Microclimate conditions of bat boxes occupied by New Zealand's native long-tailed bat (*Chalinolobus tuberculatus*) in Hamilton City

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Abstract

Globally, land clearance has resulted in the destruction of bat habitat features such as tree roost cavities. Installation of artificial roosts, also known as bat boxes, is intended to mitigate such losses. However, bat boxes are often installed with limited understanding of conditions such as temperature stability and relative humidity required by the target bat species. In New Zealand, long-tailed bat/pekapeka-tou-roa (*Chalinolobus tuberculatus*) populations largely favour tree cavities for roosting, and populations have been documented across a range of habitats including native forest, agricultural land, and within urban areas such as Hamilton City. Temperature and relative humidity have been identified as important roost selection factors for *C. tuberculatus*, but these properties have never been assessed in New Zealand bat boxes.

To understand microclimate conditions within bat boxes occupied by *C. tuberculatus* in relation to natural roosts, environmental loggers were installed in Kent and Schwegler type roost boxes in Hamilton City, and natural roost cavities near Hamilton and Pukekohe. For further comparison, loggers were also installed near the top and bottom of Grand Canyon Cave, a known roost for *C. tuberculatus*. Fortnightly surveys of Hamilton City bat boxes were conducted using an endoscopic camera mounted on a 15 m telescopic carbon fibre pole or evening watches of tree roosts. This provided box occupancy rates and allowed comparisons to be made between temperature and relative humidity within bat boxes and natural roosts in relation to occupancy.

Twenty-nine (63 %) of the 46 monitored bat boxes had confirmed occupation, with generalised linear mixed modelling (GLMM) indicating that sheltered Kent boxes were more likely than exposed Kent boxes to be occupied. Modelling also indicated that there was no significant effect of box chamber on occupation. However, microclimate conditions of Kent boxes were less stable than natural roosts, particularly exposed boxes, although the differences may not have been substantive enough to be physiologically relevant to *C. tuberculatus*. On average, bat boxes were generally warmer or similar to ambient conditions on a diel cycle, while natural roosts were warmer than ambient at night and cooler during the day. Although heat tolerance of *C. tuberculatus* is unknown, criteria used for similar species indicated that two exposed Kent boxes experienced a limited number of potential overheating events (>40 °C). The microclimate conditions in Grand Canyon Cave indicated differences between the top and bottom of the cave, with the top of the cave having similar thermal

properties to tree cavity roosts. Generalised linear mixed modelling indicated that there was no significant effect of box thermal conditions on occupation rates.

Although microclimate differences between the inner and outer chambers of Kent type boxes were potentially too small to be physiologically relevant to *C. tuberculatus*, microclimate stability and box exposure should be considered during installation. Providing a range of internal microclimates is likely to support the range of thermoregulatory requirements of the population. Future research should consider the development of boxes with improved microclimate stability, and designs which facilitate the thermoregulatory requirements of *C. tuberculatus* during different reproductive phases.

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Chapter One: Introduction

Bats (Chiroptera) are a mammalian order comprising 1500 species and are present in all global terrestrial habitats apart from polar regions (Russo et al., 2024; Simmons & Cirranello, 2025). They represent the fastest-radiating mammalian order (Teeling et al., 2005) and are highly diverse in their morphology, diet, behaviour, ecology, and physiology (Jennings et al., 2004; Voigt & Kingston, 2015). Bats also fulfil important ecological roles and provide ecosystem services, such as through regulating insect populations and pollination (Voigt & Kingston, 2015). Of the approximately 1300 species assessed by the International Union for Conservation of Nature (IUCN), over 40 % are listed as data deficient, extinct, near threatened or higher, and over 70 % of species' populations are considered to be decreasing or unknown (IUCN, 2025).

Over half a bat's life is spent roosting, making roosts an important resource for reproduction, energy conservation, socialisation, and protection from predators and weather (Kunz, 1982). The types of roosts used by bats vary considerably, especially amongst Yangochiropterans (previously Microchiroptera), spanning natural and artificial features including caves, tree cavities, rock crevices, flaky bark, foliage, branches, mine tunnels, buildings, bridges, and purpose-built bat boxes (Kunz, 1982; Rueegger, 2016). Some bat species are obligate users of one roost type, for example, *Lonchophylla dekeyseri* is only known to roost in caves (Oliveira et al., 2022). In comparison, other bat species (especially temperate-region Yangochiropterans) have more generalist roosting habits. For example, *Eptesicus fuscus* is known to use a wide range of roost features including caves, buildings, tree cavities, and bat boxes, varying throughout its geographic range and depending on the roost's particular purpose (i.e., for hibernacula, maternity roosts, night roosts, or non-reproductive roosts) (Agosta, 2002).

Roost microclimate

Specific drivers of roost selection appear to vary and have been shown to include proximity to foraging habitat/water/forest edge, tree/cavity dimensions and height, internal temperature and humidity, and tree species (Boonman, 2000; Encarnação et al., 2005; Kunz & Lumsden, 2003; Naďo & Kaňuch, 2015; Robinson et al., 2023; Sedgeley, 2001; Sedgeley & O'Donnell, 1999a, 1999b). Roost microclimate (i.e., internal temperature and humidity) has been shown

