meeting the conditions (temperature, humidity, vapour pressure deficit) for potential heat stress in three occupied roost structure types in southern British Columbia, Canada, between 31 March and 31 August, 2019 and 2021. Numbers in brackets indicate the total number of observations with bold font indicating the roost with the greatest proportion of time satisfying each microclimate parameter condition.

Microclimate Parameter	Year	Roost Structure Type		
		Buildings	Condo	Bat Boxes
Sample size (# of 15-minute increment datapoints)	2019	44,352	13,728	85,129
	2021	44,256	14,784	82,646
Tnz Temps (32 - 40 °C)	2019	0.05 (2,346)	3.6e-4 (5)	**0.13 (10,712)**
	2021	0.08 (3,676)	0.03 (446)	**0.16 (13,132)**
Temp > 40 °C	2019	0	0	**0.01 (622)**
	2021	0.17 (770)	0	**0.03 (2,190)**
RH > 90%	2019	0	0	**0.41 (34,954)**
	2021	0.26 (11,652)	0	**0.48 (39,643)**
VPD <1.0 kPa	2019	0.02 (1,015)	0	**0.46 (37,921)**
	2021	0.40 (17,948)	0	**0.50 (41,318)**
HIs ≥108	2019	0.04 (1,799)	0.03 (415)	**0.17 (14,570)**
	2021	0.08 (3,523)	0.01 (147)	**0.21 (17,486)**

Table 2.5. Qualitative summary of general findings for microclimate parameters measured in occupied box, building and condo roosts between 31 March and 31 August 2019 and 2021, in the Kootenay and Okanagan regions of southern British Columbia Canada.

Parameter	**Year**	**Description and magnitude of roost differences**
Temperature (T)	2019	Most variability and extremes in boxes, least in condos
	2021	Most variability and extremes in boxes, least in condos
Relative Humidity (RH)	2019	100%: in all occupied boxes (≤88% in buildings, ≤ 77% in the condo)
	2021	100%: in all occupied boxes, infrequently in buildings and never in the condo
Vapour Pressure Deficit (VPD)	2019	Lowest in boxes ($\bar{x}$ range 0.54 – 1.38 kPa, SE 0.01) 1.5-4X lower in Kootenay boxes than in Okanagan boxes
	2021	Lowest in boxes ($\bar{x}$ range 0.67 – 1.39 kPa, SE 0.01) 2-4X lower in Kootenay boxes than in Okanagan boxes
Heat Stress Indices (HIs)	2019	Highest in boxes (maximum, 335 °C during pregnancy; $\bar{x}$ lactation 109 °C, SE 0.39) HIs > 108 occurred in all Kootenay boxes HIs > 108 did not occur in the condo or buildings
	2021	Highest in boxes (maximum, 335 °C during pregnancy; $\bar{x}$ lactation 113 °C, SE 0.45) HIs > 108 up to seven times more frequent than in 2019, occurred in all Kootenay boxes and one building HIs > 108 did not occur in the condo

Table 2.6. Summary of AICc results for the top-rated *a priori* models potentially predictive of responses a) roost temperature (TEMP), b) roost relative humidity (RH), and c) Steadman Heat Index (HISs) within roost structures (buildings, boxes and the bat condo) between 31 March ad 31 August, 2019 and 2021, in the Kootenay and Okanagan regions of British Columbia. Site and year were random effects for all models. Parameters included acoustic occupancy status (AcOCC), roost type (TYPE; building, box or condo), roost orientation (OR), roost volume (RVOL), reproductive stage (STAGE), day or night period (PERIOD) and study region (REGION).

Response	**Model**	**Parameters**	**df**	**loglik**	**AICc**	**delta**	**weight**
TEMP	M15	AcOCC + OR + PERIOD + STAGE	17	-783016.4	1566067	0.00	0.854
	M11	TYPE + AcOCC + PERIOD + STAGE	14	-783029.8	1566088	20.97	0.088
	M14	AcOCC + PERIOD + STAGE	12	-783032.0	1566088	21.25	0.058
RH	M16	AcOCC + OR + PERIOD + STAGE + REGION	18	-374956.7	749949.4	0.00	0.870
	M15	AcOCC + OR + PERIOD + STAGE	17	-374959.7	749953.5	4.09	0.113
	M10	TYPE + AcOCC + OR + PERIOD + STAGE	19	-374959.6	749957.2	7.78	0.018
HIs	M16	AcOCC + OR + PERIOD + STAGE + REGION	18	33970.96	-67905.9	0.00	0.990
	M14	AcOCC + PERIOD + STAGE	12	33959.69	-67895.4	10.53	0.005
	M11	TYPE + AcOCC + OR + PERIOD + STAGE	14	33960.92	-67893.8	12.08	0.002
	M15	AcOCC + OR + PERIOD + STAGE	17	33963.70	-67893.4	12.51	0.002

MODELLING

Of nineteen candidate models assessed (Table 2.1) for each response variable (roost T, roost RH, and roost HIs), roost occupancy (AcOCC) was significant in all top model predictions for T, RH and HIs within roosts (Table 2.5). The top model for temperature (M15, delta = 0.00), with predictive variables occupancy (AcOCC), orientation (OR), period (day or night) and reproductive stage (STAGE), accounted for 85.4% of the variability in my data. The top model for both RH and HIs (M16) described 99.0% of variability in my data and included variables AcOCC, PERIOD (day or night), STAGE and REGION. Orientation (OR), included in M16, was significant ($\Pr(>|z|) = 0.02663$) for southwest oriented roosts but not statistically significant for all other orientations ($\Pr(>|z|) > 0.05$).

DISCUSSION

In both 2019 and 2021 the highest maximum daily roost temperatures that I observed in my study were always in bat boxes. In 2019 only bat boxes experienced temperatures in the critical thermal maxima range (T_{cmax}, > 40 °C to ≤ 44 °C, as known for *M. lucifugus* and *M. yumanensis*). In 2021 (hotter year), temperatures also reached T_{cmax} in both buildings, but one-third as often as in bat boxes. Boxes were occupied 83% of the time T_{cmax} temperatures were recorded, and on at least ten occasions during high temperatures, I observed bats (through the side ventilation slit) roosting near the sensor, confirming exposure to the conditions. Buildings constantly were occupied but, as there are innumerable microsites for roosting within buildings, and bats were observed shifting microsite locations within these roosts, precise location of bats in relation to the fixed sensors at the time of T_{cmax} was unknown (i.e., temperatures experienced by the bats may have been different from those recorded).

Contrary to my expectation that roost temperatures in buildings would most often be within focal taxa thermoneutral zone (TNZ), roost microclimates were within T_{nz} (32 °C to ≤40 °C) less than 25% of the time, between 31 March and 31 August in 2019 and 2021. In both years, roost temperatures were below the lower summer critical thermal minima as known for *M. lucifugus* and *M. yumanensis* (T_{cmin}, 32 °C) the greatest proportion of time in both 2019 and 2021, across all occupied roosts. The temperature range I chose for T_{cmin} (< 32 °C) analysis may be too broad to be biologically relevant, particularly in my chosen EARLY season (31 March – 22 May); in early spring, local ambient and roost temperatures fell below 0 °C, and bats are likely to be spending time in deep torpor to save energy while insect prey are scarce (Willis, Brigham & Geiser, 2006). Dividing T_{cmin} into several narrower temperature range categories might better account for optimal torpor use thresholds and partitioning the spring season into two or more timing windows may better reflect colony arrival or formation (or a majority thereof).

While temperature profiles did vary between structure types, humidity profiles were the most conspicuous difference between building, bat condo and bat box microclimates. Colonial (clustered) roosting in the small space of a bat box likely explains why the RH of occupied boxes in my study seldom dropped below 100%, particularly during pregnancy and lactation in the Kootenay region boxes. It is possible that residual moisture within an occupied bat box may have resulted in erroneous high RH readings even after bats had left the roost to forage. Given that all bat box HOBOs did fluctuate to values below 100%, I believe sensor saturation (producing inaccurate RH readings) was not a substantial issue and that my sensors were functioning correctly. Relative humidity was lower in Okanagan bat boxes, likely in large part due to the more arid climate. Unoccupied boxes never exceeded 80% in either region, reflecting the lack of respiring bats. This aligns with other findings that bat occupancy significantly modifies roost RH, via respiration (Bartonička & Řehák, 2007; Rensel, Hodges & Lausen, 2023). Rensel *et al.* (2023) found bat boxes containing at least 20 bats (as determined by PIT-tag reads) reached 100% RH in her high humidity coastal study area during the reproductive season. Despite colony sizes in buildings or the condo being orders of magnitude larger than in occupied bat boxes, documenting RH of 100% was comparatively rare in buildings and was never recorded in the bat condos (although sensors were not directly inside baffles so it is possible that RH in roosting chambers was higher than recorded RH).

In my study, vapor pressure deficit in occupied bat boxes in the Kootenay region was extremely low relative to boxes in the Okanagan, a region that is hotter and more arid. Warm air can hold more moisture, resulting in lower relative humidity but the actual amount of water vapour in the air will determine evaporative cooling potential. At a given high temperature, bats roosting in the more arid Okanagan (high vapor pressure deficit) boxes would be better able to lose heat through evaporation (through the skin and lungs, McKechnie *et al.* 2019) than their counterparts in Kootenay boxes (low vapour pressure deficit). It is the combination then, of high humidity and high temperature (i.e., extreme microclimates) that can lead to heat stress (Buzan & Huber, 2020); this highlights the need for researchers to include measures of humidity (absolute or relative) to facilitate calculations of vapour pressure deficit and a heat stress index. Humidity regularly is investigated in bat hibernacula (e.g., (Perry, 2013; Klüg-Baerwald & Brigham, 2017; Blejwas *et al.*, 2021; Boyles *et al.*, 2022)), but is typically underrepresented in microclimate studies of maternity roosts (but see (Bartonička & Řehák, 2007; Rensel *et al.*, 2023).

Based on my field observations and previous studies of bat behaviour in relation to high heat (e.g., Licht and Leitner 1967, Lourenço and Palmeirim 2004, Crawford *et al.*, 2022) and colony formation inside small roosts (Rensel *et al.*, 2023), I believe an HIs corresponding to a combination of 40 °C and 100% relative humidity is a defensible upper threshold of interest. Despite the limitations of heat stress indices, at a HIs of 108, roost conditions may subject bats to heat stress resulting in behavioural or physiological responses (at best) or mortality (Lausen *et al.*, 2022). Occupied bat boxes produced high (potentially lethal) heat stress index values in all three reproductive stages and in both years in the Kootenay region. This is in contrast to condos that never exceeded the HIs threshold, and buildings that exceeded the threshold very infrequently in 2019. That occupied boxes in the Kootenay exceeded the HIs threshold three times more often than Okanagan boxes illustrates the importance of investigating regional differences in similar structures. It also demonstrates the need to account for humidity in heat stress – despite a typically warmer climate, bats occupying boxes in the more arid Okanagan experienced potentially lethal heat stress conditions far less often than their counterparts in the Kootenay.

While local ambient conditions were significantly warmer and drier at all study sites in 2021 than in 2019, the occupied bat condo (Condo D) displayed the most stable temperature and humidity, of all three roost types (buildings, condo and bat boxes), within and between years. Even during the 2021 heat wave, Condo D had the narrowest temperature fluctuation range. The unoccupied condo (Condo C) had lower mean temperatures and RH than Condo D, possibly due to differing design or increased ventilation relative to Condo D; while it may take some time for bats to accept a new roost, the cooler microclimate may at least partially explain why it has remained unoccupied (two years post-construction at the end of this study). Low microclimate variability (i.e., buffered from extremes in temperature or humidity) in a roost may be most beneficial at the height of summer (when ambient temperatures peak) and for juveniles that benefit from thermal stability.

Overall, condos did not experience extreme microclimates that could result in heat stress (i.e., high temperature and high relative humidity); buildings had slightly more variable microclimates with rare instances of extremes in temperature and humidity. Both of these roost types have large roost volume and a highly heterogenous range of available microsites, allowing bats to move within the roosts to choose different microclimate conditions according to their physiological need or preference. By contrast, roost volumes are small in bat boxes and bats would be constrained to a narrow range of microclimates.

Bat boxes, with the highest temperature variability relative to other roost types, may be most energetically beneficial to females in spring during early gestation. At this time, they can take advantage of a box that heats up quickly during the day to provide passive energy prior to evening foraging. Bat boxes were subject to extreme microclimates twice as often (on average) as other roost types; my data suggested that the bat box roosts were occupied the vast majority of the time during these extremes, predisposing occupants to potential heat stress. Given the potential lethality of hot and humid conditions, which is more likely to occur when bats are clustered in groups (Rensel *et al.*, 2023), future research into maternity roost structures should include considerations of humidity, vapour pressure deficit and maximum heat index values.

Reproductive female Little Brown and Yuma have higher metabolic rates during lactation than any other life stage (Gittleman & Thompson, 1988), yet cluster together with offspring and other adults in warm roosts. In anthropogenic structures, they are able to form colonies orders of magnitude larger than would be possible in natural (tree cavity) roosts, further influencing roost microclimates. Heat stress susceptibility is influenced by reproductive status; Snoyman *et al.* (2012) found nursing female flying foxes, *Pteropus* *poliocephalus,* were more vulnerable to high temperatures than males or non-reproductive females due to clustering, use of warmer roost microclimates and lactation-driven metabolic heat production. Further, heat stress has been shown to reduce milk yield and nutritional (fat and protein) composition in domestic livestock (Gantner *et al.*, 2011)(Lee *et al.*, 2023); it is unknown if similar effects might occur in bats due to high heat stress index values in roosts. While heat tolerance limits and heat stress impacts depend on species-specific physiology, the behavioural and metabolic reasons for heightened thermal susceptibility in female flying foxes are applicable to my focal species.

During my study, I observed behavioural signs of hyperthermia, such as bats with wet fur (presumably from urination) crowding at box entrances, wing-fanning (in buildings), and roost microsite switching, in both years (details in Appendix 2). Contrary to findings by Lourenço and Palmeirim (2004) that bats left boxes at 40 °C, bats in my study remained in boxes the majority of the time high temperatures occurred. However, as Lourenço and Palmeirim (2004) did not report humidity conditions, the role of humidity in their study is unknown. In my study I observed bats leaving boxes in only one instance - during the heatwave of 2019 (25 May – 03 June) at a bat box in the Kootenay region. This 2019 heatwave occurred when many of the ~300 females in this colony were in late-stage pregnancy; the metabolic heat generated by a full-term fetus, combined with high roost temperature and humidity (42 °C and 100% as measured in the bat box via my HOBO dataloggers) may have led to heat stress that caused bats to risk leaving the box during the day. In the 2021 heatwave (25 June – 03 July), adults and pups in various stages of development (from furless neonates to larger, dark-furred juveniles) were seen crowding at the box entrance, however none of the bats left the boxes to roost elsewhere. Conditions experienced at the opening of the bat box would have been less severe than those measured by the microclimate dataloggers in the top part of the bat boxes; it is possible that the heat stress conditions were tolerable at the entrance of the bat box where the bats gathered.

Despite roosts reaching temperatures ≥ 44 °C (lethal; (Licht & Leitner, 1967; O'Farrell & Studier, 1970), I did not observe any mortalities that could definitively be attributed to high temperatures. This is similar to findings by Crawford and O'Keefe (2022), who did not observe mortalities in 2019 (during study period) - though they did note 17 (suspected heat-induced) mortalities in 2020 (after study period) -- but contrary to documented mortalities at bat boxes in Spain (Flaquer *et al.*, 2014), Australia (Griffiths *et al.*, 2021) and Canada (Lausen *et al.*, 2022). Differences in mortalities at bat boxes across the globe may be a result of regional differences (and thus relative importance to heat stress) in humidity (Buzan & Huber, 2020). Even within a species, regional differences in heat stress tolerance may exist due to acclimation or acclimatisation (e.g., Noakes *et al.*, 2016; Collier *et al.*, 2019). Bats are known to have species-specific high base-level expression of heat-shock proteins (HSP) that confer some cellular protection from high temperatures (Chionh *et al.*, 2019). Despite this, there are still species-specific limits to heat (duration and intensity) tolerance. High HSP expression, acclimation or acclimatisation history do not negate the potential for cumulative, long-term impacts of repeated or prolonged heat stress that may occur even at sublethal temperatures (Van de Ven *et al.*, 2020) or in combination with high humidity levels.

If bat boxes are to properly mitigate for loss of maternity roosts, they must provide the same or better roosting conditions as the roost(s) they are meant to replace. They must support appropriate microclimates through all phenological stages of reproduction and in all weather conditions, allowing for dissipation of heat at times, while conserving it at others. Given bat boxes' typically poor buffering capacity, high variability (design, microclimate), and elevated potential for causing heat stress, it is unlikely that a single box will fulfill the roosting needs of reproductive females over the entire season (Holroyd *et al.*, 2023). Warm roost microclimates are critical in helping females alleviate the energetic burden of gestation and lactation but microclimate extremes may render a roost suboptimal. The use of sub-optimal roosts (at either microclimate extreme) may reduce an individual's reproductive success or survival probability (Barclay, 2012); as females exhibit high roost fidelity (Lewis, 1995), one must consider the relationship between roost structure type, microclimate (including humidity) and the reproductive success of the bats that repeatedly use them. It is equally important to consider the regional and landscape context. Adjacent roosting options (natural or artificial) offering diverse microclimate options may be needed if microclimates transition to extremes. As heat waves and climate extremes are projected to increase in intensity and duration (IPCC 2021; (Coffel *et al.*, 2018)), risks of reproductive failure or mortality from hyperthermia in overheating roosts likely will be amplified in the future.

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CHAPTER 3. ESTIMATING REPRODUCTIVE SUCCESS OF BATS IN BUILDINGS AND BAT BOXES USING SURROGATE MEASURES

INTRODUCTION

Bats can use torpor (the deliberate reduction in body temperature and metabolic rate) to avoid an energetic deficit (Barclay et al. 2001). Torpor is particularly useful during periods of adverse weather or low availability of insect prey (Lausen and Barclay 2002; Willis et al. 2006; Grinevitch et al. 2009). While torpor reduces energetic demands, it can delay fetal development and parturition in pregnant females (Racey and Swift 1981) and reduce milk production in lactating females (Wilde et al. 1999). Thus females using torpor during the reproductive period may experience negative fitness consequences (Lausen and Barclay 2006; Dzal and Brigham 2013).

In order to avoid the potential fitness consequences of using torpor during the reproductive period, some bat species also employ behavioural strategies that are critical to balancing energy needs and fitness outcomes. While sociality can be of value through allomaternal care of young (Silk 2007; Heldstab et al. 2017), it is the energetic savings via social thermoregulation that is a key benefit of communal roosting (Kerth et al. 2001; Sedgeley 2001; Lausen and Barclay 2002; Kerth 2008). As group size can significantly influence temperature and humidity within a roost structure (Willis and Brigham 2007), communal roosting allows energy that would otherwise be needed for homeothermy to be used for life processes such as gestation and growth. Thus, communal roosting and the selection of optimal habitats (i.e., that support behavioural and physiological adaptations for saving energy), have important implications for reproductive success.