to be important for roost selection (Bartonička & Řehák, 2007; Kerth et al., 2001; Sedgeley, 2001). This can largely be explained by the energy conservation strategies of bats and how they relate to thermal requirements. A large proportion of bats engage in energy-saving temporal heterothermy, employing daily or multiday torpor (hibernation), when conditions are suboptimal due to inclement weather or low prey availability (Geiser & Stawski, 2011; Stawski et al., 2014; Turbill et al., 2024). As homeotherms, bats must expend energy specifically to produce heat to maintain a constant body temperature, and their comparatively small size facilitates rapid heat loss to the environment (Speakman & Thomas, 2003). Additionally, the metabolic needs of flying animals such as bats are higher than animals which utilise less metabolically-demanding locomotion methods such as running (Norberg, 1996), especially in smaller animals (Alexander, 2005). As ambient temperatures cool, the metabolic cost of remaining normothermic increases. In some cases, bats engage in voluntary hypothermia to circumvent these heightened energy demands through the use of torpor. Torpor involves a reduction in metabolic rate (MR) below basal metabolic rate (BMR), reducing energy expenditure, and usually occurs through voluntary hypothermia with body temperatures sometimes falling to 1–3 °C and MR 0.5 % of BMR at reduced ambient temperatures (e.g., below 25 °C) (Geiser, 2004; Geiser & Brigham, 2000; Speakman & Thomas, 2003). Torpor bouts have also been recorded in response to high ambient temperatures (> body temperature), where bats limit metabolic rate in order to reduce heat production, allowing them to tolerate these higher temperatures while conserving energy and water (Reher & Dausmann, 2021). In all cases, for energy savings to be achieved the metabolic cost of arousal (return to normothermy and normal MR) at the end of a torpor bout must not exceed the energetic savings gained, and therefore torpor behaviour is more commonly observed in smaller species due to their larger surface area to body ratio (Speakman & Thomas, 2003). However, torpor has been recorded in larger bat species e.g., the *Pteropus poliocephalus*, in response to low ambient temperatures following adverse weather conditions which likely led to increased energy costs and reduced food availability (Turbill et al., 2024). In the case of hypothermic torpor, passive rewarming – whereby the bat warms with increasing ambient temperatures rather than active rewarming mechanisms such as shivering – can reduce metabolic costs of arousal (Currie et al., 2015). Consequently, bats may select roosts based on whether the roost thermal profiles support maximal energy savings via torpor (Turbill, 2006; Turbill & Geiser, 2006; Turbill et al., 2003), or allow bats to maintain normothermy at low metabolic cost (e.g., if roost temperatures remain within the

thermoneutral zone, or via social thermoregulation) (Marroquin et al., 2023; Russo et al., 2017; Willis & Brigham, 2007).

Studies have shown that bats which engage in long bouts of multiday torpor (hibernation) select hibernacula with cooler, more stable temperatures and higher humidity, such as caves, which allow body temperatures to remain stable but maximise energy savings (McClure et al., 2020; Perry, 2012). Outside of the hibernation season or for bats which do not hibernate, roost microclimates must balance energy conservation against reproductive success. Male and non-reproductive individuals, especially those at lower temperate latitudes, have been shown to select thermally unstable roosts which support rapid entry into torpor and passive arousal (Turbill, 2006; Turbill et al., 2003). Such thermally unstable roost types were also selected by temperate-zone tree-roosting bats throughout winter (Turbill & Geiser, 2008). Reproductive females often do not enter torpor as frequently, for as long, or as deeply (Besler & Broders, 2019; Johnson & Lacki, 2013; Solick & Barclay, 2006), likely due to resulting reductions in foetal development and milk secretion rates caused by reduced maternal body temperatures, additionally, females may receive thermoregulatory assistance via their social roosting habits (Racey & Swift, 1981; Turbill & Geiser, 2006; Wilde et al., 1999; Willis & Brigham, 2007). However, torpor patterns in reproductive females can differ between pre- and post-natal states, during different stages of pregnancy, and between species. For example, pre-natal females enter torpor less frequently, but bouts are deeper and longer than in post-natal females (Besler & Broders, 2019; Johnson & Lacki, 2013; Solick & Barclay, 2006). Consequently, maternity roosts may be warmer, supporting the development of non-volant pups, more thermally stable and warm quickly during the day; although post-natal roosts are generally warmer at night and more thermally stable than pre-natal roosts (Chruszcz & Barclay, 2002; Lausen & Barclay, 2003; Lourenço & Palmeirim, 2004; Racey & Swift, 1981; Rueegger, 2016; Solick & Barclay, 2006). Optimal roost microclimates and torpor use may also vary between species and geographic range (Besler & Broders, 2019; Czenze et al., 2017; Rueegger, 2016; Solick & Barclay, 2007). For example, Czenze et al. (2017) demonstrated that winter torpor frequency, arousal patterns, and roost choice differed between two geographically distinct populations of New Zealand's lesser short-tailed bat, *Mystacina tuberculata*. The lower-latitude, Hauturu/Little Barrier Island population experienced warmer temperatures than the higher-latitude inland Pureora forest population, and utilised short torpor bouts more frequently, aroused more often at warmer sunset temperatures, and selected thermally unstable roosts.

Bat boxes

Globally, land clearance is a major driver of declining wildlife populations (Hogue & Breon, 2022) and has led to a reduction in available tree cavities and other habitat structures (Eyre et al., 2010; Le Roux et al., 2014). Tree cavity-roosting bats may therefore face survival pressures and population declines, especially in regions where cavities can take decades to form naturally (Vesk et al., 2008). Urban development can have a negative impact on bats (Jung & Threlfall, 2015), and their generally slow life histories increase susceptibility to threats as slow breeding rates reduce the ability of populations to quickly recover after loss (Barclay & Harder, 2003).

Purpose-built artificial roosts, such as bat boxes, have been in use for over a century to increase roost availability where natural cavities have been lost (Mering & Chambers, 2014; Rueegger, 2016). Bat box designs vary considerably, but generally describe vertical cylindrical, laminar, or rectangular structures with one or more chambers and entry/exit holes at the base or side of the structure (Martin Bideguren et al., 2018). They are typically constructed from wood or woodcement (a mixture of wood shavings and cement). Woodcement boxes appear to be preferred by bats in Europe, but are not well-tested in other regions (Rueegger, 2016). Despite known use of a variety of bat box designs, most occupation records are from species not classified as threatened under the IUCN Red List and the use of bat boxes as maternity roosts is uncommon (Mering & Chambers, 2014; Rueegger, 2016). Also, boxes may not sufficiently offset natural roost losses, as they may not be used by bats at the same rate of natural roosts, indicating that box designs may not be suitable for some species (Lindenmayer et al., 2017; Rueegger et al., 2018).

Drivers of box occupation

It is likely that microclimate requirements for a species to occupy a box vary depending on specific physiological requirements, as well as reproductive and developmental stages (Bartonička & Řehák, 2007; Brittingham & Williams, 2000; Kerth et al., 2001; Lourenço & Palmeirim, 2004; Rueegger et al., 2020). For example, *Pipistrellus pygmaeus* have been shown to select warmer boxes (~4 °C higher mean temperatures) when pregnant versus when lactating (Bartonička & Řehák, 2007), while pregnant *Myotis bechsteinii* may favour colder boxes (18.2 °C) and move to warmer boxes during and after lactation (21.3 °C) (Kerth et al., 2001). Other studies have not differentiated roost choice between stages of reproduction but

indicate selection of warmer boxes even where there are risks of high temperatures (Brittingham & Williams, 2000; Lourenço & Palmeirim, 2004). In contrast, Rueegger et al. (2020) observed that bat box temperature was not important for *Chalinolobus gouldii*, but *Nyctophilus geoffroyi* favoured warmer (black, sun-exposed) boxes. Consequently, it has been suggested that box design and installation should consider species-specific requirements – including variability in these requirements during different seasons and reproductive stages (Rueegger, 2016). Despite these observations, species-specific microclimatic requirements are often understudied and even more rarely are intraspecific preferences assessed, which would otherwise help to build a broader picture of population-level roost requirements.

Solar exposure of bat boxes is often considered during box installation and when assessing occupation (Rueegger, 2016). Solar radiation has been shown to directly impact internal roost temperatures (Griffiths et al., 2017), although, studies assessing box use relative to exposure are not consistent in their findings. Studies often fail to assess winter occupation of boxes, as many investigations are conducted at higher latitudes where bats often migrate to hibernacula, such as caves, during the winter. For example, Dillingham et al. (2003) found greater box occupancy in sunny-facing and exposed boxes by bats in southern Oregon, while Flaquer et al. (2006) indicated that Spanish *Pipistrellus pygmaeus* preferred east-facing boxes. Neither study directly measured box microclimate, but Dillingham et al. (2003) proposed that bats of the coastal Pacific northwest USA would be more limited by the need to conserve heat while roosting, rather than a need to avoid overheating and therefore favoured sun-exposed boxes. While Flaquer et al. (2006), suggested that dry westerly winds reducing temperatures and humidity may have led to avoidance of west-facing and a preference for east-facing boxes. It has been observed that *Myotis sodalis* selected shaded boxes in spring and exposed boxes in summer, potentially due to exposed boxes being warmer and better supporting the need for reduced torpor during reproductive phases in summer, while shaded boxes in spring provided protection from winds and unstable temperatures but still received some sun due to leaves not having fully returned to deciduous trees (Crawford et al., 2026). Kerth et al. (2001) found higher overall occupancy by *Myotis bechsteinii* of black-painted, exposed boxes (overall mean 22.3 °C), but no difference in occupancy of shaded black (18.2 °C) vs shaded white (17.1 °C) boxes. However, occupancy rates varied depending on reproductive stage, as pre-natal females selected shaded boxes (no box colour preference) while post-natal bats favoured the black, exposed boxes (Kerth et al., 2001). Contrastingly, a study by Fukui et al. (2010) indicated that post-natal adult female *Vespertilio sinensis*

favoured bat boxes installed at shaded sites, although no maternity roosts were formed and so this likely reflected preferences of non-reproductive individuals.

Overheating boxes

High temperatures and overheating of bat boxes have been identified as a concern, as it may lead to bats experiencing heat stress and mortality (Crawford & O'Keefe, 2021; Flaquer et al., 2014). There likely exists inter- and intraspecific variation in the upper thermal tolerance of bats, but studies broadly suggest roost temperatures above 40 °C to be outside tolerance ranges (Bartonička & Řehák, 2007; Crawford & O'Keefe, 2021; Flaquer et al., 2014; Lourenço & Palmeirim, 2004; Martin Bideguren et al., 2018). However, *Eptesicus fuscus* and *Myotis lucifugus* in Pennsylvania, USA continued roosting in boxes with internal temperatures between 44–53 °C (Brittingham & Williams, 2000). Bats exposed to air temperatures above normothermic body temperatures must engage in active cooling, such as evaporative cooling, which can cause dehydration (Herreid & Schmidt-Nielsen, 1966; Maloney et al., 1999). Therefore, selecting day roosts with temperatures which do not exceed their thermoneutral zone is important for reducing energy expenditure and conserving water.

Overheating risk in bat boxes can be reduced by adjusting box design and installation practices. Factors such as chamber volume (relative to surface area) and vertical space, box aspect and sun exposure, colour, building material, and the use of insulating layers have all been shown to impact internal box microclimates and risks of temperature extremes (Bakken & O'Keefe, 2025; Flaquer et al., 2014; Godinho et al., 2020; Lourenço & Palmeirim, 2004; Martin Bideguren et al., 2018). Bakken and O'Keefe (2025) demonstrated that southerly-facing (towards the sun) rocket-style bat boxes were more thermally stable, although results from Godinho et al. (2020) suggest that the impact of box aspect may vary seasonally, as *Chalinolobus gouldii* preferred east- and southwest-facing (away from the sun) boxes in summer, and northwest-facing (towards the sun) boxes in winter, although results were not consistent across sites. Dark box surfaces have been consistently shown to increase internal box temperatures and lead to reduced thermal stability, compared to lighter-coloured boxes (Bakken & O'Keefe, 2025; Flaquer et al., 2014; Griffiths et al., 2017; Lourenço & Palmeirim, 2004; Martin Bideguren et al., 2018). Martin Bideguren et al. (2018) found that overheating events did occur more frequently in southerly-facing (towards the sun) bat boxes, although the effect was not statistically significant. This same study also demonstrated that boxes with

greater internal volume relative to external surface area, along with boxes constructed from rice chaff, were less prone to overheating, although in the case of the rice chaff boxes this may have been due to their light colouration. Boxes constructed from woodcement have been shown to have increased overheating risk, but typically these boxes are coloured darker than wooden boxes so this may be a function of increased solar radiation absorption (Flaquer et al., 2014; Martin Bideguren et al., 2018).