For communal bats, the quality of roosting habitat relates to the potential for energy savings (O’Donnell and Sedgeley 2006). Selection of optimal roosts results in energy expenditures amounting to less than 25% of a bat’s daily energy budget for roosting, despite more than half (63%) of each day being spent in the roost (Burnett and August 1981). Roosting and energetic requirements vary based on time of year, sex and reproductive status (Chruszcz and Barclay 2002; Lausen and Barclay 2002) so the factors influencing roost quality may be especially important for reproductive females, given that their energetic and water needs are the highest of any phenological stage (Adams and Hayes 2008; Lintott et al. 2014; Patriquin et al. 2019).

A microclimate that provides a buffer from ambient temperatures likely is one of the most important factors in roost selection and quality (Hamilton and Barclay 1994; Sedgeley 2001; Mering and Chambers 2014). Selection of roosts with microclimates within a species' thermoneutral zone (TNZ, the range of ambient temperatures wherein resting body temperature can be maintained without the need for additional heat production or heat dissipation) should facilitate homeothermy. Any energy savings realized by selection of optimal roost habitat can then be used to support gestation and lactation during the reproductive period.

Artificial roost structures may be particularly critical for synanthropic species in providing habitat that would otherwise be scarce or unavailable (Fenton 1997; Kunz and Lumsden 2003). In human-altered landscapes, high quality natural roosting habitat features such as tree cavities are often limited (Kunz 1982; Whitaker et al. 2006). Buildings or other anthropogenic structures may provide energetic benefits to bats that choose to roost in them, and may be more advantageous than natural roosting habitats in some cases (Johnson et al. 2019). Further, the longevity of an anthropogenic structure, relative to more ephemeral natural roosting options, provides greater habitat security for bats (particularly females) that display a high degree of fidelity to roosting locations. This reliability means reproductive females may not need to expend energy searching for, or moving to, new roosts within a breeding season.

Roosting in anthropogenic structures such as buildings may enhance annual or lifetime fitness; Lausen and Barclay (2006) found that female bats using buildings during the reproductive season were more likely to have greater reproductive success than conspecifics using nearby natural refugia. In addition to possibility of greater reproductive success (e.g., Altweg *et al.*, 2014; Goldingjay *et al.*, 2015), there may be thermoregulatory (i.e., energetic) benefits (Lausen and Barclay 2006) or improved protection from weather extremes (Cowan et al. 2020) for bats roosting in anthropogenic structures, relative to natural roosts.

Artificial roosting habitat may however result in direct and indirect detrimental effects to bats. Bats in urban areas are exposed to higher depredation by free-roaming domestic cats, particularly when concentrated at a maternal roost (Threlfall *et al.*, 2013; Ancillotto *et al.*, 2013) or subject to higher parasite loads than bats in more ephemeral roosts (e.g., (Brittingham and

Williams 2000; Reckardt and Kerth 2007; Bartonička and Růžičková 2013) In urban or semi-urban areas, the use of anthropogenic structures for roosting also may bring bats into conflict with people. Humans may intentionally kill bats at roosts in random acts of vandalism, due to zoonotic disease fears or because they are considered a nuisance when roosting in buildings (Mickleburgh et al. 2002)(O'Shea *et al.*, 2016). Dietz *et al.* (2009) reported that bats can become accidentally trapped inside buildings leading to mortality. This is a particular danger if exclusion or eviction of bats from buildings occurs during the maternity season, as non-volant young may be left behind as females leave the roost to forage. Further, landscapes near human settlements (where artificial roosts are predominantly found) are often modified such that foraging habitat is reduced, degraded or absent (Lintott et al. 2014), resulting in greater energy expenditures to access distant high quality foraging areas. Artificial habitats could be acting as ecological traps if animals that choose to use them experience reduced fitness (e.g., Klein et al., 2007); this reduced fitness may have population level repercussions and be an example of misplaced conservation effort (Ford et al. 2021).

Bat boxes, sometimes referred to as bat houses, are artificial refugia used as a conservation tool and have been assumed to benefit bats (Rueegger 2016). They may be installed by well-intentioned people to enhance roosting options (Dillingham et al. 2003), used in biodiversity offsets for loss of tree roosts (Le Roux et al. 2016; Rueegger et al. 2019), or provided as replacement habitat, such as when bats are evicted from buildings (Brittingham and Williams 2000). While bat boxes can vary in design style, size and construction materials, there are a limited number of bat species that will use a bat box as roosting habitat. Furthermore, as the reproductive success (i.e., fitness implications), of bats that chose to roost in bat boxes is poorly understood, it is unclear if bat boxes provide suitable replacement for buildings or natural cavity roosting habitat (Griffiths et al. 2017). Despite the relatively small number of bat species that are known to use bat boxes, simple occupancy is often taken as a sign of "success". While many studies (e.g., (Mering and Chambers 2014; Hoeh et al. 2018; Arias et al. 2020; Fontaine et al. 2021) have examined the occupancy and temperature profiles of various styles of bat boxes, the fitness (annual or lifetime) implications of using bat boxes is rarely measured (but see Griffiths *et al.,* 2021, Griffiths *et al.,* 2020). Empirical evidence is needed to properly evaluate positive or negative impacts to bats (Griffiths et al. 2021) as well as the bat communities where bat boxes are deployed (Griffiths et al. 2020). Investigation into the efficacy and implications of bat boxes as artificial habitat has increased in recent years (e.g., (Rueegger 2016; Griffiths et al. 2017; Crawford and O'Keefe 2021) but has not kept pace with their widespread use.

Bats using boxes may not experience the benefits intended by those providing artificial roost structures, but instead suffer reduced reproductive success (e.g., (Brittingham and Williams 2000) or mortality (Flaquer et al. 2014). International published accounts of bat mortalities at bat boxes include (Flaquer *et al.,* (2014) and Crawford and O'Keefe (2021); within British Columbia (BC), a significant bat box mortality event is described in Lausen *et al*. (2022). Bat boxes that decrease reproductive success (Brittingham and Williams 2000) or elevate mortality rates (Flaquer et al. 2014) would be functioning as ecological traps (Robertson and Hutto 2006) for bats that continue to roost within them. A decrease in annual or lifetime fitness could have population-level repercussions.

While mortalities at bat boxes are conspicuous and thus easily quantified, measuring the fitness implications of roosting in these artificial refugia is challenging. In addition to survival, the timing and number of successful reproductive events are key to the fitness of an individual (McGraw and Caswell 1996; Coleman and Barclay 2012). Accurate measures of fitness require tracking individuals, often over several years (if not the lifetime of the individual) to create long-term data sets (e.g., (Brommer et al. 2002; Frick et al. 2010).

In the absence of complete information on lifetime reproductive success and lifetime recruitment, short-term proxy measures may allow some inferences to be drawn for individual annual fitness (Coulson et al. 2006; Dobson et al. 2020). In this study, I sought to compare the annual reproductive success of bats roosting in three types of anthropogenic structures (buildings, a bat condo and bat boxes), using surrogate measures to estimate reproductive success and juvenile development. The surrogate measures I chose were reproductive state (i.e., pregnant or not obviously pregnant) for reproductive success of adult females, and morphological measures (mass, forearm length, and metacarpal ossification) for juvenile development.

I investigated two synanthropic and sympatric bat species - Yuma Myotis (*Myotis yumanensis*) and Little Brown Myotis (*M. lucifugus*), hereafter referred to as Yuma and Little Brown, respectively. Little Brown once were ubiquitous across North America, but their population has been decimated in eastern North America by the introduced fungal pathogen, *Pseudogymnoascus destructans (Pd)*, causing white-nose syndrome (WNS) (Cheng et al. 2021). WNS has been not confirmed in the majority of Yuma range (western North America from central BC to northern Mexico), however *Pd* and WNS has been confirmed in Yuma in Washington State (WDFW 2021). Potential population impacts to Yuma and Little Brown in western North America are currently unknown. Yuma and Little Brown are morphologically similar, although Little Brown are generally heavier with a longer forearm (Lausen et al. 2022). Differentiating between these species in the field where they co-occur is most reliably done using a combination of morphological and acoustic characteristics (Weller et al. 2007; Luszcz and Barclay 2016).

Both of my focal species have similar reproductive and roosting ecology: they are long-lived and slow to reproduce, having one pup in a year (Fenton and Barclay 1980; Braun *et al.,* 2015). Even within each species, parturition is asynchronous (Cockrum 1955); the earliest date of confirmed parturition in my southeast BC study area is June 14 for Yuma (S. Dulc, unpublished data) and June 16 for Little Brown (BCCBP 2021). Altricial young of both species are capable of flight within 21 - 28 days, however weaning and independence may occur well after volancy (Barclay and Harder 2003). Natural roosts include tree cavities and crevices (Fenton and Barclay 1980; Braun et al. 2015), but most documented maternity roosts within BC are in anthropogenic structures where these bats can form very large colonies (Lausen et al. 2022). Fidelity to roost sites is high (Willis and Brigham 2004; Lausen and Barclay 2006; Dixon 2011) and females of both species are known to use (and may co-occur in) anthropogenic structures as maternity roosts (Braun et al. 2015; Lausen et al. 2022).

As both Yuma and Little Brown in my study area use buildings and bat boxes during the summer to raise young (BCCBP 2021), my research questions were:

1. Are the rates of pregnancy the same for bats roosting in buildings and in boxes?
2. Do juvenile bats in buildings exhibit accelerated growth relative to juveniles in bat boxes?
3. Are there fitness implications of roosting in a bat box compared to a building, based on pregnancy rates and juvenile development in each roost structure?

Study area and sites

My study sites were located near the town of Creston, British Columbia (approximately 49°N latitude, -116°W longitude), at the southeastern end of Kootenay Lake. Warm, dry summers and cool, wet winters typify the climate in our study area. Average high and low temperatures are 27 °C and 12 °C in summer, and 12 °C and -5 °C in winter, respectively. The annual precipitation ranges from 450 - 670 mm, with June and December being the wettest months of the year on average (ECCC 2022).

I studied maternity colonies in buildings (3), one large bat condo, and bat boxes (a total of three boxes at two sites) (Fig. 3.1). All sites were potentially mixed Yuma/Little Brown species roosts, however the precise species ratio within roosts was unknown. Each of these maternity roosts has been part of an annual exit-count program to monitor occupancy and approximate colony size for several years as part of the Kootenay Community Bat Project (see https://bcbats.ca/regions/kootenays/). Details and images for each roost structure can be found in Chapter 1 and Appendices A and B of this thesis.

Two building roosts were on private, semi-forested rural land on the eastern shore of Kootenay Lake. Building A (BLDG A), an inhabited log home exposed to full day sun, has an unfinished attic with a hayloft-style entrance facing north. Building S (BLDG S) is a windowless, doorless unoccupied cabin, shaded in all directions by mature trees. Colony sizes in BLDG A and BLDG S are estimated at 3,000 and 800 bats, respectively. The third building (BLDG X) was a large interpretive centre at the western edge of the Creston Valley Wildlife Management Area (CVWMA) wetland complex. An estimated 400 bats used the roof space of the covered patio area; however, this aging building was demolished in the winter of 2019 and thus could not be included in 2021 research. The bat condo (CONDO D, estimated colony size 7,000 bats) is a very large, raised, wooden structure with multiple interior baffled roost boxes hanging from the ceiling, a central interior open area and hopper-like hinged doors closing below the chambers.

All bat boxes were four-chambered maternity-style boxes constructed of plywood and located on private rural residential land at the southern end of the study area. Colony sizes for bat BOX T and BOX R are approximately 800 and 300, respectively. BOX R is a single, south-facing (full day solar exposure) maternity box mounted on a metal pole. BOX T is a complex of four maternity boxes, erected as two box-pairs). Each pair is mounted on opposite sides (back-to-back) of a wooden post; front chambers are oriented in each cardinal direction (i.e., one pair is east-west oriented and one pair is north-south oriented). The space between boxes around a pole is enclosed to provide additional roosting space. Only one box-pair is occupied by the colony at any given time (i.e., bats were not observed to roost in both box-pairs simultaneously), I consider the boxes for this colony as a single roost, BOX T.

METHODS

Roost and ambient microclimate data were collected at each study site using HOBO data loggers (MX2302A or U23 Pro V2; Onset Corporation, USA). Detailed microclimate data collection methods are provided in Chapter 2. I also obtained daily and monthly (March – August) precipitation data, for both 2019 and 2021, for the Creston area from Environment Canada (ECCC 2022).

CAPTURE AND PROCESSING PROCEDURES

Together with field assistants, I conducted bat captures 19 May - 21 June 2019 (adults only) and 13 July - 28 August 2019 (adults and volant juveniles). In 2021, I conducted captures 14 May - 19 June (adults only) and 18 July - 31 August (adults and volant juveniles). I suspended capture during the presumed peak period of parturition within our study area (end of June to mid-July) to avoid very late-stage pregnancy and to prevent prolonged separation of neonates from their mothers during the critical nursing period in early post-parturition. I targeted capture to occur once per week at each site, during appropriate weather conditions (above 10 °C, wind < 12 km/h, no precipitation); I did not conduct capture during suboptimal conditions.

For bat capture in 2019, I used a combination of free-standing, two-bank Austbat harp trap (Titley Scientific Ltd, Columbia, MO), 38 mm mesh mist nets (Avinet Research Supplies, Portland, ME) and custom-made two-bank harp traps (1 inch PVC pipe frame, 30 lb fishing line strings and a PVC bag). In 2021, due to changes in protocols and permitted activities, I captured bats exclusively using custom-made (PVC) or Austbat (Titley Scientific Ltd, Columbia, MO) harp traps at all sites.

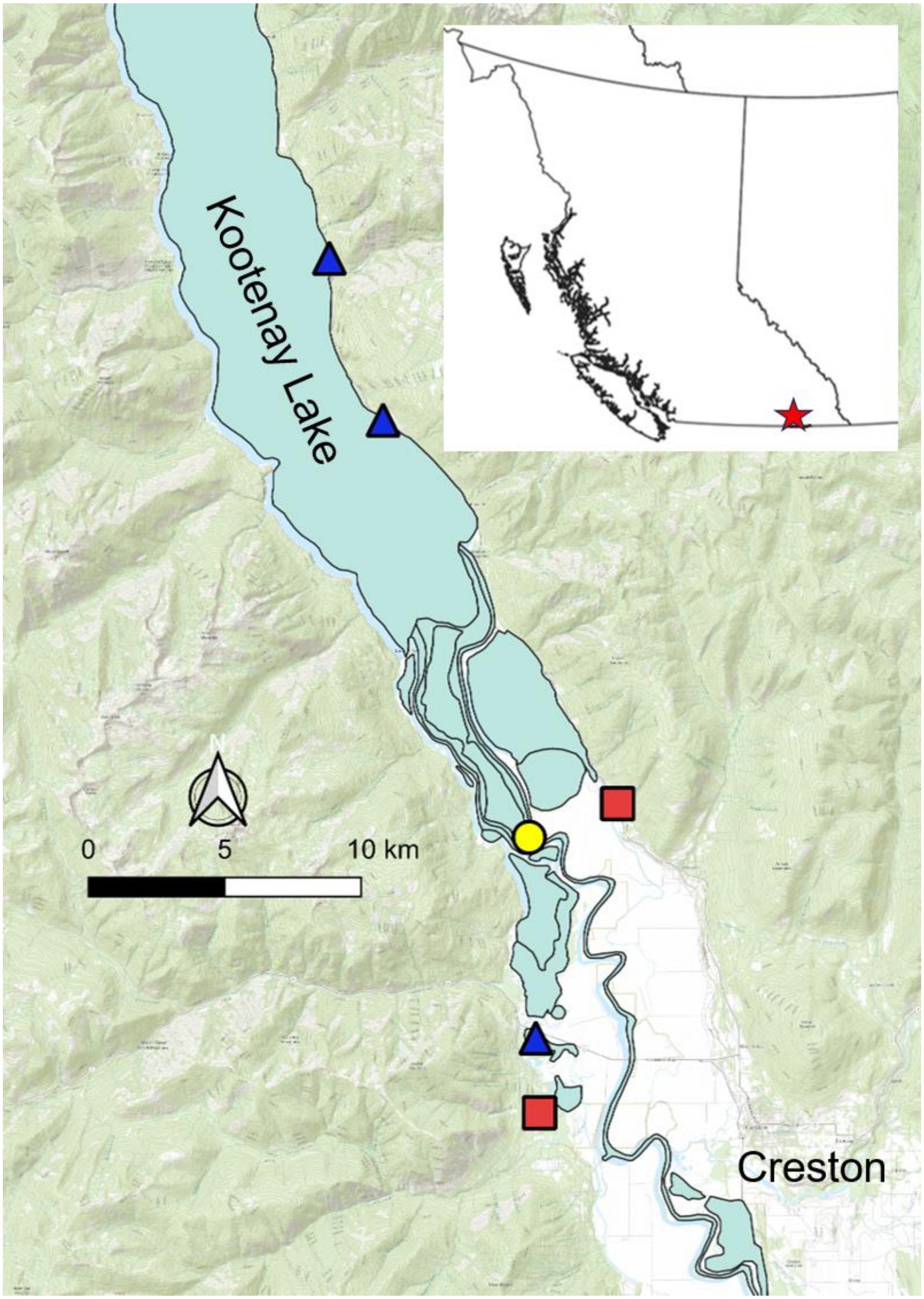

Figure 3.1. Locations of maternity roost study sites (2019-2021) - buildings (triangles), bat boxes (squares) and bat condo (circle) - relative to the town of Creston and Kootenay Lake in southeastern British Columbia, Canada (inset).

I used acoustic and morphometric characteristics to identify bats to species ((Yuma, MYYU); Little Brown, MYLU); if acoustics/morphometrics were ambiguous or intermediate, a combined species label, YULU, was used. I then determined sex and assessed current reproductive status of adult females as ‘not obviously pregnant’ (NOP) or ‘pregnant’ (PG) by gentle palpation of the abdomen. I recorded additional morphometrics and fastened uniquely numbered, lipped aluminum bands (Porzana Limited, East Sussex, United Kingdom) on the forearm of adult bats.

For bats captured in July and August, I determined age class (adult or volant juvenile) by examining the metacarpal phalanges (typically the fourth) for shape and degree of ossification (as per Brunet-Rossinni and Wilkinson 2009). For volant juveniles, I recorded sex, species, mass (nearest 0.1 g), forearm length (nearest 0.01 mm), and the epiphyseal gap (e-gap) of the fifth metacarpal (nearest 0.025 mm). The e-gap measurements consisted of four distinct sub-units (Fig. 3.2): total gap (TG), metacarpal plate (MP), secondary center of ossification (SC) and phalangeal plate (PP). Calcification of bone occurs as juveniles grow and the size of these four cartilaginous e-gap sub-units will change with time. Each subunit was measured to assess the relative degree of bone ossification at a finer scale than simple presence or absence of an e-gap; any differences in e-gap measurements between roost sites were used as an indicator of relative juvenile development and surrogate for juvenile “success”. I transilluminated the wing by gently stretching it over a transparent I-Seeing µRuler M (Qingying E&T LLC, Shanghai, China) micrometer ruler taped to a small battery-operated 32 LED work-light (Fig. 3.2). With the fifth metacarpal joint directly aligned beside and over the ruler hatch marks (Fig. 3-3), I recorded the number of marks, viewed through a 10X jeweller’s loupe, per epiphyseal gap sub-unit (TG, MP, SC, and PP). I generally did not band juvenile bats, apart from 52 juveniles that were banded in late August 2019 at Condo D as part of an ongoing, longer-term monitoring program in place since 2011.