*New Zealand long-tailed bat (***Chalinolobus tuberculatus***)*

New Zealand has two extant, resident bat species which are the only native terrestrial mammal species – the long-tailed bat, *Chalinolobus tuberculatus* (Vespertilionidae) and the lesser short-tailed bat, *Mystacina tuberculata* (Mystacinidae). Both are Yangochiropterans and *C. tuberculatus* is considered critically endangered while *M. tuberculata* is considered vulnerable, primarily due to habitat loss and predation (O'Donnell, 2021a, 2021b). *Chalinolobus tuberculatus* is a small (8–11 g) aerial insectivore which forages at forest edges and roosts in a range of features including tree cavities, under flaky bark, and in caves (O'Donnell et al., 2021). They are also known to occupy bat boxes and buildings, including as maternity roosts (O'Donnell, 2010, 2024; Robinson et al., 2023). *Chalinolobus tuberculatus* individuals are known to switch between solitary and communal roosts, but reproductive females typically form communal maternity roosts during the breeding season, while males and non-reproductive females often roost alone (O'Donnell & Sedgeley, 1999). In large forests where available roosts can be assumed to be abundant, *C. tuberculatus* have low roost fidelity and will typically switch roosts every 1–3 nights, although they have been shown to exhibit higher fidelity of solitary roosts (O'Donnell & Sedgeley, 1999; Sedgeley & O'Donnell, 1999a, 1999b). Generally, low roost fidelity is more common amongst bat species which roost in less permanent features such as foliage, and where roost availability is high (Lewis, 1995). However, this may vary within species due to factors such as location and sex. For example, Brigham (1991) proposed that roost fidelity of *Eptesicus fuscus*, which have a large geographic range and utilise a range of roost types, depended on the availability of the population's chosen roost type. *Eptesicus fuscus* roosting in "rare roosts" such as buildings had higher rates of roost fidelity than those roosting in "abundant roosts" such as tree cavities. This may also be true of *C. tuberculatus*, although in urban and rural settings where roost features are likely limiting, they have been recorded to have higher rates of roost fidelity and re-use than in areas of extensive forest (Dekrout, 2009). In native forest, *C.*

tuberculatus appear to select natural roost features which are not directly obscured by surrounding vegetation, are higher from the ground than random, and in taller, larger trees (Sedgeley & O'Donnell, 1999a, 1999b). Post-natal maternity roosts of *C. tuberculatus* have been recorded both in poorly and well-insulated roost features (Sedgeley & O'Donnell, 2004), but Sedgeley (2001) determined that maternity roost features (pre- and post-natal) were well insulated from ambient fluctuations in temperature and humidity, with higher humidity means (95.4 % vs 92.8 %), and temperature maximums experienced later in the day (21.5 vs 19.1 hours), compared to non-roost cavities. In a study of summer male *C. tuberculatus* and maternity roosts in a plantation forest (*Pinus radiata*, *Eucalyptus fastigata*, and *E. regnans*) in south Waikato, New Zealand, maternity roosts were closer to water sources, and male roosts were located in areas where the vegetation was more open (Borkin, 2011).

Bats and boxes in Hamilton City

Chalinolobus tuberculatus are more prevalent in expansive native forest areas actively managed by the Department of Conservation, but fragmented populations are also present in both rural and urban areas such as Hamilton City (Caskey & Tempero, 2022; Daniel & Williams, 1984; Dekrout et al., 2014; Robinson et al., 2023). Hamilton City is located in the central North Island and is surrounded by high intensity pastural land, with only 1.6 % of the original native vegetation extent remaining (Leathwick et al., 1995). The city's notable natural characteristics are the Waikato River and the vegetated gully systems branching from it, which contain parks and reserves. *Chalinolobus tuberculatus* have been detected most frequently in these southern gullies e.g., the Mangaonua and Mangakotukutuku (Caskey & Tempero, 2022), which typically contain less fragmented vegetation than other parts of the city (Crewther & Parsons, 2017).

A local cross-organisation advocacy group, Project Echo, installed 27 wooden, Kent-style bat boxes (Figure 1.1) throughout Hamilton's urban parks in 2011 (Robinson, 2022). The first occupation of these boxes was confirmed in January 2018 by Davidson-Watts (2019) and included the discovery of a maternity roost. This same study also confirmed natural roosts within and around the city, such as at the Narrows Campground, and indicated that the Hamilton *C. tuberculatus* population home ranges may encompass both peri-urban areas and the southern urban gully systems within the city. Urban infrastructure development projects in Hamilton City, such as in the Peacockes greenfield zone and the Southern Links roading

development, have been assessed as likely to have a significant impact on *C. tuberculatus* in the south of the city through loss of roosting habitat (Davidson-Watts, 2019). As partial mitigation of these impacts, over 100 bat boxes have been installed in the city's southern gully systems since 2019. Ten of these were Schwegler 2F woodcement bat boxes, with the remainder wooden Kent-style boxes. At least seven of these Kent boxes were of a modified design, featuring two chambers, an openable lid, and a wooden lip below the outer chamber, installed in late 2024 (F. Fisher, pers. comm., March 2025). The remaining boxes were simple double-chamber designs (Figure 1.2). There is no evidence that the Hamilton City *C. tuberculatus* population uses the Schwegler 2F bat boxes (AECOM New Zealand Limited, 2022), however, the species is known to use this box type in south Canterbury, New Zealand, albeit at low (10 %) occupancy rates (O'Donnell, 2024).

Figure 1.1 Two of the original 27 wooden Kent-style bat boxes installed by Project Echo in Hamilton City in 2011. Left: A single-chamber design; right: a triple-chamber design.

Figure 1.2 Types of bat boxes installed as part of the "Southern Links" development project since 2019. Left: wooden double-chamber Kent-style box; middle: Schwegler 2F woodcement box; right: wooden double-chamber modified Kent-style box.

Bats outside of Hamilton City

Grand Canyon Cave Scientific Reserve is one of the few confirmed cave roosts for *C. tuberculatus*. The cave is located in the Mangaotaki Valley karst area, amongst agricultural and horticultural land, where approximately 30 % of the original extent of native vegetation is estimated to remain (Harding, 1997). The cave is a tunnel cave about 350 m long, 5–9 m wide, and up to 30 m high, with a 15 m x 7 m entrance to the north and a 10 m x 6 m entrance to the south (O'Donnell, 2002; pers. obsv.) (Figure 1.3). *Chalinolobus tuberculatus* have been regularly recorded roosting in the cave since about 1959 (O'Donnell, 2002).

Figure 1.3 Grand Canyon Cave roost site. Top: View of the northern cave entrance from afar, showing surrounding regenerating forest and agricultural land; bottom-right: looking out of the northern entrance to the cave; bottom-left: looking out of the smaller, southern entrance to the cave.

The Franklin area incorporates the Pukekohe and Waiuku urban centres and rural surrounds, in the southern part of the Auckland region west of State Highway 1. It is located in an area dominated by agriculture, horticulture and urban areas with only 1.5 % of its original native

vegetation extent remaining (Emmett et al., 2000). *Chalinolobus tuberculatus* populations have been monitored in the area since 2021, with approximately 40 confirmed roost features primarily in *Beilschmiedia tarairi*, *Vitex lucens*, *Podocarpus totara* var. *totara*, and *Hesperocyparis macrocarpa* (N. Bansall, pers. comm., March 2026).

Research objectives

Urban development threatens the availability of suitable roost features for populations of *Chalinolobus tuberculatus* persisting in urban areas and rural surrounds. Consequently, conditions may be placed on development projects to mitigate roost loss through the installation of bat boxes. However, minimal research has been conducted to-date on the suitability of the internal conditions of these boxes for *C. tuberculatus* roosting. This research aims to improve this understanding through assessing the microclimate conditions of bat boxes in Hamilton City and fulfilling the following objectives:

Objective 1: Determine the rate of box occupation by *Chalinolobus tuberculatus*, and whether this varies according to box chamber, and exposure. This will be achieved by conducting fortnightly occupation surveys of a selection of bat boxes in Hamilton City from January-October 2025.

Objective 2: Microclimate (temperature and relative humidity) data from bat boxes and natural roosts will be compared, and used to determine the effect of box chamber, season, and exposure, along with identification of potential overheating events within roosts.

Objective 3: Findings from occupation surveys and microclimate analyses will be used to determine the effect of internal box temperature on occupation rates.

The learnings from these objectives will provide insight into the suitability of bat boxes as tools for mitigating losses of natural *C. tuberculatus* roosts in New Zealand and help to inform design and installation of bat boxes to improve this suitability.

Chapter Two: Methods

Study areas

Natural and artificial roosts located at eight sites within Hamilton City, Waipa District, Waikato District, and Waitomo District in the North Island of New Zealand were utilised for this study (Figure 2.1).

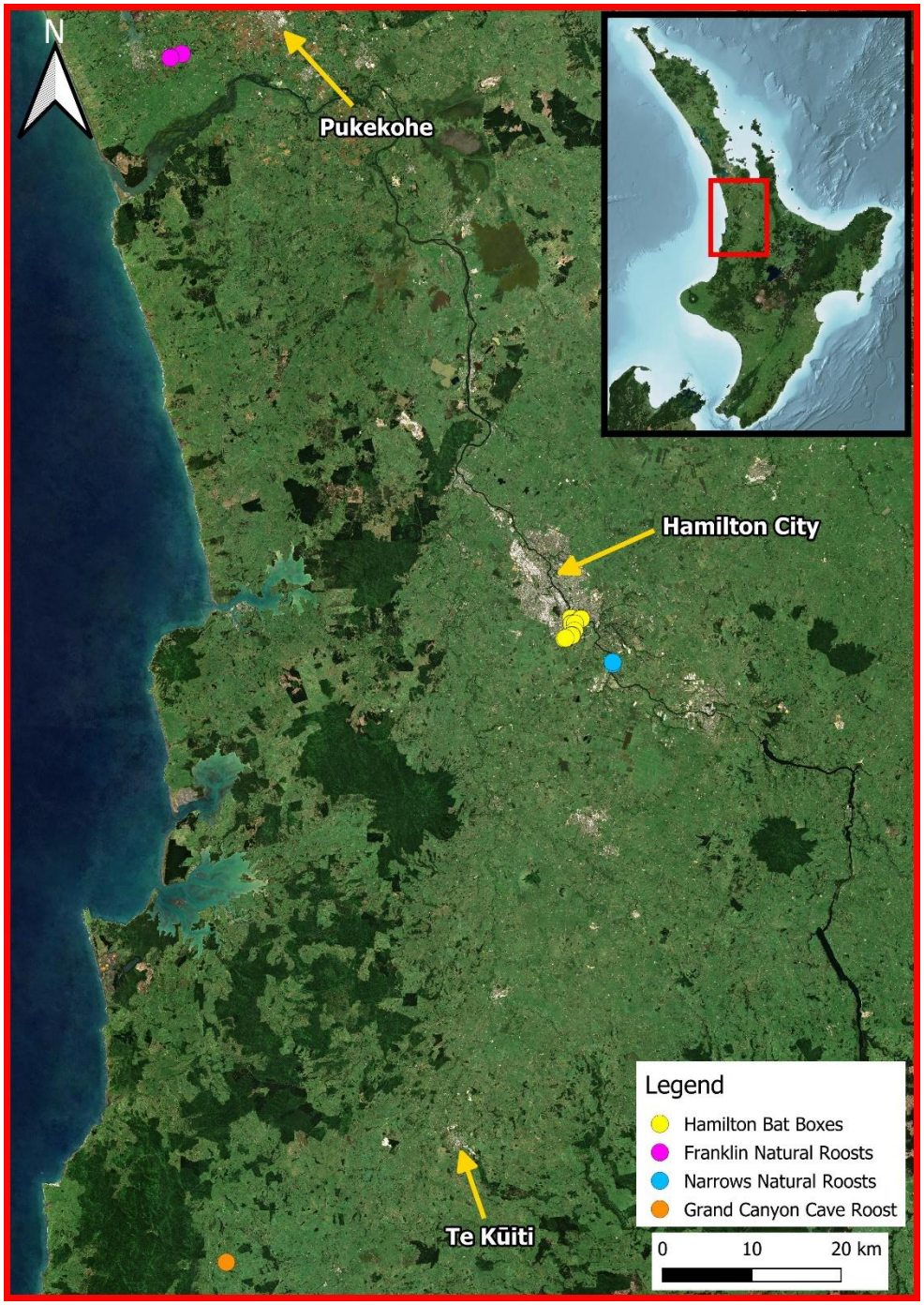

Figure 2.1 Map of the roost site locations within the Waikato Region in the North Island of New Zealand, with main urban centres labelled.