DATA ANALYSIS

For all capture data (2019 and 2021), I excluded observations that were incomplete or appeared to have been inaccurately recorded. I analyzed adult and juvenile capture data separately, assessed intra- and inter-year differences (for site and other effects) and considered species individually and grouped together for both data sets. I used alpha = 0.05 as a statistical significance threshold. For modeling response variables against roost microclimate data, I considered 32 °C and 40 °C to be the lower and upper limits, respectively, of the bats' summer TNZ for both species (Studier and O'Farrell 1976; Braun et al. 2015). I used R Version 4.2.2 (R Core Team, 2022) for all statistical analyses.

To analyze adult female reproductive success, I calculated the proportion of PG to NOP females for pre-parturition (May and June) captures in each year (2019 and 2021) at each roost. I compared rates of observed pregnancy between roost types, between sites within each year (to determine site effects) and within sites over both years (to determine interannual differences) using χ^2 and Fisher's exact tests with simulated p-values (based on 2000 replicates) to account for small sample sizes.

To compare relative juvenile development between sites, I used mass (M), forearm (FA) and e-gap measures (TG, MP, SC, PP) as surrogate metrics of relative growth. I compared juvenile morphological data from capture events that were within two days or less of each other (e.g., paired comparison between juveniles captured at a site on 20 July and those captured at a different site on 22 July). This reduced the potential influence of time between capture events on bat growth between respective site sampling intervals, for both intra- and inter-annual comparisons. I used Welch's T-test for each juvenile morphological measure (M, FA, TG, MP, SC, and PP) by structure type and site and assessed differences in means (with 95% confidence intervals), both within and between years using Tukey's HSD by site and by roost type.

I created generalized linear mixed effects models with R package GLMMTLB (Brooks *et al.*, 2017) using pregnancy status (gestational period 23 May to 14 June) and mass-to-forearm ratio (MFA) as response variables for adult and volant juvenile data, respectively. I chose roost type, cumulative amount of time that roost temperature was within the TNZ, maximum and minimum roost temperatures and humidities, and species as predictive variables; I included sex as a predictive variable for juvenile data modelling (Table 3.1). All models are presented in (Table 3.2). I checked residuals for dispersion and homogeneity issues using DHARMa (Hartig 2022) and used AICc in R package MuMIn (Bartoń 2009) to assess models. Criteria used in model selection were deltaAICc values ≤ 2 and weight greater than 0.01; I used $P < 0.05$ as the significance level for predictor variables.

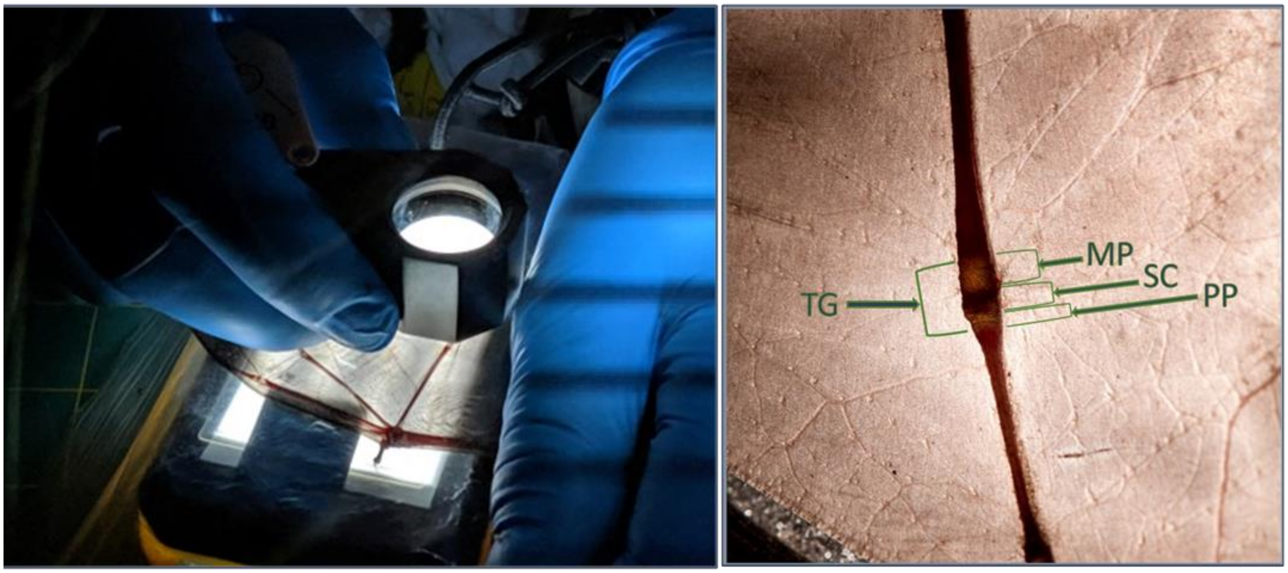

Figure 3.2. Researcher viewing the transilluminated wing (left) of a volant juvenile bat to measure the epiphyseal gap (right). As many as four distinct measurements of the epiphyseal gap were recorded for each juvenile bat: total gap (TG), metacarpal plate (MP), secondary center of ossification (SC) and phalangeal plate (PP). (Photo: S. Dulc).

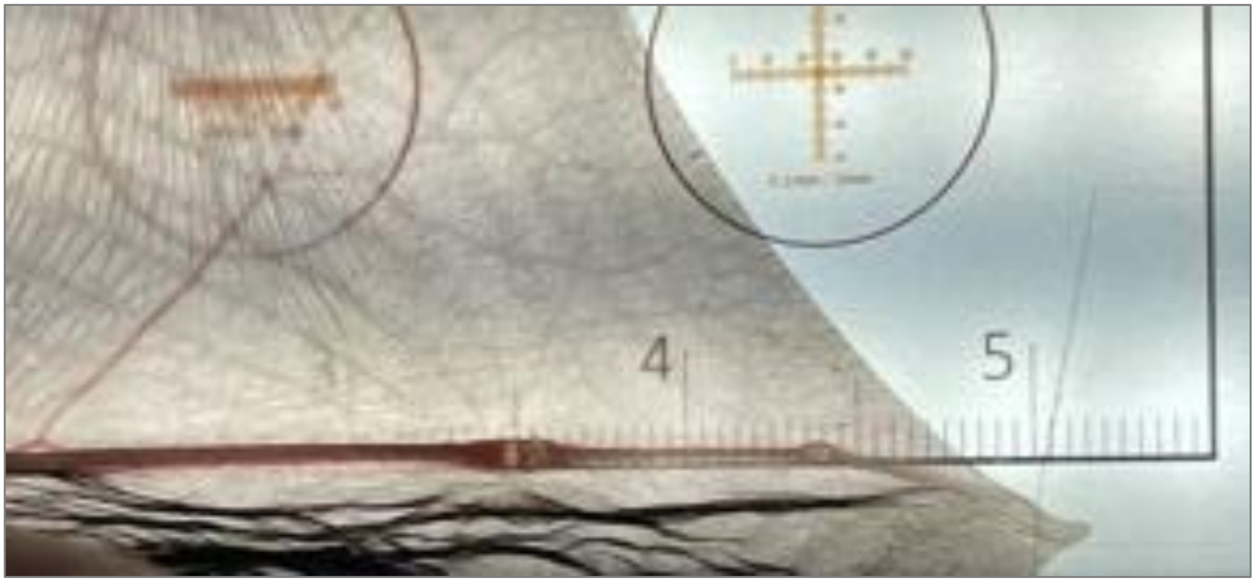

Figure 3.3. Transilluminated wing of a juvenile bat with e-gap positioned over a micrometer ruler for measurement. (Photo: S. Dulc).

Table 3.1. Description of modelling parameters investigated as potentially predictive of surrogate measures of success for two Myotis species (*Myotis lucifugus* and *M. yumanensis*) roosting in three types of roost structures (buildings, a bat "condo", and bat boxes) in the Kootenay region of southeastern British Columbia, Canada in 2019 and 2021. *Because of the morphological similarities of the focal taxa, the designation 'YULU' was assigned to individual captured bats that could not be confidently assigned to either species.

Parameter abbreviation	Description	Possible values/categories
TNZTIME	Cumulative amount of time roost temperature was within the summer thermoneutral zone (32-40 °C; Studier and O'Farrell, 1976; Braun *et al*., 2015) for focal taxa.	Percentage of total data points
MAXTEMP	Maximum recorded roost temperature	Maximum value from data up to the date of capture
MINTEMP	Minimum recorded roost temperature	Minimum value from data up to the date of capture
MAXRH	Maximum recorded roost relative humidity	Maximum value from data up to the date of capture
MINRH	Minimum recorded roost relative humidity	Minimum value from data up to the date of capture
TYPE	Roost structure type	Building, box or condo
SPP	Species identification for captured bats	Yuma (MYYU), Little Brown (MYLU), or *YULU (uncertain)
SEX	Sex of juvenile bats captured	Female or male

Table 3.2. Generalized linear mixed-effects models used to compare adult pregnancy rates (during gestation 23 May to 14 June) as well as juvenile morphometric data (during volancy 18 July to 31 August) between roost sites/types in the Kootenay region of southeastern British Columbia, Canada in 2019 and 2021. Ambient temperature and relative humidity was a fixed covariate, SITE and YEAR were random effects in all models; interaction terms are denoted by an asterisk (*). Response variables were pregnancy status ("pregnant" or "not obviously pregnant") for the adult data set and ratio of mass (g) to forearm length (MFA) for the juvenile data set; both response variables were considered proxies for reproductive success.

Model	Data Set(s)	Variables
1	Adult, juvenile	TNZTIME
2	Adult, juvenile	MAXTEMP
3	Adult, juvenile	MAXRH
4	Adult, juvenile	MINTEMP
5	Adult, juvenile	MINRH
6	Adult, juvenile	TYPE
7	Adult, juvenile	SPP
8	Adult, juvenile	TNZTIME + MAXTEMP
9	Adult, juvenile	TNZTIME + MAXTEMP + MAXRH
10	Adult, juvenile	TNZTIME + MAXTEMP + MAXRH + MAXTEMP*MAXRH
11	Adult, juvenile	TNZTIME + MINTEMP
12	Adult, juvenile	TNZTIME + MINTEMP + MINRH
13	Adult, juvenile	TNZTIME + MINTEMP + MINRH + MINTEMP*MINRH
14	Adult, juvenile	TNZTIME +TYPE
15	Adult, juvenile	TNZTIME + MAXRH + MINTEMP + MINRH
16	Juvenile only	SEX
17	Juvenile only	SEX + SPP
18	Juvenile only	TNZTIME + SEX
19	Juvenile only	TNZTIME + SEX + SPP

RESULTS

In 2019 and 2021, cumulative precipitation was lower and mean monthly temperatures were slightly higher than the 30-year norms for Creston (see Chapter 1 herein). Cumulative precipitation (31 March – 31 August) in Creston was 158 mm in 2019 and 88 mm in 2021 (versus the 30-year average of 255 mm, ECCC 2022); rainfall in 2021 was roughly half (in frequency and amount) of what the study area received in 2019 (ECCC 2022). Between 31 March and 31 August, mean monthly temperatures ranged from 3.3 ° C – 21.4 ° C in 2019 (within ±1.0° C of 30-year average) and from 5.3 ° C – 25.7 ° C in 2021 (≥ 5.1° C above 30-year average). Daily temperature extremes for the 30-year norm range from a minimum of -1.0° C (March) to a maximum of 27.2° C (August); March daily minimums were -2.6 ° C (2019) and -0.1 ° C (2021) while maximum daily temperature was 28.6° C in 2019 (August) and 33.9 ° C in 2021 (July).

I captured 1316 adult females in 2019 over 35 nights and 1229 adult females over 36 nights in 2021. Of these, pre-parturition captures were 432 and 558, with 69% (2019) and 95% (2021) being *Myotis yumanensis* (Fig. 3.4). I captured 925 volant juveniles in 2019 and 718 in 2021, again the vast majority being *M. yumanensis*. Table 3.3 provides a breakdown of sample sizes by site type (building/box/condo), species and year.

ADULT FEMALE PREGNANCY RATES

By roost type, pregnancy rates were significantly higher at the condo and at building roosts compared to bat boxes in both 2019 (χ 2 = 13.11*, df =4*, *P = 0.011*) and 2021 (χ 2 = 53.3*, df =4*, *P < 0.001*). In 2019, mean pregnancy rates were 75.7% (SE = 0.064) at the condo, 70.7% (SE = 0.033) at buildings and 42.4% (SE = 0.053) at bat boxes (Fig. 3.5). In 2021, mean pregnancy rates were 85.7% (SE = 0.034) at buildings, 80.8% (SE = 0.049) at the condo, and 64.6% (SE = 0.032) for box-roosting females (Fig 3.5). Rates of observed pregnancy were also significantly higher (χ 2 = 72.558, df = 5, P <0.001) in 2019 than in 2021 within roost types (Fig. 3.5).

At the individual roost level, rates of pregnancy for all species were significantly different between sites in 2019 (Fisher's Exact test, *P* = 0.0025) and in 2021 (Fisher's Exact test, *P* = 0.011). In 2019, pregnancy rates were highest in Building X (83.3% ± 0.083 SE, n=36) and

Table 3.3. Number of adult (pre-parturition) and juvenile (post-volancy) *Myotis yumanensis (MYYU)*, *M. lucifugus (MYLU)* and YULU (assigned if acoustic and morphological characteristics were indeterminate) captured at each maternity roost type in the Kootenay region of British Columbia in 2019 and 2021. *Numbers for 2021 do not include Building X.

Roost type		Capture	Number of adults			Number of juveniles		
(Site)	Year	nights	MYYU	MYLU	YULU	MYYU	MYLU	YULU
Buildings	*2019*	*17*	*149*	*59*	*17*	*386*	*28*	*9*
(A, S, X)*	*2021*	*14*	*191**	*3*	*23*	*341**	*5*	*16*
Condo	*2019*	*5*	*61*	*3*	*51*	*269*	*1*	*1*
(Condo D)	*2021*	*7*	*104*	*0*	*0*	*129*	*0*	*0*
Boxes	*2019*	*13*	*89*	*0*	*3*	*226*	*1*	*4*
(R and T)	*2021*	*15*	*237*	*0*	*0*	*226*	*0*	*1*
Totals	***2019***	***35***	***299***	***62***	***71***	***881***	***30***	***14***
	2021	***36***	***532***	***3***	***23***	***696***	***5***	***17***

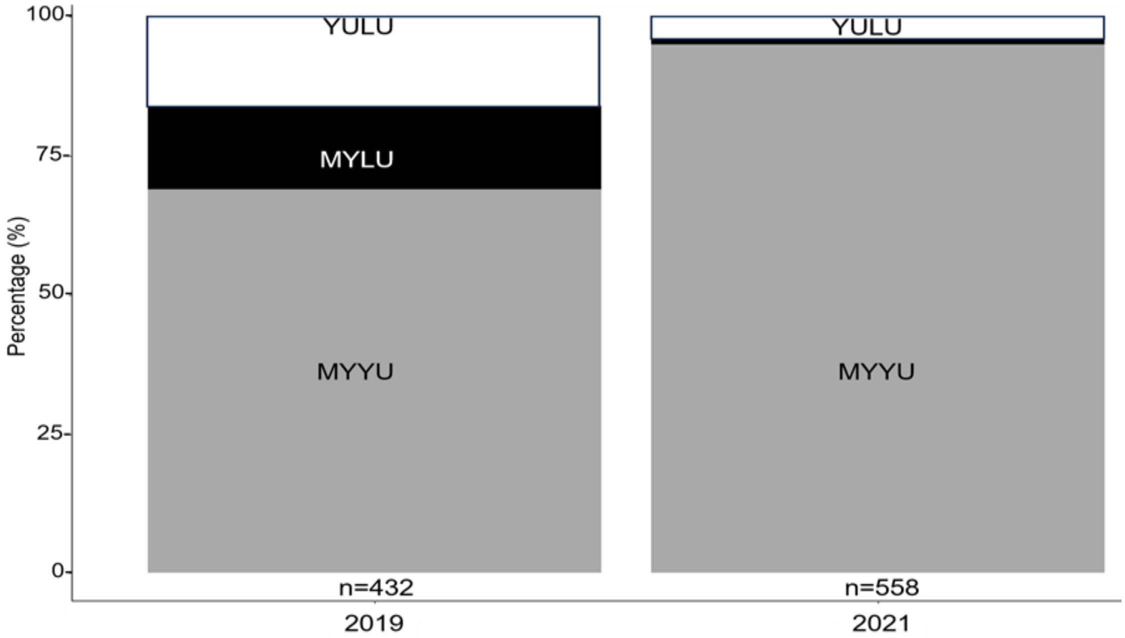

Figure 3.4. Proportion of adult female bats identified to *Myotis lucifugus* (black), *M. yumanensis* (grey), and "YULU" for indeterminate species identifications (white) in pre-parturition capture events at all (building, box and condo) maternity colonies in the Kootenay region of British Columbia in 2019 and 2021.

lowest at Box T (40.0% ± 0.053 SE, n = 89) (Fig. 3.6a). In 2021, the observed pregnancy rate (all species) was highest in Building S (89.9% ± 0.044 SE, n= 128) and lowest at Box R (53.9% ± 0.042 SE, n=143) (Fig.3.6b). All roosts except Box R had higher observed pregnancy rates in 2021 than in 2019 (Table 3.4); interannual differences were only statistically significant for Box T ($\chi 2$ = 63.2, df = 1, P <0.001), where pregnancy rate in 2021 was double that of 2019 (Fig. 3.6).

AICc rankings for the 15 candidate models (see Table 3.1) I evaluated as potentially explanatory for pregnancy rates are provided in Table 3.5. The best model for my data included MINTEMP, MINRH and an interaction between MINTEMP and MINRH as statistically significant (Pr |<z| < 0.001); TNZTIME was also included in this model however it was not a statistically significant variable (Estimate = -7.50; SE = 4.68; Pr |<z| = 0.109).

JUVENILE MORPHOMETRICS

As 97% of juveniles captured at boxes were identified as MYYU, I excluded MYLU and YULU from morphometric comparisons. I found that juveniles, regardless of sex, had smaller mass in 2019 than during the same time in 2021 (F test, df = 1, P < 0.001) at all sites (Fig. 3.7) and thus I kept juvenile analyses separate by year. In general, juvenile females (♀) were larger (M$\overline{x}$ (P < 0.001, adjusted R-squared = 0.05215) and FA$\overline{x}$ ((P < 0.001, adjusted R-squared = 0.05215)) relative to juvenile males (♂) in both years. I did not separate juvenile sex data by site as the capture ratio was consistently 1.5♀:1♂ across all sites.