All artificial roost (bat box) sites were situated within Hamilton City, located in seven Hamilton City Council reserves (Figure 2.2) in the south of the city where bat activity is highest (Caskey & Tempero, 2022). Hamilton Gardens contains a variety of native and exotic vegetation among enclosed, themed gardens, and the wider park-like grounds. Dillicar Park is a small reserve which forms part of the Waikato River walkway and is dominated by a mixture of native and exotic tree species. Sandford Park forms a major part of the Mangakotukutuku gully system and is dominated by mature *Pinus radiata* and is a known area of high *Chalinolobus tuberculatus* activity, including two bat boxes regularly used as maternity roosts (Caskey & Tempero, 2022; O'Sullivan, 2021; Robinson et al., 2023). Peacockes Reserve Esplanade is dominated by exotic tree species such as *Pseudotsuga menziesii* and *Acacia melanoxylon*, and a bat box here has previously been observed in use as a maternity roost (Robinson et al., 2023). Fitzroy Park consists of a community sports field and playground, bordered by mature vegetation such as *Eucalyptus* spp. and *Acacia melanoxylon*. Te Anau Park has similar features to Fitzroy Park, although the *Eucalyptus* spp. trees are larger and more dominant. Resthills Reserve contains rolling park-like grounds with large *Eucalyptus* spp. predominant.

Figure 2.2 Map of the 46 monitored bat boxes in Hamilton City.

Natural roost features were monitored at three locations across the Waikato Region (Figure 2.1). The Narrows site was located on the true left bank of the Waikato River, just upstream from the Narrows Bridge and approximately 4 km southeast of Hamilton City. It consisted of park-like grounds with dominant, mature *Quercus* spp. and *Robinia pseudoacacia*. Roosts were previously confirmed at this site in 2018 (Davidson-Watts, 2019) and three potential roosts suitable for monitoring were selected for the study (Natural Roosts 1–3). The Franklin

site was located approximately 11 km west of the Pukekohe urban centre. Populations of *C. tuberculatus* were known to roost in the pūriri-taraire (*Vitex lucens–Beilschmiedia tarairi*) forest fragments and scattered mature trees situated amongst the rolling hills in this area. The monitored roosts (Natural Roosts 4–6) were located in two forest fragments approximately 1 km apart and had previously been confirmed as maternity roosts (N. Bansal, pers. comm., December 2024). The Grand Canyon Cave site was located approximately 28 km southwest of the Te Kūiti urban centre, amongst steep farmland and forest fragments. It is known to be a communal roost site for *C. tuberculatus* (O'Donnell, 2002).

Occupation monitoring of bat boxes

A preliminary visual survey of 114 Hamilton City bat boxes was carried out in December 2024, primarily to assess box condition, accessibility, and signs of occupation by *C. tuberculatus*, such as staining from urine/faeces or lack of visible cobwebs. Box types included eight Schwegler 2F boxes and several designs based on the Kent bat box. The majority (75) of the surveyed bat boxes were double-chamber Kent style boxes. Results from this survey were used to inform the final selection of boxes for regular occupation monitoring. Boxes which couldn't be located, easily accessed, or were in a condition unlikely to encourage occupation (e.g., rotted, upside-down) were excluded from further assessment. Additionally, boxes were included in the survey group if occupation had been previously recorded, or they were near to otherwise selected boxes, in addition to 10 Kent style boxes which were later installed for the microclimate assessment.

Each roost was classified either as "sheltered" or "exposed", which was determined based on its level of canopy cover, distance to the edge of the stand of trees, and predicted exposure to prevailing winds depending on topography, aspect, and surrounding vegetation. The final 46 bat boxes (Table 2.1) were monitored approximately fortnightly for 7–8 months from January–September 2025, excluding August, and with monitoring for some boxes continuing into October to support the microclimate assessment.

Table 2.1 The 46 monitored bat boxes in Hamilton City and their respective site locations, year of installation, number of chambers, box type, exposure category, and months monitored for occupancy (year is 2025 unless otherwise specified). NB: no occupancy monitoring was conducted during the month of August 2025.

Box ID	Site	Year Installed	Number of chambers	Box Type	Exposure Category	Months monitored
3	Hamilton Gardens	2011	3	Kent	Exposed	Jan-Sep (opportunistic)
3B	Hamilton Gardens	2011	2 (left & right)	Kent	Exposed	Jan-Sep (opportunistic)
BB68	Hamilton Gardens	2019	2	Kent	Exposed	Jan-Sep
BB69	Hamilton Gardens	2019	2	Kent	Sheltered	Jan-Oct
U6	Hamilton Gardens	2025	2	Kent	Sheltered	Apr-Oct
BB70	Hamilton Gardens	2019	2	Kent	Sheltered	Jan-Sep
BB66	Dillicar Park	2019	2	Kent	Sheltered	Jan-Sep
BB67	Dillicar Park	2019	2	Kent	Exposed	Jan-Sep
BB41	Sandford Park	2019	2	Kent	Sheltered	Jan-Sep (opportunistic)
BB42	Sandford Park	2019	2	Kent	Exposed	Jan-Oct
U7	Sandford Park	2025	2	Kent	Exposed	May-Oct
BB45	Sandford Park	2019	2	Kent	Exposed	Jan-Oct
U4	Sandford Park	2025	2	Kent	Exposed	Apr-Oct
BB46	Sandford Park	2019	2	Kent	Exposed	Jan-Sep
BB47	Sandford Park	2019	2	Kent	Exposed	Jan-Oct
U8	Sandford Park	2025	2	Kent	Exposed	May-Oct
BS09	Sandford Park	2019	1	Schwegler 2F	Sheltered	Jan, Mar-Oct
14	Sandford Park	2012	3	Kent	Sheltered	Dec ‘24, Feb-Sep
U9	Sandford Park	2025	2	Kent	Sheltered	Jul-Oct
15	Sandford Park	2012	3	Kent	Sheltered	Dec ‘24, Feb-Sep
U10	Sandford Park	2025	2	Kent	Sheltered	Jul-Oct
BB53	Peacockes Reserve Esplanade	2019	2	Kent	Exposed	Feb-Sep
BB54	Peacockes Reserve Esplanade	2019	2	Kent	Sheltered	Feb-Sep
BBS1	Peacockes Reserve Esplanade	2024	2	Modified Kent	Sheltered	Feb-Sep
BBS3A	Peacockes Reserve Esplanade	2024	2	Kent	Sheltered	Feb-Sep
BBS3B	Peacockes Reserve Esplanade	2024	2	Modified Kent	Sheltered	Feb-Sep
BBS5	Peacockes Reserve Esplanade	2024	2	Modified Kent	Sheltered	Feb-Sep
BB34	Fitzroy Park	2019	2	Kent	Sheltered	Jan-Sep
BB35	Fitzroy Park	2019	2	Kent	Sheltered	Jan-Sep
BB36	Fitzroy Park	2019	2	Kent	Exposed	Jan-Sep
BBF5B	Fitzroy Park	2024	2	Modified Kent	Sheltered	Jan-Sep
BBF6B	Fitzroy Park	2024	2	Modified Kent	Sheltered	Jan-Sep
BS01	Fitzroy Park	2019	1	Schwegler 2F	Exposed	Mar-Oct
17	Te Anau Park	2012	2	Kent	Sheltered	Jan-Oct
U3	Te Anau Park	2025	2	Kent	Sheltered	Apr-Oct
BB20	Te Anau Park	2019	2	Kent	Sheltered	Mar-Sep
BB22	Te Anau Park	2019	2	Kent	Sheltered	Feb-Sep
BB27	Te Anau Park	2019	2	Kent	Sheltered	Feb-Sep
BB28	Te Anau Park	2019	2	Kent	Exposed	Jan-Oct
U5	Te Anau Park	2025	2	Kent	Exposed	Apr-Oct
BB08	Resthills Reserve	2019	2	Kent	Exposed	Jan-Sep
BB09	Resthills Reserve	2019	2	Kent	Exposed	Jan-Oct
U1	Resthills Reserve	2025	2	Kent	Exposed	Apr-Oct
BB10	Resthills Reserve	2019	2	Kent	Sheltered	Jan-Sep
BB11	Resthills Reserve	2019	2	Kent	Sheltered	Feb-Oct
U2	Resthills Reserve	2025	2	Kent	Sheltered	Apr-Oct

Boxes were primarily monitored with an endoscopic camera (Dongguanshi Qianyu Electronic Technology Co. Ltd., China) on a 15 m telescopic carbon fibre pole, inserted just past the entrance of the bat box chamber to obtain a visual of the box interior (Figure 2.3). Alternatively, an infrared video camera (Equinox Z2, Bushnell) was used for evening roost watches if the mounted box height exceeded 15 m or when bats were likely to be present based on historic occupation patterns, audible vocalisations, or guano observed falling from the box. Roost emergence counts of boxes 14 and 15 (Sandford Park) were conducted fortnightly for one hour following sunset using the infrared video cameras. Footage was reviewed using Media Player (Microsoft Corporation, version 11) with the total count of bats, number of pups, and banded bats (those marked with a single metal ring on one wing) recorded.

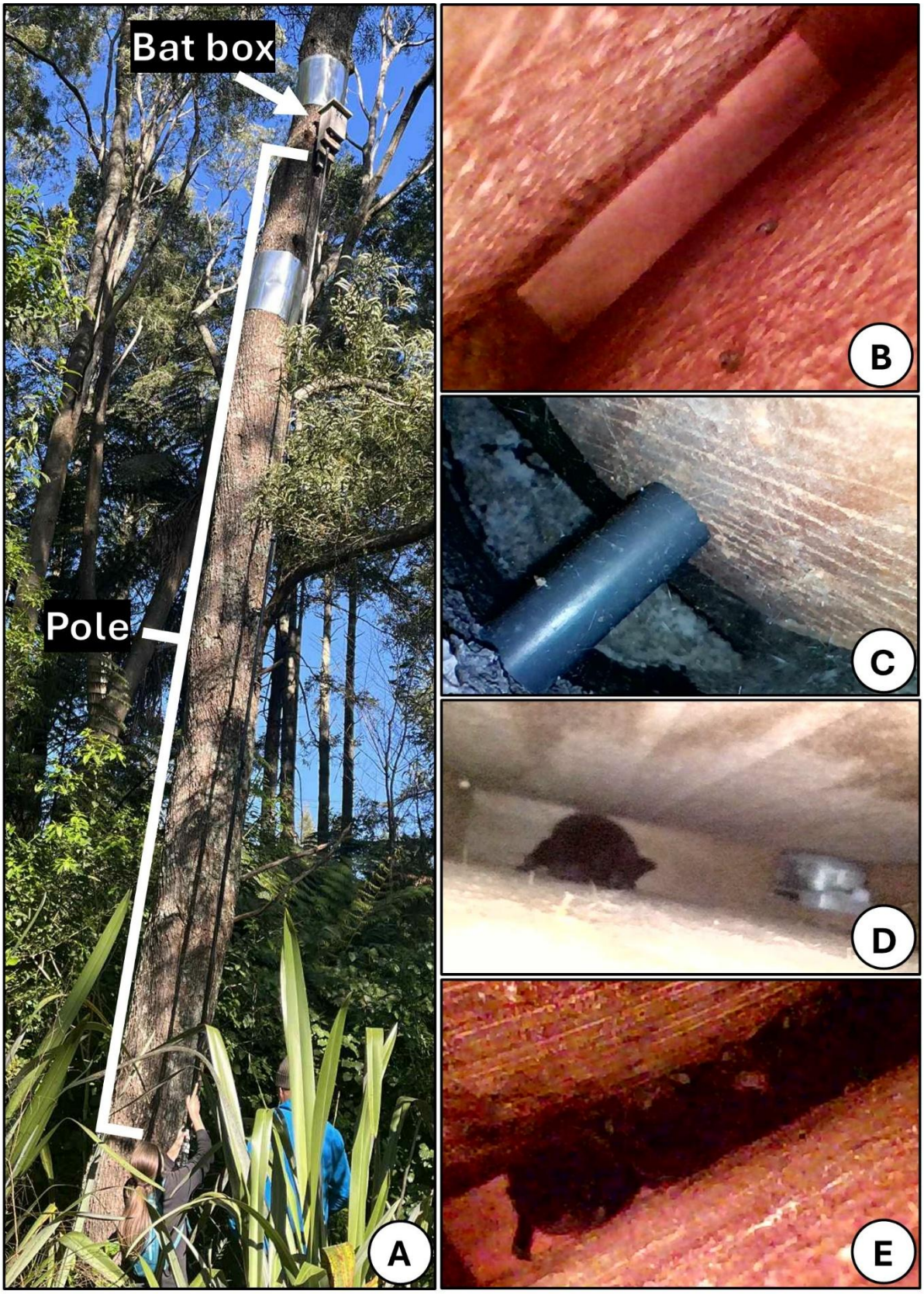

Figure 2.3 Bat box monitoring with an endoscopic camera attached to a telescopic pole. A: Using the pole with the endoscope to view the interior of a double-chamber Kent bat box. B–E: Endoscope images of the interior of (B) an empty Kent bat box chamber, (C) an empty Schwegler 2F bat box, (D) a Kent box chamber with a single roosting bat and a HOBO MX2201 datalogger, (E) a Kent box chamber with ≥4 roosting bats.