In 2019, I found no evidence of a difference in any of the juvenile morphometric means (M, FA, TG and SC) in 56% of comparisons (9/16; Welch's two sample T-test, P >0.05) between juveniles in boxes and those in other roosts. For the remaining 44% of comparisons (7/16) in 2019, I found significant differences (Welch's two sample T-test, P < 0.05), with juveniles in bat boxes were less developed in 6 of these 7 comparisons (i.e., had lower mean M, shorter FA, smaller TG, or larger SC) compared to juveniles in buildings or the condo (Table 3.6). In 2021, I found no statistical difference (Welch's two sample T-test, P >0.05) in any juvenile morphometric means in 70% of comparisons (n=20) between boxes and other roost types (Table 3.5). In the 30% of comparisons when a statistically significant difference was found in 2021, juvenile morphometrics in bat boxes were always less advanced (lower mean M, shorter FA, smaller TG, or larger SC) than their counterparts in buildings or the condo (Table 3.5).

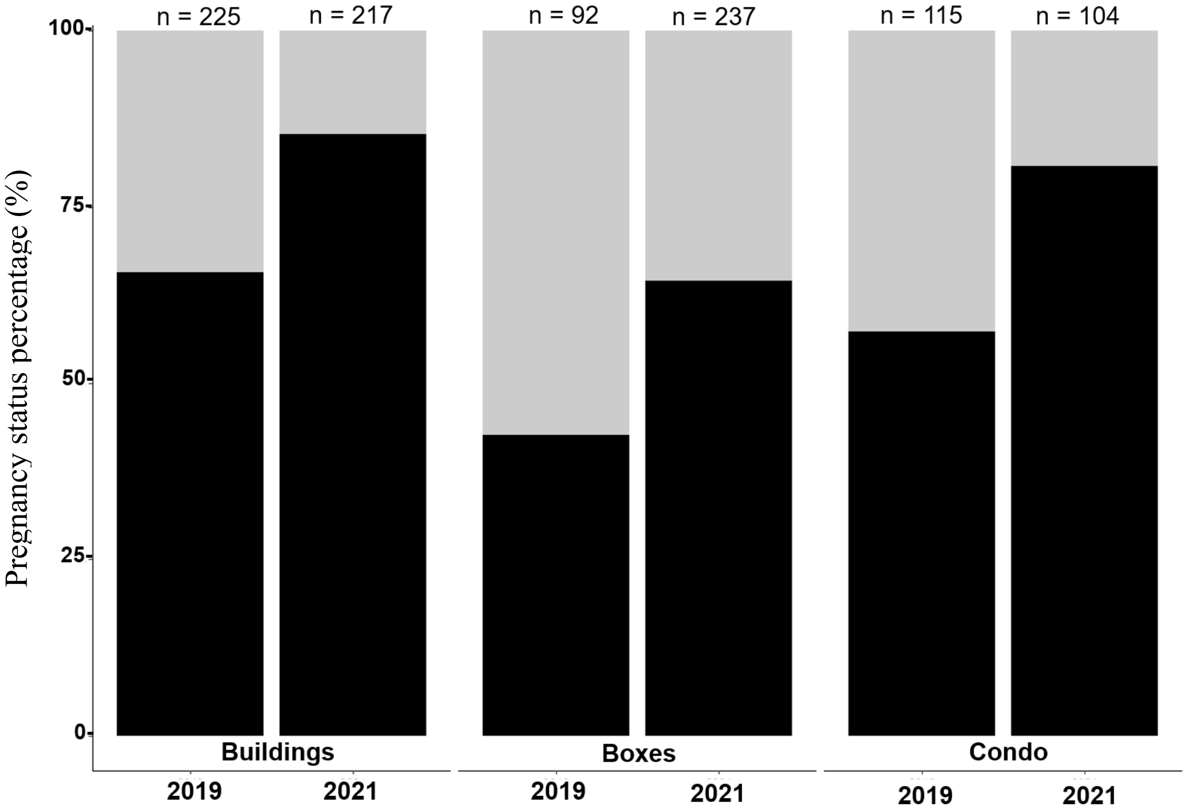

Figure 3.5. Interannual differences in proportion of reproductive adult female *Myotis* bats assessed as pregnant (black) or not obviously pregnant (grey), during examination of bats captured 14 May and 21 June, in 2019 and 2021 aggregated by roost type (buildings, boxes and condo) in the Kootenay region of British Columbia. Differences were significant within roost types between years at alpha = 0.05 (χ *2 = 72.558, df = 5, P <0.001).* Total sample sizes are shown at the top of each bar.

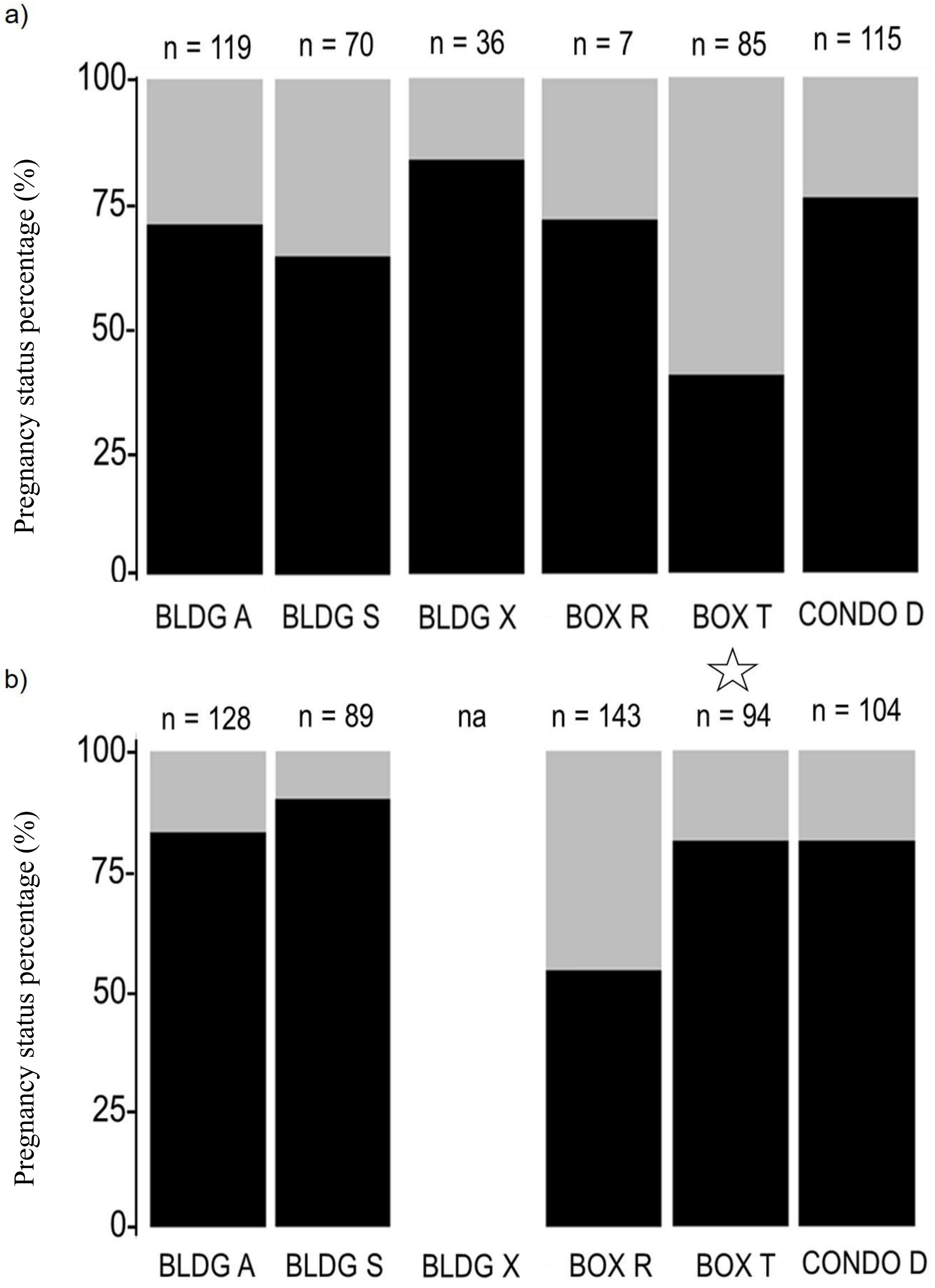

Figure 3.6. Percentage of adult female *Myotis* bats assessed as pregnant (black) or not obviously pregnant (grey), during examination of bats captured between 14 May and 21 June, in a) 2019 and b) 2021 at each maternity roost study site in the Kootenay region of British Columbia. Total sample sizes are shown at top of each bar and statistically significant within-site differences between years are indicated by a star. Building X (present in 2019) was no longer standing in 2021 and thus could not be included.

Table 3.4. Percentage of adult female *Myotis* bats assessed as pregnant or not obviously pregnant during examination of bats captured between 14 May and 21 June, in 2019 and 2021 at each maternity roost study site in the Kootenay region of British Columbia, Canada.

Roost Name	**Type**	**2019** **Pregnant (%)**	**SE**	**n**	**Pregnant (%)**	**2021** **SE**	**n**
Bldg A	Building	70.5	0.046	119	82.8	0.053	89
Bldg S	Building	64.3	0.060	70	89.9	0.044	128
Bldg X	Building	83.3	0.083	36	na	na	na
Condo D	Condo	75.7	0.047	115	80.8	0.049	104
Box R	Box	71.4	0.189	7	53.9	0.042	143
Box T	Box	40.0	0.053	89	80.9	0.054	94

Table 3.5. Summary of AICc results for assessed models relating the observed pregnancy status (response variable) of *Myotis* bats at maternity roosts in the Kootenay region of British Columbia to possible explanatory variables in 2019 and 2021. The top-rated model (Model 13) is highlighted in bold font and includes the cumulative amount of time roost temperatures were within the summer thermoneutral zone (TNZTIME), minimum roost temperature (MINTEMP), minimum relative humidity (MINRH), and an interaction between minimum temperature and minimum relative humidity (MINTEMP*MINRH). The second and third-rated models (# 7 & 8; deltaAICc < 20) are shown for information purposes. Parameters for all models are provided in Table 3.2.

Model	**Model Parameters** (Estimate; SE; *P*-value)	**df (K)**	**logLik**	**AICc**	**delta AICc**	**weight**
13	**TNZTIME** (Est.=-7.50; SE=4.68; Pr(>|z|) =0.109) **+ MINTEMP** (Est.=-0.48; SE=0.08; Pr(>|z|) =1.2e-10) **+ MINRH** (Est.=-0.07; SE=0.02; Pr(>|z|) =9.6e-06) **+ MINTEMP*MINRH** (Est.=-0.01; SE=0.001; Pr(>|z|) =1.6e-10)	**7**	**-466.296**	**946.7**	**0**	**1**
7	SPP	5	-477.593	965.2	18.54	0
8	TNZTIME + MAXTEMP	6	-476.811	965.7	19.00	0

In five building-condo comparisons in 2019 and 2021, I found statistically significant differences (Welch's two sample T-test, $P > 0.05$) in at least one morphometric measure; in all cases juvenile morphometrics in the condo were more developmentally advanced than in building roosts (Table 3.7). Details (sample sizes, means, *p*-values and 95% confidence intervals) for all comparisons of 2019 and 2021 juvenile data are provided in Appendix E.

AICc rankings for the 19 candidate models (Table 3.1) for juvenile response variable mass to forearm ratio (MFA) are presented in Table 3.8. The top-ranked model (model 18), explaining 51.4% of the variability in my data, included cumulative amount of time roost temperatures were within the summer thermoneutral zone (TNZTIME; estimate = - 0.00924; SE = 0.001; z = -9.02) and the sex of an individual (SEX; estimate = - 0.00404; SE = 0.001; z = -7.18), both statistically significant model terms (Pr |<z| < 0.001). TNZTIME and sex were also significant variables in the second-ranked model (model 19), explaining 25.8% of the variability in juvenile morphometrics. Species (SPP) was also an included variable in model 19, however the difference between MYLU (intercept) and either MYYU or YULU was not statistically significant (Pr |<z| = 0.593 and Pr |<z| < 0.158, respectively). The third-ranked model, explaining 22.2% of the variability in juvenile morphometric data included TNZTIME, MINTEMP, MINRH and an interaction between MINTEMP and MINRH; all variables in this latter model were statistically significant (Pr |<z| < 0. 001).

DISCUSSION

I found pregnancy rates among sites differed between roost types within year and, to a lesser degree, between years. Box-roosting bats typically, but not always, had a lower rate of pregnancy than building-roosting bats. This wide variation in pregnancy rates within and between roost structures suggests that not all roost structures, regardless of type, are created equal. It also highlights the importance of multi-year sampling to capture interannual differences, whether they are intrinsic (e.g., natural population variation) or extrinsic (e.g., due to weather conditions or resource availability).

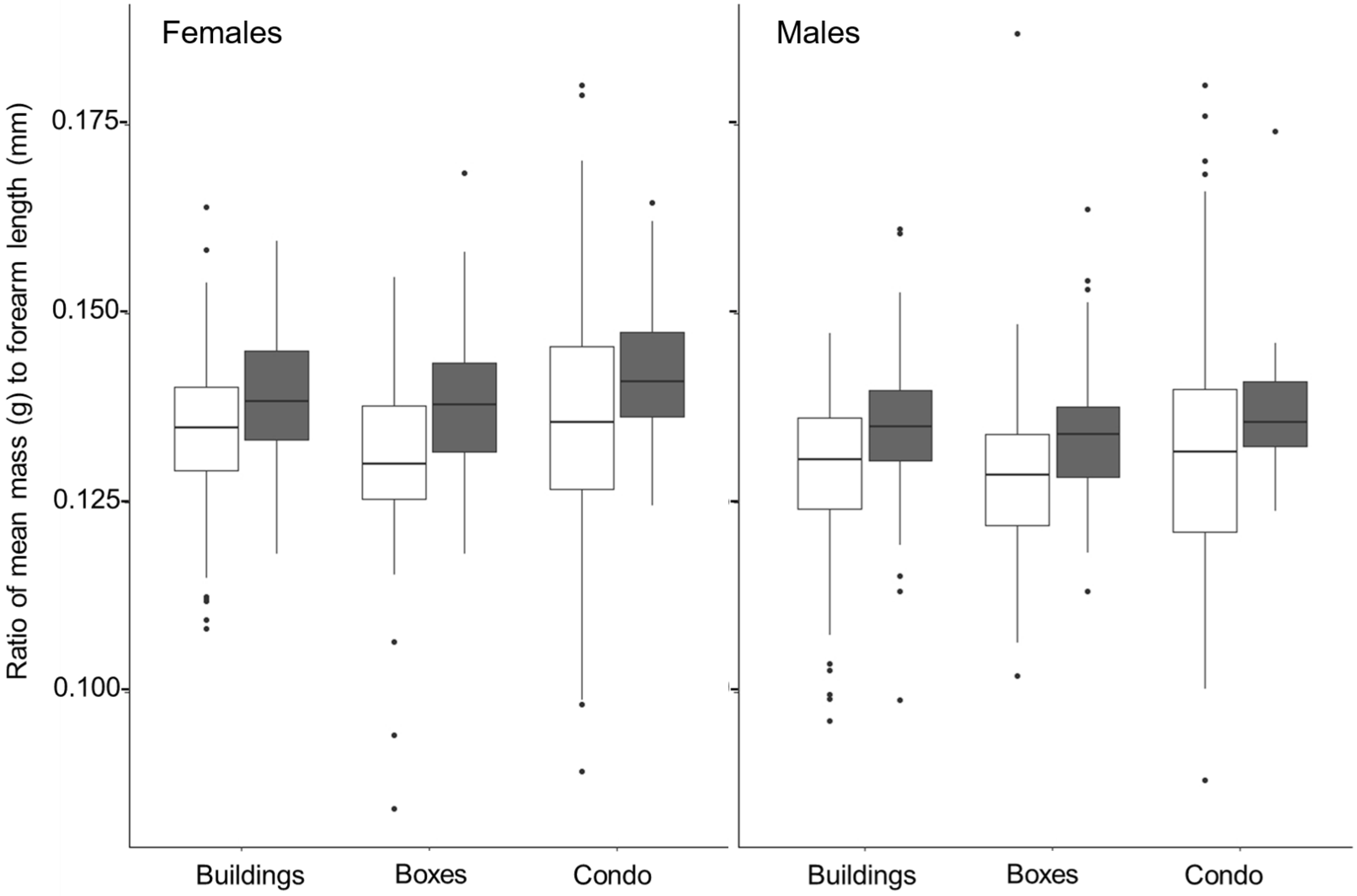

Figure 3.7. Boxplots for 2019 (white) and 2021 (grey) the ratio of mass to forearm for volant juvenile female (left) and male (right) Myotis bats captured at building, bat box and bat condo maternity roosts in the Kootenay region of British Columbia. All interannual differences were significant (F test, df = 1, P < 0.001).

Table 3.6. Summary of statistically significant (Tukey's HSD, $P \leq 0.05$) differences of volant juvenile *Myotis yumanensis* morphometric means from comparisons of building- or condo-roosting juveniles to box-roosting juveniles in 2019 and 2021. Morphometric means compared were mass, M; forearm length, FA; total epiphyseal gap, TG; secondary center of joint ossification, SC. Symbols < and > in column headings signify directionality of the (presumed) more developmentally advanced state for that measure. The roost type (building, BLDG; condo, CONDO; bat box, BOX) with evidence of more advanced juvenile development is noted in each morphometric column. Non-significant differences in morphometric means are noted with "ns". Details (sample sizes, degrees of freedom and p-values) for all comparisons of 2019 and 2021 juvenile data are provided in Appendix E

		Roosts Compared		**Evidence of advanced juvenile morphometric**			
Year	**Capture Dates**	**Building or Condo**	**Box**	**$M\bar{x}$** >	**$FA\bar{x}$** >	**$TG\bar{x}$** <	**$SC\bar{x}$** >
2019	July 27/28	Bldg X	T	BLDG	BLDG	BLDG	ns
	Aug 7/8	Bldg S	T	ns	ns	BOX	BLDG
	Aug 8/9	Bldg S	R	BLDG	ns	BOX	BLDG
	Aug 9/10	Condo	R	CONDO	ns	CONDO	CONDO
	Aug 19/20	Bldg X	T	BLDG	BLDG	ns	ns
	Aug 20/22	Bldg S	T	BLDG	ns	BLDG	BLDG
	Aug 27/28	Condo	R	BLDG	ns	ns	ns
2021	July 26/27	Condo	R	ns	ns	CONDO	ns
	Aug 1/2	Bldg A	T	ns	BLDG	ns	ns
	Aug 25/26	Bldg A	T	ns	BLDG	ns	ns
	Aug 26/28	Condo	T	CONDO	CONDO	ns	ns
	Aug 28/29	Condo	R	CONDO	ns	ns	ns

Table 3.7. Summarized results of volant juvenile morphometric comparisons between buildings (A, S) and the bat condo (Condo) roosts in the Kootenay region of British Columbia during 2019 and 2021. Morphometric means (mass, M; forearm length, FA; total epiphyseal gap, TG; secondary center of joint ossification, SC) were compared using Welch's t-test and statistical significance at $P < 0.05$; non-significant differences are noted with "ns". Symbols < and > in column headings signify directionality of the (presumed) more developmentally advanced state for that measure. The roost with evidence of more advanced juvenile development is noted (bold font) in each morphometric column.

		Roosts Compared		**Evidence of advanced morphometric**			
Year	**Capture Dates**	**Building Roost**	**Bldg or Condo**	**M$\bar{x}$ >**	**FA$\bar{x}$ >**	**TG$\bar{x}$ <**	**SC$\bar{x}$ >**
2019	July 30/31	S	Condo	S	ns	ns	ns
	Aug 10/11	A	Condo	Condo	ns	ns	ns
2021	July 20/21	A	S	S	A	A	ns
	July 28/29	A	S	ns	ns	A	ns
	Aug 05/06	A	S	ns	ns	A	ns
	July 19/20	S	Condo	ns	Condo	ns	ns
	July 27/28	S	Condo	ns	ns	Condo	ns
	Aug 04/05	S	Condo	Condo	ns	Condo	ns

Table 3.8. Summary of AICc results for assessed models with (weight > 0.002) potentially predictive of the observed mass-to-forearm ratio (response variable) of volant juvenile *Myotis* bats at building, bat box and condo maternity roosts in the Kootenay region of British Columbia during 2019 and 2021. All models are conditional on SITE and YEAR. The three top-rated models (with delta AIC ≤ 2) are highlighted in bold font; models with weight <0.002 are not shown. Interaction terms are noted with an * between variables. Parameters for all models are provided in Table 3. 2.

Model	**Predictive Variables** (Estimate; Std. Error; z-value; Pr(>|z|)	**K**	**logLik**	**AICc**	**deltaAICc**	**weight**
18	**TNZTIME** (-0.00924; SE = 0.001; z = -9.02; Pr(>|z|) < 2e-16) **SEX** (-0.00404; SE = 0.001; z = -7.18; Pr(>|z|) < 6.92e-13)	**4**	**4736.723**	**-9465.4**	**0.00**	**0.514**
19	**TNZTIME** (-0.00924; SE = 0.001; z = -9.02; Pr(>|z|) < 2e-16) **SEX** (-0.00404; SE = 0.001; z = -7.18; Pr(>|z|) < 6.92e-13) **SPP-MYYU** (-0.00124; SE = 0.002; z = -0.53; Pr(>|z|) = 0.593) **SPP-YULU** (-0.00430; SE = 0.003; z = -1.41; Pr(>|z|) =0.158)	**6**	**4738.048**	**-9464.0**	**1.38**	**0.258**
13	**TNZTIME** (-8.8e-03; SE = 1.2e-03; z = -6.96; Pr(>|z|) < 3.5e-12) **MINTEMP** (-8.5e-04; SE = 2.4e-04; z = -3.49; Pr(>|z|) < 0.0001) **MINRH** (-2.7e-04; SE = 7.7e-05; z = -3.50; Pr(>|z|) < 0.0001) **MINTEMP*MINRH** (-2.6e-05; SE = 6.7e-06; z = 3.90; Pr(>|z|) = 9.6e-05)	**7**	**4738.906**	**-9463.7**	**1.68**	**0.222**
9	TNZTIME, MAXTEMP, MAX RH	6	4732.951	-9453.8	11.57	0.002

While my overall results suggest building- and condo-roosting females may have greater reproductive success than box-roosting females, this was not the case at all sites nor in all years. The pregnancy rates in my study area, as estimated by my surrogate measure of pregnancy over two years, suggest interannual variation in pregnancy was site-specific and not necessarily correlated to roost structure type (i.e., not based on whether the roost was a box, a bat condo or a building). Overall, pregnancy rates of adult females that I captured at maternity roosts in both 2019 and 2021, were within the ranges published by Barclay *et al.* (2004) for *M. lucifugus* and *M. yumanensis* (27.5% - 100% and 31% - 100%, respectively). These data were for the same species and at the same latitude as my study but investigated a variety of roost types (buildings, trees, caves) and random samples, while my study only included targeted (non-random) maternal colonies in anthropogenic structures. The narrower range in my data may reflect differences in roost types under study, random versus targeted maternal colony sampling, or climate variation between the populations that were studied. Pregnancy rates in my study were generally lower than the 87% - 99% reported for *M. lucifugus* in a barn by Frick *et al.* (2010).

The cumulative time that roost temperatures were within the summer thermoneutral zone (TNZTIME, 32 °C – 40 °C) of my focal taxa occurred in the top-ranked model as a potential predictor for observed pregnancy status but was not a statistically significant variable ($P > 0.05$). That TNZTIME was not significant may be due to the relatively small proportion of time that roost temperatures were within the TNZ (see Chapter 2 herein), particularly prior to parturition. If both reproductive and non-reproductive adult females returned to maternity colony roosts, aligning with findings by Frick *et al*. (2010), this would confound modelling. Further, an individual’s fat reserves would influence the probability of successfully reproducing (Barclay *et al*., 2004; Reimer and Barclay 2023), likely overriding roost microclimate variables in observed pregnancy rates. Johnson and Lacki (2014) found that roost microclimate or external weather variables did not explain reproductive condition but did explain the frequency of torpor use.

The site or roost type differences I observed in early season pregnancy rates in 2019 may reflect delayed gestation progress as opposed to lower reproductive success. The relatively cool, wet spring of 2019 may have necessitated a greater use of torpor for females, delaying gestation and hindering our ability to detect the physical evidence of pregnancy for females captured in spring. This may explain why minimum temperature (MINTEMP) was a statistically significant ($P < 0.05$) potential predictor for observed pregnancy status. Bats that were not obviously pregnant could have given birth later during the summer. Furthermore, a pregnancy detected in spring may not have resulted in a successfully fledged offspring. Inclement weather, as experienced in my study area in 2019, may have resulted in a female foregoing reproduction (through an aborted fetus or similar to results reported by Burles *et al.* (2009). This appears to align with findings of Grindal *et al.,* (1992), who reported that high levels of spring precipitation resulted in delayed reproduction and lower overall reproductive rates (possibly via termination of pregnancy) for Yuma and Little Brown in the Okanagan region of BC. Similarly, cold and wet spring weather resulted in lower reproductive success for Little Brown in the temperate Pacific northwest (Burles et al. 2009). As spring weather influences the duration of gestation and timing of parturition (Racey 1982; Frick et al. 2010), the cool, wet spring conditions likely led to low pregnancy rates observed at all of my study sites in 2019.

Bat boxes, typically less well-buffered from ambient temperatures (Rowland et al. 2017; Griffiths et al. 2018; Hoeh et al. 2018), may have prompted adult female occupants to use torpor more frequently in 2019, delaying fetal development relative to building-roosting females. This could explain the low observed pregnancy rates at boxes in spring of 2019. It follows that the significantly higher observed pregnancy rates at boxes in 2021, relative to 2019, may be attributable to less frequent torpor use in the warmer spring of 2021, facilitating fetal development.

If females that roost in buildings in our study area became pregnant sooner, or experienced accelerated gestation, parturition would occur earlier relative to bats roosting in boxes. Earlier parturition and subsequent earlier weaning would maximize the amount of time a post-lactating female has to regain energy stores prior to hibernation. Accelerated gestation also would be advantageous for offspring; earlier parturition dates will give young a longer period to grow, master flight and prey capture, exploit foraging opportunities, and store energy as fat. For example, Lausen and Barclay (2006) found that parturition and fledging occurred up to two weeks sooner for juvenile *Eptesicus fuscus* raised in buildings compared to those in rock roosts. This would increase the probability of overwinter survival for both juveniles and adults and positively influence future breeding outcomes, as reported by Frick *et al.* (2010) for *M. lucifugus.* With high first-year mortality rates for Little Brown (0.23 – 0.46), survival probability was positively correlated with parturition date; pups born earlier in the season (in late May) were more likely to survive their first winter than those born in mid-July (Frick et al. 2010). Longer post-weaning and pre-hibernation time, coupled with favourable roost microclimates, allows greater accumulation of fat reserves, better long-term survival, and higher lifetime fitness potential for adult females and young of the year (Linton and Macdonald 2018; Johnson et al. 2019).

In the comparative ranking of models for juvenile development, cumulative time in thermoneutral zone (TNZTIME) was a significant variable in the top-ranked model. Despite roost temperatures between 32 °C – 40 °C occurring only 25% of the time or less at each roost in 2019 and 2021 (see Chapter 2 results herein), greater amounts of cumulative time in optimal thermal conditions (see Chapter 2, Figure 2.3) appears to have benefited juvenile growth (mass to forearm ratios, MFA). . Passive warming provided by optimally warm roosts may lower the energetic requirements to maintain homeothermy, particularly important for juvenile growth and development. This would be most important when adult females are out foraging at night and the juveniles are left behind in roosts that may or may not retain enough heat to stay within the species thermoneutral zone.

Sex was also an important model in the top-ranked juvenile development model. As in previous studies, I observed sexual dimorphism in Little Brown (Fenton and Barclay 1980) and Yuma Myotis (Braun et al. 2015), with females typically larger than males. Species was a variable in the second highest ranked model however, it was not a statistically significant variable. There are at least three nonexclusive reasons for this: 1) While Little Brown are typically a larger species than Yuma myotis (Lausen *et al.,* 2022), Little Brown myotis tends to arrive at maternity sites in spring in this area at least a month earlier than Yuma myotis (C. Lausen, pers. comm.). Species may thus have been a relatively uninformative parameter (Arnold 2010; Leroux 2019) for predicting juvenile MFA, because differences in timing of birth may be masked by inherent size differences between the species. 2) The relative scarcity of Little Brown myotis captured in my study may have under-represented this species in my analyses. 3) The error (or range) in the MFA response data may have exceeded any effect of species on MFA, rendering species unimportant in modelling relative juvenile development.

In my study, neither post-natal nor overwinter survivorship of juveniles could be ascertained to determine the relative success (within year and between year) of offspring from different roost types. Similarly, I was unable to track the reproductive status of any individual (i.e., to determine if an individual bat that was pregnant in May/June gave birth or was nursing later in the season). This was likely due in part to exceptionally low within-year recapture rates of banded adult females (0.9%, *n* = 14/1482, in 2019; 1.1%, *n* = 15/1416, in 2021). The ability to recapture bats was likely challenged in part by very large colony sizes at some sites and unknown roost switching behaviour, as these are factors that may influence recapture probabilities (Kunz et al. 2009). For example, Rensel *et al.* (2023) found that after young achieved volancy, adults were more likely to switch roosts, relative to late pregnancy and early lactation stages. As weaning occurs after juvenile volancy is achieved (Barclay and Harder 2003), juveniles likely switch roosts with their mothers. The increased potential for roost switching at this time would have lowered the probability of recapturing adult or juvenile bats.

Adults and juveniles using unknown satellite roosts, of mixed types, would certainly have influenced my data and subsequent modelling efforts. Roost switching is a possibility at all sites as none of the sites appeared isolated by the surrounding landscape matrix and I did not conduct radiotracking to know if bats switched roosts mid-summer. Differences in local habitat characteristics, such as distance to preferred foraging areas or alternate roosts (as well as quantity or quality), may have a greater influence on reproduction and growth than the variables I investigated. The effects of local habitat variables may be more pronounced in years with adverse weather conditions.

Precipitation, and to a lesser extent temperature, has been found to affect insect biomass (Welti et al. 2022; Dalton et al. 2023) and abundance (Gruebler et al. 2008; Stack Whitney et al. 2016; Dalton et al. 2023). Although I did not measure prey availability or density, insect abundance was likely lower in the cooler, wetter spring of 2019 compared to 2021. The warmer, drier conditions of 2021 would have led to greater foraging opportunities (longer or more frequent periods) for both mothers and offspring. Further, the quality and quantity of milk produced by female bats may have been higher due to better weather and foraging in 2021 relative to 2019. For example, Quesnel *et al.* (2017) found that environmental conditions that affected foraging resulted in variable milk protein and lipid content; better forage correlated with higher quality milk and, in turn, increased offspring survival probability. A measure of insect (prey) abundance would have been a useful inclusion as it may have explained the increase of pregnancy rates and advanced juvenile development at all sites in 2021. If abundance of insect prey varied by site, this may also have explained the shift in sites with the highest and lowest pregnancy rates between 2019 and 2021.

The reproductive benefits of roosting in buildings have been identified in some areas and for some bat species. Indeed, reproductive success is improved for some synanthropic species living in human structures such as big brown bat, *Eptesicus fuscus* (Lausen and Barclay 2006), and Kuhl's pipstrelle, *Pipistrellus kuhlii* (Ancillotto et al. 2015). Johnson *et al.,* (2019) found that where summer temperatures are cool and the active growing season is short, buildings provide critical maternity habitat for Little Brown bats (*Myotis lucifugus*).

My study supports that, at least in some years, certain buildings may provide higher-quality maternity habitat for Little Brown or Yuma Myotis than bat boxes. However, results of my study also suggest that roosting in a bat box may, depending on the box and the year (including biotic and abiotic variables), have benefits that are not realized in all types of building roosts. As not all artificial refugia (buildings or boxes) are created equally (e.g., Neubaum *et al.,* 2007; Jeong *et al.,* 2022), protecting or restoring natural roosting habitats for bats is imperative. It is likely that providing a range of refugia (both natural and anthropogenic), with a variety of microclimates and foraging habitats, will offer synanthropic species such as Yuma and Little Brown the greatest flexibility in choosing suitable maternal habitat.

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CHAPTER 4. CONCLUSION

THESIS SUMMARY

Are boxes used by reproductive female bats an effective conservation tool (in that they provide suitable artificial roosting habitat) when compared to buildings or bat condos? To my knowledge, there is a paucity of research on the true fitness implications of roosting in a bat box and this is the first study to use surrogate measures of fitness to compare maternity colonies in boxes with those in other anthropogenic roost structures. In 2019 and 2021, I studied maternity roosts of *Myotis lucifugus* and *M. yumanensis* residing in each structure type to reveal the relative differences, in an attempt to inform discussions on this overarching question. For each roost, I characterized the available microclimates (temperature, relative humidity, vapour pressure deficit and temperature - humidity indices as an estimate of heat stress potential) and compared microclimates by structure type. Among roosts and roost types, I compared surrogate measures of reproductive success, specifically, adult female pregnancy rates and juvenile growth/development.

The main findings of my research relating to roost microclimates were:

- Temperatures in all roosts were most often (70%) below 32 °C (the presumed thermoneutral zone summer lower limit) and within the summer TNZ 25% of the time during the breeding season in all roosts, regardless of type. This was the case in both years, despite local ambient conditions being much warmer in 2021 than in 2019.
- Temperatures > 44 °C (presumed lethal) and 100% RH occurred in occupied boxes both years and in one building in 2021 only; these conditions were more frequent in 2021.
- Vapour pressure deficits (VPD) for occupied bat boxes were 1.5 – 4 times lower (i.e., less evaporative cooling capacity) in the Kootenay region than in the Okanagan.
- Heat Stress Indices (HIs) for bat boxes were up to 1.5 times higher than for buildings or condo roosts in both study years.
- HIs exceeding my threshold of 108 (HIs value at 40 °C and 100% relative humidity) occurred in all occupied Kootenay region boxes in both years but

were more frequent in 2021; HIs > 108 were more frequent in the Kootenay than in the arid Okanagan, despite the latter generally being the hotter of the two regions.

- HIs > 108 were extremely infrequent in building roosts (< 2% and in 2021 only) and never occurred in the bat condo.
- Microclimates were most stable (and not subject to extremes) in bat condos, relative to boxes and buildings, in both study years. Bat boxes had the least stable microclimates (greater variability and more frequent extremes in all parameters) in both study years.
- Bat boxes remained occupied the majority of the time when microclimate extremes occurred.

My main research findings relating to reproductive success and juvenile growth were:

- Pregnancy rates were highest in buildings and lowest in boxes in both years but dependent on year at the site level; i.e., higher pregnancy rates for each roost type in the warmer, drier 2021 but this was not necessarily the case for individual roosts.
- Juveniles were more developmentally advanced (based on morphometric measures) in buildings or the bat condo than in bat boxes; this was more frequently observed in the cooler, wetter 2019 study year.
- Roost type (i.e., box, building or condo) was not a significant predictor of pregnancy or juvenile development and individual roosts performed differently in each year. The cumulative amount of time roost temperature was within the summer TNZ was a term in the top-rated model for each surrogate measure of reproductive success.

LIMITATIONS AND FUTURE RESEARCH RECOMMENDATIONS

While my results suggest that bat boxes in my study area were not functioning as ecological traps, caution in extrapolation is required. Cowan *et al.* (2021) suggest that the study of artificial habitat efficacy and implications is nascent and future research should include impacts at both the individual and population level. My study was short-term, conducted over two non-consecutive years, and not a mark-recapture effort, thus I was limited to using surrogate measures of unknown individuals to estimate annual reproductive success and juvenile development at a small number of roost sites. These aggregate annual estimates based on surrogate measures may not correspond closely to lifetime fitness of an individual (Dobson *et al.*, 2020) and are unsuitable for making inferences about potential population-level impacts. Long-term datasets, involving known (i.e., marked) and genetically identified (in the case of morphologically similar conspecifics) individuals are needed to illuminate the fitness consequences of using artificial habitat and provide greater insight into potential population-level effects of artificial refugia such as bat boxes.

A further limitation of my research is that I did not investigate natural roosts used by my focal taxa, such as tree deformities (cavities, crevices, or flaking bark). Comparing buildings versus bat boxes is warranted given the increasing societal pressure to evict bats from buildings (e.g., real estate disclosure forms, BCREA (2020); zoonotic disease spill-over fears, Wang & Anderson, 2019)) and the frequent provision of bat boxes as mitigation for lost roosts (Griffiths *et al*., 2017; Arias *et al*., 2020). Bat boxes (or buildings) may not be an appropriate substitute for natural habitats (but see Lausen *et al.* 2006), thus a comparison of anthropogenic to natural roosts is necessary. As with any artificial habitat, the suitability and quality of these structures for bats will depend on "how closely they mimic natural conditions" (Valdez, Gould & Garnham, 2021). In other words, anthropogenic habitat must meet or exceed the reproductive success facilitated by natural maternal roosting habitat. Long-term monitoring of bat boxes (e.g., Griffiths *et al*., 2020) and natural roosts, incorporating measures of reproductive success, is needed for a more accurate assessment of the fitness implications of providing these artificial refugia, relative to the structures in which these species would have evolved.

A comparison of microclimate profiles in natural roosts to those in anthropogenic roosts may elucidate the characteristics that lead to roost selection. The addition of variables such as hours of solar exposure, amount of shading (or canopy cover) , height of roost, and air speed – all factors that may influence microclimate and roost selection (e.g., Jung *et al.,* 2004; O'Keefe and Loeb, 2017) - that I did not consider in my analysis may be informative. Adding measures of thermal conductance and surface reflectance could aid in understanding the thermal buffering capacity of bat boxes (Crawford *et al*., 2022; Crawford *et al.,* 2024).

Alternative construction materials such as fiber-cement board (Rueegger, 2016; Bideguren *et al.*, 2019) for bat boxes that may ameliorate overheating risks are worth exploring. Further, incorporating different types of anthropogenic structures, such as bat condos (or mini-condos), mechanically-carved cavities (e.g., Rueegger, 2017; Griffiths *et al.*, 2018) and bark-mimics (e.g., Adams *et al.*, 2015) into roost microclimate studies and management programs may provide valuable insights; as an example, Griffiths *et al.,* (2022) found mechanically-carved hollows provided effective buffering from extreme temperatures and the condo studied herein had the most stable microclimate of all three roost types.

I would strongly encourage new maternity roost microclimate studies to measure relative humidity along with temperature, to allow calculation of absolute humidity and vapour pressure deficits. Similar to Rensel *et al*. (2023), my data in the Kootenay (see Chapter 2 herein) demonstrated that 100% relative humidity was common in occupied bat box maternity colonies. By contrast, the bat box maternity colonies I studied in the Okanagan did not achieve this extreme humidity, likely reflecting the more arid climate. This could be a critical consideration for bat box use in humid regions; heat waves in such areas present a much greater threat to bats roosting in confined spaces such as bat boxes, than to colonies in similar structures in desert-like climates. Counter- intuitively, our assumptions about maternity roosts that are at ‘high risk’ and ‘low risk’ of heat stress or heat-induced mortality may be incorrect. Based on my data, bat boxes in moist climates (e.g., inland temperate rainforest zone of the Kootenay; DellaSala *et al*., 2021) may be more likely to present a heat stress and possibly a mortality risk, than boxes in dry (hotter) climates. Regional differences in humidity - and thus evaporative cooling potential - may explain why mass mortality events attributed to overheating have been observed in Kootenay and coastal areas of BC to date (Lausen *et al.,* 2022), but have not occurred in the Okanagan. Understanding not just roost temperature data, but humidity conditions in bat boxes, is needed to properly understand evaporative cooling potential (as vapour pressure deficit, VPD) within a roost. Even for species without known TNZ or heat stress thresholds, VPD profiles may help identify roosts (or regions) that are at higher risk of overheating where active management or interventions may be required. The inclusion of VPD measures also will facilitate roost comparisons across broad geographic locations and between studies.

Published research on the consequences of artificial habitat provision to individual fitness, populations and to bat community structures is lacking (but see Griffiths *et al.*, 2017, 2019, 2020). Long-term mark-recapture studies are needed to measure fitness costs at each of these levels. Given low first winter survival rates for young of year (Lentini *et al.*, 2015), exploring options for non-invasive and inexpensive methods of mark-recapture (e.g., wing biometrics; Amelon *et al.,* 2017) for juvenile bats is an area for further research. This would improve the inferential power of future research on juvenile survivorship or growth rates. Further, incorporating measures of prey densities, foraging distances and other landscape variables will lead to a more fulsome understanding of the factors that may influence the annual fitness of adults and juveniles in maternity colonies.

MANAGEMENT AND CONSERVATION IMPLICATIONS

Preventing loss of existing natural habitats should be a priority for management and conservation of bats, along with restoration of degraded natural habitats (e.g., Lacki 2018). Bat boxes, or other types of artificial refugia, may be most appropriate in human-modified landscapes to enhance otherwise limited roosting options for certain species (Kunz *et al.*, 2006). To be effective surrogates for natural habitats, however, bat boxes must be appropriately placed, maintained and monitored (Brittingham & Williams, 2000; Holroyd *et al.*, 2023) to ensure they are providing functional, safe and long-lasting artificial roosting habitat for females and young.

Artificial refugia also may be beneficial beyond the provision of habitat for target species. Researchers may find population monitoring logistically less challenging and more effective in artificial habitats (e.g., (Flaquer, Torre & Ruiz-Jarillo, 2006; Matthias *et al.*, 2021); than in natural habitats. The provision of artificial refugia can be an important tool in education and outreach; conservation organizations can increase community engagement (in specific programs) and awareness of conservation issues or broad conservation goals by highlighting artificial habitats (e.g., (Torre *et al.*, 2021).

It is important however, for researchers and resource managers to recognize when providing artificial refugia is inappropriate, as there are implications to the conservation or management of wildlife and overall ecosystem health. Firstly, any misalignment in artificial habitat quality and preference may lead to population decline and decreased ecosystem function. Secondly, conservation resources (e.g., funding, equipment, materials, personnel) are often limiting, and thus wildlife management should focus on the most effective and efficient use of resources. Thirdly, the provision of artificial habitats as offsets or mitigation for environmental damage caused by industrial projects is only justified with evidence supporting the efficacy and safety of their use. Artificial habitats should confer measurable benefits to the target taxa without negatively impacting sympatric species or the local ecological community. Finally, meeting conservation objectives, at a local and global scale, will be required to protect biodiversity and support ecosystem resilience in the face of climate change.

CONCLUSION

As natural habitats continue to be degraded or lost due to anthropogenic disturbance, artificial habitats may be increasingly needed in species conservation. Bat boxes have gained popularity as compensatory or enhancement tools in bat conservation, yet relatively few species (particularly in Canada) will actually use them for roosting or raising young. My investigation of two synanthropic species revealed that not all artificial habitats, even of the same type, provide the same energetic or fitness benefits. Expecting a single bat box to meet the needs of a colony over an entire maternity season is unreasonable. Those seeking to install bat boxes as alternate refugia should apply a precautionary approach and endeavour to protect (for existing roosting habitat) or provide (for artificial roosting habitat) a myriad of roosting opportunities.

My research findings have been integrated into the collaborative creation of a best management practices (BMP) guidance document (Holroyd *et al.,* 2023), of which I was a co-author, for the use of bat boxes as artificial maternity roost structures. With an emphasis on *M. lucifugus*, *M. yumanensis* and *Eptesicus fuscus*, Holroyd *et al.* (2023) synthesizes the best available information relating to bat boxes, their use and highlights knowledge gaps that remain to be studied. The BMP was intended for use by resource managers, conservation organizations or individuals and provides technical background as well as guidelines for appropriate bat box use. Acknowledging that there is no immutable rule set governing the "appropriate" use of bat boxes, four key recommendations from the BMP (Holroyd *et al.,* 2023) are:

1. Maintain existing, occupied roosts (including buildings and bat boxes) to the maximum extent possible. Reproductive females in particular display strong interannual fidelity to roosts (natural or anthropogenic) or roost areas (Lewis, 1995; Lausen & Barclay, 2006; Olson & Barclay, 2013). If overheating is observed or thought to be a threat, additional boxes should be added in the immediate area, erected to maximize a range of alternative microclimates.
2. For a building-roosting exclusion, mitigate habitat loss with multiple bat boxes (to facilitate roost switching) or a larger single roost structure (bat condo or mini-condo) to provide a variety of microclimates. Thermal suitability of bat boxes will vary temporally and spatially, based on numerous factors (Nadeau, Conway & Rathbun, 2015) and microhabitats within (Gorecki *et al.,* 2020). Thermal suitability and colony size warrant consideration of capacity and, if installing bat boxes, the number required.
3. Maintenance and monitoring are required to ensure that boxes do not deteriorate but provide safe and secure long-term roosting habitat (Menzel, 2018; Griffiths *et al.*, 2023).
4. Implement adaptive management practices to provide flexibility in responding to issues, such as for locally changing climates or other conditions that may impact bat box suitability.

This study has emphasized that mere occupancy of a bat box should not be considered a sign of “success”. Evidence of the reproductive benefits of bat boxes, not simply occupancy of these habitats, is needed to accurately assess the “success” of providing such habitats (but see McGinn *et al.,* 2022). While the provision of artificial habitat is often done with the best intentions, it is critical to understand the fitness implications (to populations and individuals) of these habitats so as not to inadvertently create an ecological trap. This requires monitoring of artificial habitats over spatial and temporal scales relevant to the target taxa (Watchorn *et al.*, 2022), and scrutiny of characteristics that may either exacerbate population declines or aid in population recovery. Without this, evaluating the true conservation value of artificial habitat is impossible. Only with certainty of artificial habitat effectiveness can resource managers ensure that these habitats will achieve the intended conservation objectives for the target species.

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APPENDIX A. DESCRIPTIONS OF MATERNITY ROOST STRUCTURES AND STUDY SITES IN THE KOOTENAY AND OKANAGAN

Building A (Kootenay)

Location: Eastern shore of Kootenay Lake, ~ 34 km north of Creston, British Columbia.

Structure Type: Occupied log home, >100-year-old

Major insolated surface: Corrugated metal roof, gable-style, sloping east and west.

Colony Size and species: 2,000 – 3,000 bats, mixed *Myotis yumanensis* and *M. lucifugus.*

Roost Location(s): Unfinished attic space, between the exterior metal roof and the cedar strapping, on exposed rafter corners, along the ridge beam and on the block chimney. The highest concentration of roosting bats is at the southern end.

Roost access: One exterior “door”, consisting of five horizontal wood slats spaced five inches apart, and several crevice-type exit points.

Adjacent Habitat: A mix of lakeshore, fir/pine forest, pasture, and sparse rural residences.

Nearest water: A natural pond (104 square-meter) with emergent vegetation approximately 20 meters west of the building; Kootenay Lake is within 170 m.

Building S (Kootenay)

Location: Eastern shore of Kootenay Lake, ~ 46 km north of Creston, British Columbia.

Structure Type: Window-less, door-less wood-framed, cedar-clad shell of a formerly occupied cabin.

Major insolated surface: Corrugated metal roof, gable-style, sloping east and west.

Colony Size and species: ~ 800 bats, mainly *M. yumanensis* and *M. lucifugus*.

Roost Location(s): Loft space open to the floor below, between the exterior metal roof and the cedar strapping, occasionally on exposed ridge beams.

Roost access: Doorway and window frames on south aspect.

Adjacent Habitat: Fir/pine forested hillside and a small, lakeshore vacation community.

Nearest water: 80 m from Kootenay Lake.

Building X (Kootenay)

Location: In the Creston Valley Wildlife Management Area (CVWMA), 11 km west of Creston, British Columbia.

Structure Type: Large wood-framed building, research and interpretive centre (demolished in winter 2019).

Major insolated surface: Corrugated metal roof, saltbox-style, mainly sloping east.

Colony Size and species: ~ 400 *M. yumanensis* and *M. lucifugus*. as well as an unknown number of *Eptesicus fuscus* (in a separate area of the building roof).

Roost Location(s): Roof of main building and covered patio roof.

Roost access: Crevices along roofline.

Adjacent Habitat: Extensive wetlands, cottonwood riparian and upland forested habitat.

Nearest water: 10 m, built on pilings within the wetland.

Condo C (Kootenay)

Location: In the Creston Valley Wildlife Management Area (CVWMA) at Corn Creek wetland, 11 km west of Creston, British Columbia.

Structure Type: Plywood and cedar bat mini-condo, installed in May of 2019 to replace the Interpretive Centre (Building X demolished in winter 2019).

Major insolated surface: Corrugated metal roof, shed-style, sloping south.

Colony Size and species: Primarily unoccupied 2019-2021 (one *Eptesicus fuscus* detected during and exit count on 26 June 2021; sparse guano and insect wings as evidence of temporary use).

Roost Location(s): central, internal “attic” space and 14 multi-chamber baffle boxes hanging from the ceiling perimeter for roosting surfaces.

Roost access: Multiple crevices in cedar siding, hatch-style doors, and abutments with log pillar supports.

Adjacent Habitat: Wetland and sloughs, Kootenay River channel and associated cottonwood riparian vegetation, upland forest within one kilometer of the condo.

Nearest water: Surrounded by wetlands, Kootenay River is 10 m east.

Condo D (Kootenay)

Location: In the Creston Valley Wildlife Management Area (CVWMA) at Duck Lake, 18 km northwest of Creston, British Columbia.

Structure Type: Large plywood and cedar bat condo, constructed in 2011 to replace a dilapidated barn.

Major insolated surface: Corrugated metal roof, shed-style, sloping south.

Colony Size and species: 4,500 - 7,000 *M. yumanensis*

Roost Location(s): Multiple interior baffled roost boxes hanging from the ceiling surrounding a central interior open space.

Roost access: Multiple crevices in cedar siding, hatch-style doors, and abutments with log pillar supports.

Adjacent Habitat: Primarily cattle grazing and hay fields immediately adjacent, bordered by the Kootenay River channel and associated cottonwood riparian vegetation to the north, south and west. Upland forest, as well as wetland and slough habitats, are within one kilometer of the condo.

Nearest water: Kootenay River is 330 m south at its closest and a side channel that connects to the river lies 200 m directly west.

Box R (Kootenay)

Location: Private rural property 12 km north of Creston, British Columbia.

Structure Type: Single, four-chambered plywood bat box, mounted on metal pole.

Major insolated surface: Plywood roof and front, south aspect.

Colony Size and species: ~ 350 *M. yumanensis* (primarily) and *M. lucifugus*.

Roost History: Installed to encourage local bat activity/roosting after the cedar siding on a neighbouring home (within 200 m) that previously hosted roosting bats was replaced with vinyl siding. Landowner reported "bulging bats" in 2018.

Adjacent Habitat: West-sloping grass yard with mature fruit and nut trees, overlooks floodplain and wetland habitat, while upland habitat is forested. four homes and two outbuildings within 500 m

Nearest water: CVWMA flood control channel 420 m to the west, Duck Lake and wetlands beyond.

Box T1/T2 & T4/T5 (Kootenay)

Location: Private rural property 11 km west of Creston, British Columbia.

Structure Type: Double, four-chambered plywood bat box pairs, mounted back-to-back on central wooden posts with predator shields.

Major insolated surface: Plywood roof and front, east-west aspect (T1/T2 box pair) and north-south aspect (T4/T5 box pair).

Colony Size and species: 800 – 1,100 *M. yumanensis* (primarily) and *M. lucifugus*.

Roost History: Installed by the homeowner to provide alternate roosting habitat for the colony of bats evicted from the home's attic (beginning in 2015).

Adjacent Habitat: Pasture, sustenance garden and mixed deciduous/coniferous forest in a rural residential, forest and wetland landscape.

Nearest water: Dugout pond (approximately 144 square meters) within 15 m of the bat boxes; CVWMA wetland complex 700 m to the northeast.

Box Kt and Kv (Okanagan)

Location: West shore of the north arm of Okanagan Lake, near Vernon, British Columbia.

Structure Type: Double, four-chambered plywood bat box pairs, mounted back-to-back on wooden posts.

Major insolated surface: Plywood roof and front, east-west aspect. Both box pairs partially shaded by large cottonwood trees and shrubs. Box Kt western aspect covered with shade cloth.

Colony Size and species: 800 – 1,200 presumed *M. yumanensis* and *M. lucifugus*.

Roost History: Installed by the cabin owners to enhance roosting habitat.

Adjacent Habitat: Small vacation cabins surrounded by mature cottonwood, pasture, and dry open pine forest.

Nearest water: Okanagan Lake 30 m to the south.

Box FLb and FLw (Okanagan)

Location: Fintry Provincial Park, northwestern shore of Okanagan Lake, British Columbia.

Structure Type: Single, four-chambered plywood bat box, mounted on wooden posts.

Major insolated surface: Tin-wrapped plywood roof, plywood front, south aspect (Box FLb) and west aspect (Box FLw).

Colony Size and species: 200 – 400 presumed *M. yumanensis* and *M. lucifugus*.

Roost History: Several bat boxes (various styles) installed by BC Parks within the campground area of this park to enhance roosting habitat. Bats also roost in the historic manor house attic space.

Adjacent Habitat: Campground in mature pine forest, cleared fields and dry open pine forest.

Nearest water: Okanagan Lake 50 m to the north.

Box OKLSd and OKLSs (Okanagan)

Location: Okanagan Lake South Provincial Park, 10 km south of Peachland, British Columbia.

Structure Type: Double (Box OKLSd) and single (Box OKLSs) four-chambered plywood bat boxes, mounted on wooden posts.

Major insolated surface: Tin-wrapped plywood roof, plywood front, south aspect (Box FLb) and west aspect (Box FLw).

Colony Size and species: 50 - 400 presumed *M. yumanensis* and *M. lucifugus*.

Roost History: Installed by BC Parks to enhance roosting habitat.

Adjacent Habitat: Lakeshore campground with mature trees, adjacent to steep pine grassland hillside.

Nearest water: Okanagan Lake within 100 m.

Box SOd and SOe (Okanagan)

Location: Sun-Oka Provincial Park, seven kilometers north of Penticton, British Columbia.

Structure Type: Double (Box SOd) and single (Box SOe) four-chambered plywood bat boxes, mounted on wooden posts.

Major insolated surface: Tin-wrapped plywood roof, plywood front, north-south aspect (Box FLb) and south aspect (Box SOe).

Colony Size and species: 50 - 300 presumed *M. yumanensis* and *M. lucifugus*.

Roost History: Installed by BC Parks to enhance roosting habitat.

Adjacent Habitat: Day-use area with beach, lawn, mature trees, residential areas and agricultural fields; some cottonwood riparian along Trout Creek outflow into lakel

Nearest water: Okanagan Lake within 50 m.

Table A.1. Summary of select structure details for *Myotis yumanensis / M. lucifugus* maternity roosts studied in the Kootenay region of British Columbia (2019 – 2021).

Site name	**Roost type**	**Max. colony size (est.)***	**Year Install / Built**	**Roost aspect**	**~ Roost Volume (m^3)**	**~ Roost Dimensions W x D x H (m)**
BLDG A	Building	3,000	~1920	all	118	5 x 12 x 2
BLDG S	Building	800	~1930	West	165	3 x 9 x 6
BLDG X	Building	350	1974	all	unknown	unknown
CONDO D	Large Condo	7,000	2011	all	44	6 x 6 x 2
CONDO C	Mini condo	1**	2019	all	10	2 x 2.5 x 2
BOX R	Single Maternity Box	350	2017	South	0.04	0.56 x 0.1 x 0.70
BOX T1/T2	Double Maternity Box	900[ŧ]	2011	East/ West	0.08	2 X (0.56 x 0.1 x 0.70)
BOX T4/T5	Double Maternity Box	900[ŧ]	2011	South/ North	0.08	2 X (0.56 x 0.1 x 0.70)

** Condo C remained unoccupied during my study with the exception of a single *Eptesicus fuscus* that was detected during an exit count on 26 June 2021.

[ŧ] Located at the same site, only one box pair was occupied at a time. Typically, Box T1/T2 was occupied in early spring and T4/T5 was occupied during the summer season.

Table A.2. Summary of select structure details for *Myotis yumanensis / M. lucifugus* maternity roosts studied in the Okanagan region of British Columbia (2019 – 2021).

Site name	**Roost type**	**Max. colony size (est.)***	**Year Install / Built**	**Roost aspect**	**~ Roost Volume (m^3)**	**~ Roost Dimensions W x D x H (m)**
BOX Kv	Double Maternity Box	800	2010	East/ West	0.108	2 X (0.6 x 0.12 x 0.75)
BOX Kt	Double Maternity Box	1,200	2010	East/ West	0.078	2 X (0.56 x 0.1 x 0.70)
BOX FLb	Single Maternity Box	400		South	0.039	0.56 x 0.1 x 0.70
BOX FLw	Single Maternity Box	100		West	0.039	0.56 x 0.1 x 0.70
BOX OKLSd	Double Maternity Box	400		East/ West	0.078	2 X (0.56 x 0.1 x 0.70)
BOX OKLSs	Single Maternity Box	200		South	0.039	0.56 x 0.1 x 0.70
BOX SOd	Double Maternity Box	300		South/ North	0.078	2 X (0.56 x 0.1 x 0.70)
BOX SOs	Single Maternity Box	300		South	0.039	0.56 x 0.1 x 0.70

Appendix B. Photos of Myotis Maternity Roosts in the Kootenay and Okanagan

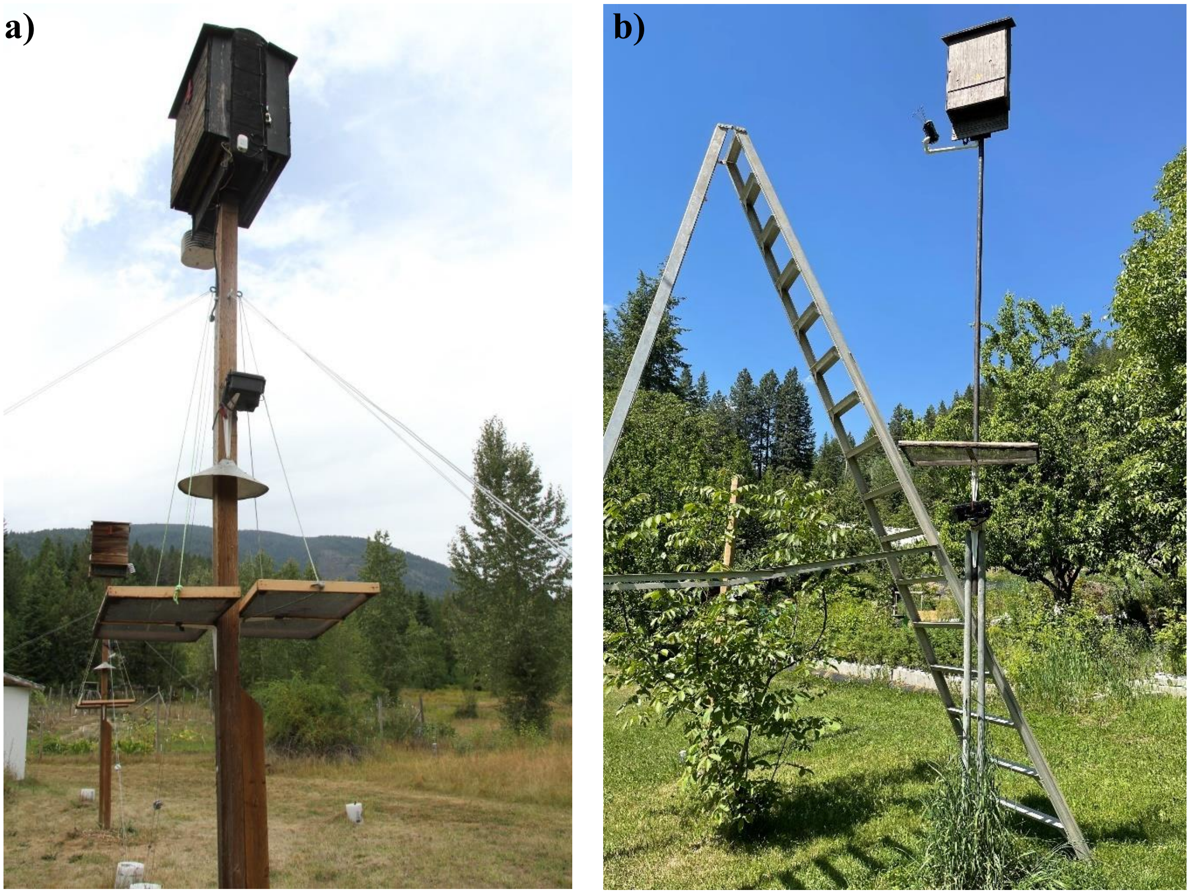

Figure B.1. Bat box maternity roosts studied in the Kootenay region of British Columbia, Canada (2019-2021) were four-chambered maternity boxes (a) mounted on wood posts in pairs (back-to-back); T1/T2 (background) and T4/T5 (foreground) and (b) mounted on a metal pole; Box R. (Photos: SDulc).

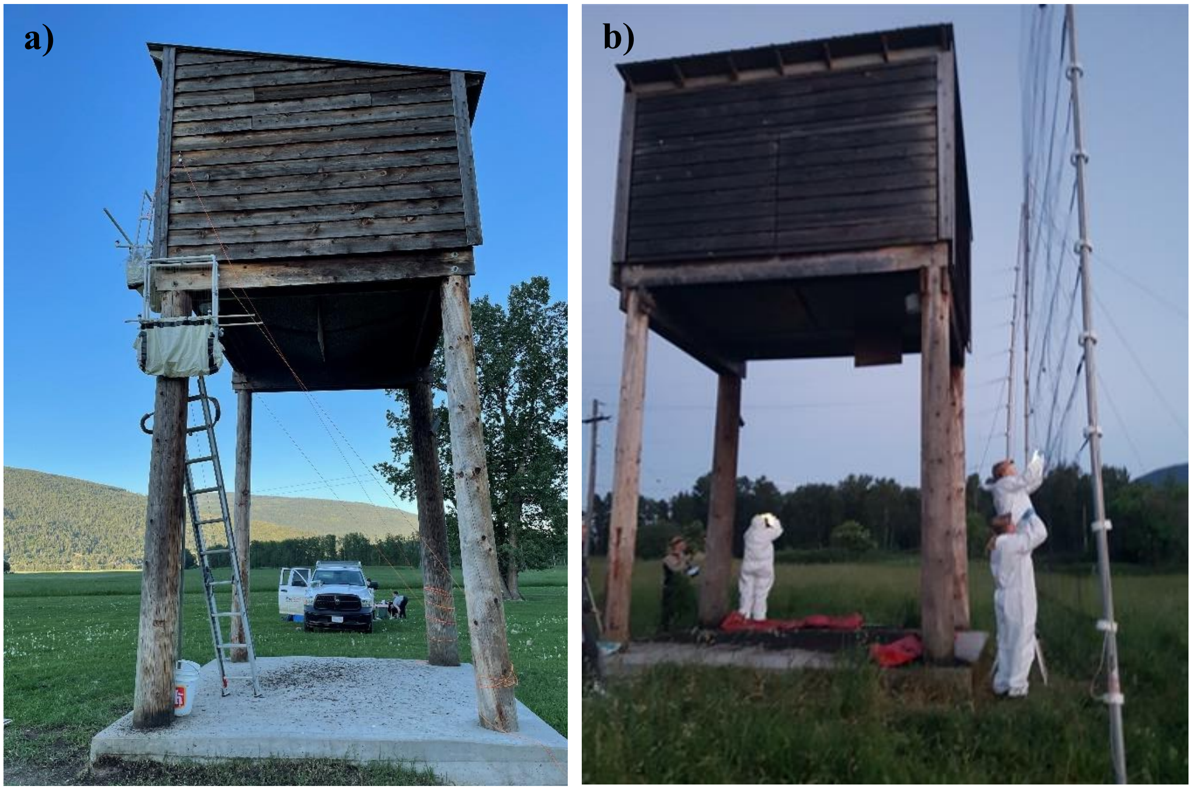

Figure B.2. Exterior view of bat Condo D, a) photo: S. Dulc and b) photo: Emily de Freitas maternity roost in the Kootenay study area of British Columbia, Canada. Baffled roost boxes within the structure are similar to those in the mini-condo (Condo C), pictured in Figure B.3b.

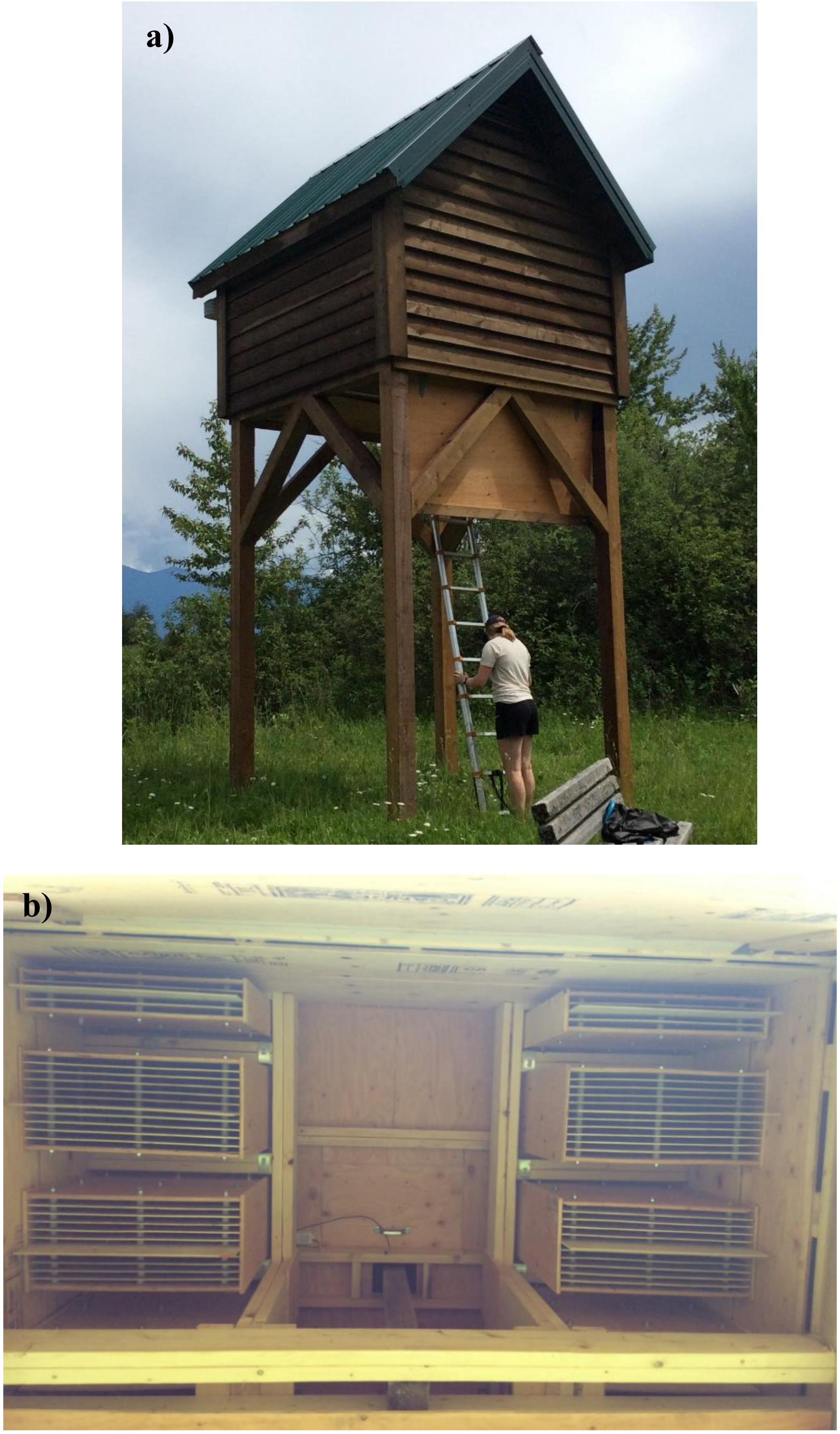

Figure B.3. Exterior (a) view of the unoccupied (as of 2021) mini-condo, Condo C and (b) interior view, looking up at half of the baffled roost boxes within the Condo C in the Kootenay region of British Columbia, Canada. (Photos: S. Dulc)

Figure B.4. Exterior and interior view of building maternity roosts in the occupied log home BLDG A (a and b) and the unoccupied cabin BLDG S (c and d) studied in 2019-2021 within the Kootenay region, British Columbia, Canada (Photos: S. Dulc).

Figure B.5. Double maternity boxes studied (2019-2021) in the Okanagan region of British Columbia, Canada included Box KT (a) and (b) at Alexis Beach (north end of Okanagan Lake) that had a shade cloth installed in front of the west face; and Box OKLSd (c) and (d) at Okanagan Lake South Provincial Park.

Figure B.6. Single maternity boxes at Fintry Provincial Park in the Okanagan region of British Columbia, Canada included Box FLb (a, b) and Box FLw (c). Box FLb is visible on the far right in the habitat photo (d) and (e) shows the lawn and manor house west of Box FLw; bats also used the attic space of the building.

Figure B.7. Bat boxes at Sun-Oka Provincial Park (Okanagan region of British Columbia, Canada) included the double maternity box SOd (a and b) at the west end of the day-use area and BOX SOe (c and d), a single maternity box adjacent to the concession building.

APPENDIX C. SUMMARY STATISTICS FOR ROOST MICROCLIMATES: TEMPERATURE, RELATIVE HUMIDITY, HEAT STRESS AND VAPOUR PRESSURE DEFICIT

The tables on the following pages provide additional details for microclimate data collected during the study of anthropogenic maternity roosts in the Kootenay region of British Columbia, Canada. Table C.1 summarizes temperature and relative humidity conditions with the potential to cause heat stress in occupied roosts during periods of unseasonally extreme weather (heat waves) in each of 2019 and 2021. Tables C.2 and C.3 provide descriptive statistics for temperature and relative humidity conditions in occupied roosts during 2019 and 2021, respectively. Tables C.4 and C.5 provide descriptive statistics for heat stress index and vapour pressure deficits calculated for occupied roosts during 2019 and 2021, respectively.

Table C.1. Comparison of temperature and relative humidity conditions conducive to heat stress (high temperature and high humidity) between Kootenay roosts during a 40-day (960 hours) monitoring period (25 May – 03 July) that coincided with a heat wave in each of 2019 and 2021. Occupied hours were based on acoustic data; roosts with an * indicate potential false positive occupancy, based on field observation (lack of guano). An ^ indicates battery failure caused missing data over a portion of the monitoring period. Data loggers were not deployed in Box Ab until August 2019.

Year	**Temperature (T) and Humidity (RH) Condition**	**BLD A**	**BLD S**	**CONDO D**	**BOX Ab**	**BOX R**	**BOX T1**	**BOX T2**	**BOX T4**	**BOX T5**
2019	*Ambient T Max (°C)*	35.0	31.0	33.5	Na	35.0	31.5	31.5	31.5	31.5
	Roost T Max (°C)	39.0	30.0	32.4	Na	43.2	36.7	39.5	40.6	41.7
	Roost RH Max (%)	71	88	76	Na	100	100	92	100	100
	Occupied Hours	888 ^	960	960	Na	960	312	312	960	960
	Total hours roost RH >90%	0	0	0	Na	167	156.5	3.5	291.25	553.25
	Potential heat stress (PHS): ***Total hours roost RH >90% AND roost T > 40 °C***	0	0	0	Na	**7.25**	0	0	**3.5**	0
	Occupied hours with PHS	0	0	0	Na	**7.25**	0	0	**3.5**	0
2021	*Ambient T Max (°C)*	44.2	41.8	41.3	40.7	44.7	40.6	40.6	40.6	40.6
	Roost T Max (°C)	48.6	47.5	37.6	55.0	48.8	52.9	47.7	52.2	45.8
	Roost RH Max (%)	100	100	81	100	100	69	61	67	100
	Total Occupied Hours	960	960	960	481 ^	960	72*	72*	960*	960
	Total hours roost RH >90%	260.25	337	0	788.5	814.5	0	0	75	545
	Potential heat stress (PHS): ***Total hours roost RH >90% AND roost T > 40 °C***	0	0	0	**40.25**	**21.25**	0	0	0	**6.5**
	Occupied hours with PHS	0	0	0	**39.5 ^**	**21.25**	0	0	0	**6.5**

Table C.2. Summary statistics for 2019 roost temperatures and relative humidities, aggregated by roost type and occupancy status, (across EARLY season (occupation of summer range, 31 March to 22 May) and three reproductive stages: PG (gestation and earliest known parturition, 23 May to 14 June); LAC (neo-natal and nursing, 15 June to 12 July); and PL (post-lactation, 13 July to 31 August. Roosts included two buildings, one bat condo and five boxes in the Kootenay region of southeastern British Columbia, Canada.

				Roost Temperature (°C)				**Roost Relative Humidity (%)**			
Year	**Type**	**Stage**	**Occupied**	**min**	**max**	**mean**	**SE**	**min**	**max**	**mean**	**SE**
2019	Building	EARLY	Yes	1.5	33.3	14.6	0.06	18.7	92.2	54.4	0.16
	Condo	EARLY	Yes	3.8	27.2	12.6	0.08	33.8	78.8	54.7	0.15
	Box	EARLY	Yes	-0.6	40.2	18.2	0.05	19.9	100	77.5	0.16
	Building	PG	Yes	8.9	39.4	23.0	0.10	10.8	87.6	46.9	0.22
	Condo	PG	Yes	12.7	29.9	20.3	0.09	31.7	70.8	54.8	0.15
	Condo	PG	No	8.8	30.3	19.3	0.11	18.4	76.9	51.6	0.24
	Box	PG	Yes	8.9	42.1	23.3	0.07	21.5	100	80.0	0.25
	Box	PG	No	6.7	36.0	20.7	0.13	22.3	66.4	44.2	0.16
	Building	LAC	Yes	8.8	37.9	21.7	0.07	22.8	89.8	59.9	0.20
	Condo	LAC	Yes	13.2	29.9	20.9	0.07	34.4	77.6	64.7	0.15
	Condo	LAC	No	9.9	29.7	18.7	0.08	25.2	80.3	62.0	0.22
	Box	LAC	Yes	10.9	43.7	26.6	0.05	26.4	100	91.2	0.15
	Box	LAC	No	6.8	36.7	23.3	0.16	25.0	80.0	42.8	0.56
	Building	PL	Yes	10.1	39.2	24.7	0.06	19.5	88.7	53.7	0.13
	Condo	PL	Yes	14.5	32.4	22.6	0.05	37.9	78.4	61.6	0.11
	Condo	PL	No	10.6	34.6	20.9	0.07	25.1	79.5	55.4	0.17
	Box	PL	Yes	10.5	47.0	25.5	0.04	28.9	100	82.6	0.14
	Box	PL	No	9.0	48.3	25.4	0.11	37.7	86.1	63.8	0.17

Table C.3. Summary statistics for 2021 roost temperatures and relative humidities, aggregated by roost type and occupancy status, across EARLY season (occupation of summer range, 31 March to 22 May) and three reproductive stages: PG (gestation and earliest known parturition, 23 May to 14 June); LAC (neo-natal and nursing, 15 June to 12 July); and PL (post-lactation, 13 July to 31 August. Roosts included two buildings, one bat condo and five boxes in the Kootenay region of southeastern British Columbia, Canada.

				Roost Temperature (°C)				**Roost Relative Humidity (%)**			
Year	**Type**	**Stage**	**Occupied**	**min**	**max**	**mean**	**SE**	**min**	**max**	**mean**	**SE**
2021	Building	EARLY	Yes	-0.2	35.5	12.5	0.06	44.9	100	85.6	0.10
	Condo	EARLY	Yes	7.7	27.9	15.2	0.07	41.9	77.8	63.3	0.12
	Box	EARLY	Yes	-3.5	40.1	17.6	0.07	15.8	100	77.3	0.20
	Building	PG	Yes	6.5	39.4	17.8	0.10	43.5	100	83.4	0.16
	Condo	PG	Yes	9.7	31.3	17.8	0.10	47.0	80.4	69.9	0.12
	Box	PG	Yes	6.9	50.1	21.9	0.07	10.4	100	89.7	0.16
	Box	PG	No	4.5	39.5	19.0	0.15	17.3	61.5	46.4	0.18
	Building	LAC	Yes	9.8	47.3	26.2	0.10	36.2	100	84	0.16
	Condo	LAC	Yes	14.0	37.6	26.0	0.09	45.3	80.5	65.6	0.12
	Box	LAC	Yes	10.3	54.7	30.0	0.07	22.0	100	79..7	0.23
	Box	LAC	No	7.7	47.7	27.2	0.13	17.3	67.6	38.6	0.14
	Building	PL	Yes	8.9	41.2	23.3	0.06	32.3	100	84.3	0.15
	Condo	PL	Yes	11.9	35.0	23.4	0.07	37.2	79.8	63.4	0.14
	Box	PL	Yes	5.7	48.9	25.4	0.04	25.3	100	81.6	0.13
	Box	PL	No	14.7	40.9	26.4	0.12	14.0	80.0	43.3	0.33

Table C.4. Summary statistics for 2019 roost heat stress index and vapor pressure deficit values, aggregated by roost type and occupancy status across EARLY season (occupation of summer range, 31 March to 22 May) and three reproductive stages: PG (gestation and earliest known parturition, 23 May to 14 June); LAC (neo-natal and nursing, 15 June to 12 July); and PL (post-lactation, 13 July to 31 August. Roosts included two buildings, one bat condo and five boxes in the Kootenay region of southeastern British Columbia, Canada.

				Roost Heat Stress Index (°F)				Roost Vapor Pressure Deficit (kPa)			
Year	Type	Stage	Occupied	Min	Max	Mean	SE	Min	Max	Mean	SE
2019	Building	EARLY	Yes	73.2	149	94.1	0.147	0.5	4.99	2.8	0.010
	Condo	EARLY	Yes	55.6	129	90.5	0.193	1.3	4.07	2.78	0.010
	Box	EARLY	Yes	76.6	229	91.4	0.222	0.0	4.93	1.38	0.010
	Building	PG	Yes	73.6	105	81.8	0.084	0.8	5.49	3.26	0.014
	Condo	PG	Yes	75.2	91.7	79.5	0.071	1.8	4.20	2.75	0.440
	Condo	PG	No	74.9	102	81.1	0.112	1.4	5.02	2.91	0.015
	Box	PG	Yes	55.6	335	84.8	0.382	0.0	4.83	1.23	0.015
	Box	PG	No	74.7	115	83.6	0.138	2.1	4.78	3.42	0.010
	Building	LAC	Yes	66.6	102	78.7	0.073	0.6	4.75	2.46	0.013
	Condo	LAC	Yes	71.2	91	76.8	0.064	1.4	4.03	2.16	0.009
	Condo	LAC	No	70.7	99.9	78.5	0.083	1.2	4.59	2.33	0.013
	Box	LAC	Yes	55.6	303	113	0.446	0.0	4.53	0.54	0.009
	Box	LAC	No	71.8	119	82.6	0.177	1.2	4.61	3.51	0.016
	Building	PL	Yes	66.9	109	79.8	0.063	0.7	4.96	2.84	0.008
	Condo	PL	Yes	70.7	108	78.0	0.063	1.3	3.82	2.36	0.007
	Condo	PL	No	71.1	100	78.9	0.058	1.3	4.61	2.74	0.010
	Box	PL	Yes	55.6	337	89.9	0.211	0.0	4.39	1.07	0.008
	Box	PL	No	66.7	187	89.8	0.378	0.9	3.84	2.22	0.011

Table C.5. Summary statistics for 2021 roost heat stress index and vapor pressure deficit values, aggregated by roost type and occupancy status across EARLY season (occupation of summer range, 31 March to 22 May) and three reproductive stages: PG (gestation and earliest known parturition, 23 May to 14 June); LAC (neo-natal and nursing, 15 June to 12 July); and PL (post-lactation, 13 July to 31 August. Roosts included two buildings, one bat condo and five boxes in the Kootenay region of southeastern British Columbia, Canada.

				Roost Heat Stress Index (°F)				Roost Vapor Pressure Deficit			
Year	Type	Stage	Occupied	Min	Max	Mean	SE	Min	Max	Mean	SE
2021	Building	EARLY	Yes	72.9	156	84.7	0.183	0.0	3.39	0.88	0.006
	Condo	EARLY	Yes	73.9	110	84.4	0.139	1.4	3.57	2.25	0.007
	Box	EARLY	Yes	55.6	218	90.5	0.236	0.0	5.17	1.39	0.012
	Building	PG	Yes	55.7	180	72.8	0.278	0.0	3.47	0.63	0.010
	Condo	PG	Yes	70.8	102	79.0	0.112	1.2	3.25	1.85	0.007
	Box	PG	Yes	55.6	335	84.8	0.382	0.0	5.50	0.67	0.010
	Box	PG	No	74.6	126	86.9	0.212	2.4	5.08	3.29	0.011
	Building	LAC	Yes	55.7	255	92.4	0.505	0.0	3.93	0.98	0.010
	Condo	LAC	Yes	70.9	134	84.2	0.222	1.2	3.37	2.12	0.007
	Box	LAC	Yes	55.6	303	109.0	0.388	0.0	4.81	1.25	0.014
	Box	LAC	No	75.0	143	87.3	0.193	2.0	5.09	3.77	0.009
	Building	PL	Yes	55.6	191	79.4	0.228	0.0	4.17	0.97	0.009
	Condo	PL	Yes	70.3	110	79.6	0.096	1.2	3.86	2.25	0.008
	Box	PL	Yes	55.6	337	84.8	0.382	0.0	4.60	1.15	0.010
	Box	PL	No	70.0	158	84.5	0.251	1.2	5.29	3.48	0.020

APPENDIX D. OBSERVATIONS OF HEAT STRESS IN BAT ROOSTS

On 12 June 2019, I observed females in BOX R hanging out of the bottom of the box chambers at the bat box entrance, fur soaking wet, in mid-afternoon. Several bats, over the course of two hours, flew from this box to the shaded trunk of a walnut tree 20 m away. One bat, appearing exhausted (by its lethargic flight), landed on the ground. It was retrieved and placed in the shade, high on the trunk of the tree, where we observed seven other bats that had already alighted on the tree. Ambient conditions at the time were 31.3 °C and 30.6 % RH; roost microclimate was 40.5 °C and 100 % RH.

I also observed instances of (suspected) heat-induced behaviour in 2021. On 01 July 2021, I observed a bat fly out of BOX T5, make several passes over the artificial pond (15 m away) to drink and then land in a low bush adjacent to the pond. Roost conditions were 40.0 °C and 53.0 % RH while ambient conditions were 38.5 °C and 19.4 % RH. During five visits to BOX R between 25 June and 03 July 2021, adults and pups of various ages (including neonates) were crowding at the entrance of the bat box with wet fur. As reported in Lausen *et al.* (2022), I installed a white shade on the box front 27 June 2021; within 30 minutes, roost temperature dropped from 44.7 °C to 43.2 °C. On 03 July 2021, bats were crowding at the bottom of BOX R with soaking wet fur (Fig. D.2.5) and one juvenile was seen crawling out of the front ventilation slit to roost on the front of the (now) shaded bat box. Microclimate within BOX R at this time was 100% RH and 41.4 °C (front chamber) to 42.3 °C (rear chamber), while ambient conditions were 35.8% RH and 35.5 °C.

On 29 June 2021, ~ 300 bats were roosting atypically in loose groups on the exposed, daylit concrete surfaces of the (Building A) attic chimney and six bats crawled into joist spaces on the floor. Microclimate (2 m from the chimney) was recorded as 46.6 °C and 40.4 % RH; ambient conditions were 36.7 °C and 28.8 % RH. On 30 June 2021, I observed bats roosting on exposed roof rafters in larger numbers than usual; numerous bats were clustered around the HOBO probe, licking wing membranes, stretching and shifting roost locations. During this time, roost microclimate was 41.2 °C and 37.8 % RH while ambient conditions were 41.3 °C and 24.2 % RH.

Figure D.2.5. Juvenile (dark fur) and adult *Myotis* (light fur) with wet fur crowd at the roost entrance of BOX R on 03 July 2021, six days after installation of a temporary sun shade during the heat wave. A juvenile can be seen crawling out of the ventilation slit on the front of the box (white arrow) where it roosted for the remainder of the site visit (approximately 30 minutes). At the time of this photo the interior roost temperature was 41.4 ℃ (front chamber) and 42.3 °C (rear chamber) and relative humidity was 100% (both chambers); ambient temperature at the same time was 35.5 ℃ with 35.8 % relative humidity. (Photo: S. Dulc).

APPENDIX E. SUMMARIES OF JUVENILE MORPHOMETRIC COMPARISONS BETWEEN MATERNITY ROOSTS IN THE KOOTENAY REGION

Table E.3. Summary of morphometric comparisons with no evidence of a difference between juvenile *Myotis yumanensis* roosting in buildings (Bldg), bat boxes (Box) and the bat condo (Condo) maternity roosts in the Kootenay region of British Columbia, Canada in 2019. Means compared were mass (M), forearm length (FA), total epiphyseal gap (TG) and secondary centre of ossification (SC) using Tukey HSD with P > 0.05 as non-significant (ns.).

Roost ID 1	**Capture Date 1**	**Roost ID 2**	**Capture Date 2**	**Tukey HSD *P*-values for each (ns.) morphometric mean**
Box T	16 July	Bldg X	17 July	0.200 (M), 0.365 (TG), 0.136 (SC)
Box R	19 July	Condo D	20 July	0.156 (M), 0.643 (FA), 0.528 (SC)
Bldg A	25 July	Box T	27 July	0.570 (M), 0.092 (TG), 0.435 (SC)
Box T	27 July	Bldg X	28 July	0.227 (FA), 0.627 (SC)
Bldg X	06 Aug	Box T	07 Aug	0.885 (M), 0.060 (FA), 0.933 (TG), 0.156 (SC)
Box T	07 Aug	Bldg S	08 Aug	0.933 (TG), 0.135 (SC)
Box R	09 Aug	Condo D	10 Aug	0.170 (FA)
Bldg X	19 Aug	Box T	20 Aug	0.667(TG), 0.218 (SC)
Box T	20 Aug	Bldg S	21 Aug	0.056 (M), 0.098 (FA)
Condo D	27 Aug	Box R	28 Aug	0.891 (FA), 0.319 (TG), 0.956 (SC)

Table E.4. Summary of morphometric comparisons with no evidence of a difference between juvenile *Myotis yumanensis* roosting in buildings (Bldg), bat boxes (Box) and the bat condo (Condo) maternity roosts in the Kootenay region of British Columbia, Canada in 2021. Means compared were mass (M), forearm length (FA), total epiphyseal gap (TG) and secondary centre of ossification (SC) using Tukey HSD with P > 0.05 as non-significant (ns.).

Roost ID 1	**Capture Date 1**	**Roost ID 2**	**Capture Date 2**	**Tukey HSD *P*-values for each ns. morphometric mean**
Box R	18 July	Condo D	19 July	0.501 (M), 0.392 (FA), 0.781 (TG), 0.392 (SC)
Condo D	19 July	Bldg S	20 July	0.860 (M), 0.127 (TG), 0.721 (SC)
Bldg S	20 July	Bldg A	23 July	0.570 (SC)
Box T	25 July	Box R	26 July	0.617 (TG), 0.210 (SC)
Box R	26 July	Condo D	27 July	0.079 (M), 0.112 (FA), 0.196 (SC)
Condo D	27 July	Bldg S	28 July	0.379 (M), 0.411 (FA), 0.749 (SC)
Bldg S	28 July	Bldg A	29 July	0.928 (M), 0.175 (FA), 0.805 (SC)
Box T	02 Aug	Box R	03 Aug	0.052 (M), 0.124 (TG), 0.318 (SC)
Box R	03 Aug	Condo D	04 Aug	0.737 (M), 0.717 (FA), 0.802 (TG), 0.836 (SC)
Condo D	04 Aug	Bldg S	05 Aug	0.396 (FA), 0.182 (SC)
Bldg A	09 Aug	Box T	10 Aug	0.179 (M), 0.427 (FA), 0.091 (TG), 0.141 (SC)
Box T	10 Aug	Box R	11 Aug	0.136 (TG)
Box R	11 Aug	Condo D	12 Aug	0.878 (M), 0.402 (FA), 0.629 (TG), 0.584 (SC)
Bldg A	25 Aug	Box T	26 Aug	0.143 (M), 0.559 (TG), 0.541 (SC)
Box T	26 Aug	Condo D	27 Aug	0.145 (TG), 0.116 (SC)
Condo D	27 Aug	Box R	29 Aug	0.512 (FA), 0.549 (TG), 0.596 (SC)
Box R	29 Aug	Bldg S	30 Aug	0.149 (M), 0.818 (FA), 0.302 (TG), 0.220 (SC)
Bldg S	30 Aug	Bldg A	31 Aug	0.441 (M), 0.670 (FA), 0.368 (TG), 0.782 (SC)

Table E.5. Summary of Welch's t-tests with statistical evidence ($P < 0.05$) of a difference in at least one morphometric mean between volant juvenile *Myotis yumanensis* roosting in bat boxes (BOX) compared to those in buildings (BLDG) or the bat condo (CONDO) in the Kootenay region of British Columbia, Canada in 2019. Morphometrics compared were mass (M), forearm length (FA), total epiphyseal gap (TG), and secondary center of joint ossification (SC). Number of juveniles captured (sample size) is provided in brackets below roost id; the roost where juveniles appeared to have more advanced morphometrics is noted in bold font. Non-significant differences are noted with "ns".

Roosts			**Welch's t-test results (df and *P*-values) for morphometric means**			
BOX	**BLDG / CONDO**	**Capture Dates**	**> M$\bar{x}$**	**> FA$\bar{x}$**	**< TG$\bar{x}$**	**> SC$\bar{x}$**
T (11)	**BLDG X** (5)	July 16/17	ns	df=10.01; *P*=0.033	ns	ns
R (12)	**CONDO** (97)	July 19/20	ns	ns	df=11.78; *P*=0.04	ns
T (59)	**BLDG A** (18)	July 25/27	ns	df=25.05; *P*=0.016	ns	ns
T (59)	**BLDG X** (21)	July 27/28	df=29.45; *P*=0.022	ns	df=38.51; *P*=0.010	ns
T (33)	BLDG S (40)	Aug 7/8	ns	ns	df=64.32; *P*=0.003	df=45.66; *P*=0.017
R (19)	BLDG S (40)	Aug 8/9	df=30.27; *P*=0.004	df=35.49; *P*<0.001	df=47.24; *P*<0.001	df=22.62; *P*<0.001
R (19)	CONDO (66)	Aug 9/10	df=31.66; *P*=0.017	ns	df=37.16; *P*=0.016	df=26.13; *P*=0.002
T (70)	BLDG X (55)	Aug 19/20	df=110.82; *P*<0.001	df=103.82; *P*=0.003	ns	ns
T (70)	BLDG S (68)	Aug 20/22	ns	ns	df=134.58; *P*<0.001	df=122.64; *P*<0.001
R (27)	**CONDO** (53)	Aug 27/28	df=76.64; *P*<0.001	ns	ns	ns

Table E.6. Summary of Welch's t-tests with statistical evidence ($P < 0.05$) of a difference in at least one morphometric mean between volant juvenile *Myotis yumanensis* roosting in bat boxes (BOX) compared to those in buildings (BLDG) or the bat condo (CONDO) in the Kootenay region of British Columbia, Canada in 2021. Morphometrics compared were mass (M), forearm length (FA), total epiphyseal gap (TG), and secondary center of joint ossification (SC). Number of juveniles captured (sample size) is provided in brackets below roost id and the roost (building, BLDG; condo, CONDO; bat box, BOX) with evidence of more advanced juvenile development is noted in bold font. Non-significant differences are noted with "ns".

Roosts			**Welch's t-test results (df and *P*-values) for morphometric means**			
BOX	**BLDG / CONDO**	**Capture Dates**	**> M$\bar{x}$**	**> FA$\bar{x}$**	**< TG$\bar{x}$**	**> SC$\bar{x}$**
R (20)	**CONDO** (30)	July 26/27	ns	ns	df=28.76; P<0.001	ns
T (57)	**BLDG A** (11)	Aug 1/2	ns	df=14.42; P=0.020	ns	ns
T (24)	**BLDG A** (29)	Aug 25/26	ns	df=50.77; P=0.038	ns	ns
T (24)	**CONDO** (41)	Aug 26/28	df=49.70; P=0.043	df=41.07; P=0.019	ns	ns
R (13)	**CONDO** (41)	Aug 28/29	df=30.37; P=0.001	ns	ns	ns

Table E.5. Summary of comparisons with statistical evidence ($P < 0.05$) of a difference in at least one morphometric mean for volant juvenile *Myotis yumanensis* between bat boxes (BOX), buildings (BLDG) or the bat condo (CONDO) maternity roosts in the Kootenay region of British Columbia, Canada in 2021. Morphometrics compared were mass (M), forearm length (FA), total epiphyseal gap (TG), and secondary center of joint ossification (SC). Number of juveniles captured (sample size) is provided in brackets below roost id; the roost with evidence of more advanced juvenile development is noted in bold font. Non-significant differences are noted with “ns”.

Roosts Compared			**Welch’s t-test results (df and *P*-values) for morphometric means**			
Roost 1	**Roost 2**	**Capture Dates**	**> M$\bar{x}$**	**> FA$\bar{x}$**	**< TG$\bar{x}$**	**> SC$\bar{x}$**
CONDO (4)	BLDG S (12)	July 19/20	ns	df=3.86; *P*=0.003	ns	ns
BLDG S (12)	BLDG A (33)	July 20/21	df=15.06; *P*=0.012	df=20.63; *P*=0.023	df=22.59; *P*=0.003	ns
BOX R (20)	BOX T (36)	July 25/26	df=45.49; *P*<0.001	df=36.45; *P*=0.003	ns	ns
CONDO (30)	BLDG S (69)	July 27/28	ns	ns	df=95.55; *P*<0.001	ns
BLDG A (57)	BLDG S (69)	July 28/29	ns	ns	df=117.91; *P*<0.001	ns
BOX R (20)	BOX T (11)	Aug 2/3	ns	df=24.96; *P*=0.020	ns	ns
CONDO (11)	BLDG S (75)	Aug 4/5	df=12.75; *P*=0.005	ns	df=22.09; *P*<0.001	ns
BLDG S (75)	BLDG A (43)	Aug 5/6	ns	ns	df=63.31; *P*<0.001	df=75.75; *P*<0.001
BOX T (61)	BOX R (21)	Aug 10/11	df=35.46; *P*<0.001	df=58.48; *P*=0.002	ns	df=33.72; *P*=0.017