Measuring the microclimate of bat roosts

Temperature and relative humidity of nineteen bat roost features at eight locations across the Waikato Region were measured from March 2025 to January 2026, including internal and ambient conditions of 12 bat boxes, six natural tree roosts, and the Grand Canyon Cave roost (Table 2.2).

Of the 12 bat boxes, ten were new double-chamber Kent bat boxes (U1–U10) with microclimate dataloggers installed in March–July 2025, adjacent or near to existing boxes. Rather than installing loggers in the existing boxes, new boxes with dataloggers were installed to avoid altering the structure of existing roost boxes or disturbing roosting bats. *Chalinolobus tuberculatus* have never been observed occupying Schwegler 2F boxes in Hamilton (AECOM New Zealand Limited, 2022), so dataloggers were installed within two of the existing Schwegler boxes as the risk of disturbance to bats was deemed to be very low.

Prior to any work on a tree with an existing box or roost feature, boxes/roosts were checked for occupation using an endoscope or infrared camera. If bats were present, work was not conducted on that tree. Where possible, a new box was installed adjacent to the existing box on the same tree, but where this was not feasible due to the presence of roosting bats, an alternative nearby tree was selected (i.e., boxes U5, U9, and U10). Site selection was also made to achieve a geographic spread across Hamilton City's southern parks and to include a range of sheltered and exposed boxes. Natural roost features were selected for accessibility and geographic spread.

Table 2.2 Roosts with microclimate dataloggers, their locations, roost type, exposure category, paired box (where applicable), months monitored, and the type of microclimate monitoring conducted (OC: outer chamber, IC: inner chamber, BC: both chambers, T: temperature, RH: relative humidity).

Roost ID	Site	Roost Type	Exposure Category	Paired box	Months monitored	Type of monitoring conducted
U6	Hamilton Gardens	Kent	Sheltered	BB69	Mar-Jan ('26)	OC (T)
U7	Sandford Park	Kent	Exposed	BB42	May-Jan ('26)	OC (T)
U4	Sandford Park	Kent	Exposed	BB45	Mar-Jan ('26)*	BC (T + RH)
U8	Sandford Park	Kent	Exposed	BB47	May-Jan ('26)	OC (T)
BS09	Sandford Park	Schwegler 2F	Sheltered	NA	Mar-Jan ('26)	T
U9	Sandford Park	Kent	Sheltered	14	Jul-Jan ('26)	BC (T + RH)
U10	Sandford Park	Kent	Sheltered	15	Jul-Jan ('26)	OC (T)
BS01	Fitzroy Park	Schwegler 2F	Exposed	NA	Mar-Jan ('26)	T
U3	Te Anau Park	Kent	Sheltered	17	Mar-Jan ('26)	BC (T + RH)
U5	Te Anau Park	Kent	Exposed	BB28	Mar-Jan ('26)	BC (T + RH)
U1	Resthills Reserve	Kent	Exposed	BB09	Mar-Jan ('26)	BC (T)
U2	Resthills Reserve	Kent	Sheltered	BB11	Mar-Jan ('26)	BC (T)
Natural Roost 1	Narrows	Knot-hole cavity	Exposed	NA	Mar-Dec	T
Natural Roost 2	Narrows	Knot-hole cavity	Sheltered	NA	Mar-Dec	T
Natural Roost 3	Narrows	Knot-hole cavity	Sheltered	NA	Mar-Aug	T + RH
Natural Roost 4	Franklin	Basal hollow	Sheltered	NA	Mar-Nov	T + RH
Natural Roost 5	Franklin	Knot-hole cavity	Sheltered	NA	Mar-Nov	T (+ RH Mar-Apr)
Natural Roost 6	Franklin	Knot-hole cavity	Sheltered	NA	Mar-Nov	T
Grand Canyon Cave	Grand Canyon Cave	Tunnel cave	NA	NA	Mar-Jan ('26)	T + RH

**inner chamber logger failed in July 2025*

Temperature and relative humidity were logged every 15-minutes using either HOBO MX2301, MX2301A, MX2302A, or MX2201 dataloggers (Onset Computer Corporation, United States of America). Pre-deployment, dataloggers were set to log simultaneously for up to one week, to assess sensor drift. Temperature readings between loggers were found to differ by <1 °C, which was considered acceptable variation. However, relative humidity readings varied up to ~5 % between the MX2301/MX2301A and MX2302A models. Therefore, data from the MX2302A loggers were adjusted using linear interpolation prior to analysis.

In addition to internal roost conditions, ambient temperature and relative humidity at each location and exposure category were recorded. The Sandford Park sheltered ambient datalogger was excluded from analyses, as it was later discovered to be exposed to direct morning sunlight. The Sandford Park exposed ambient datalogger was instead used for all Sandford Park analyses, as it was positioned only 30 m west of the sheltered ambient datalogger. Each ambient datalogger was fixed to a tree approximately 4.5 m above the

ground, within solar radiation shields at the exposed sites (Figure 2.4). In the Schwegler 2F boxes, HOBO MX2201 dataloggers were attached to the lower portion of the wooden roosting board within the chamber (Figure 2.5). In the double-chamber Kent boxes, HOBO MX2201 dataloggers, or the external sensor of HOBO MX2302A dataloggers, were installed in a top corner of the chamber with sensors facing/on the side of the open roosting area (Figure 2.5). In the natural tree roost features, MX2201 or MX2302A sensors were inserted into the highest part of the roost feature accessible without compromising potential access by bats to the interior roost cavity. HOBO MX2301 and MX2301A dataloggers were used for both ambient and internal roost microclimate readings at Grand Canyon Cave. The ambient datalogger was located approximately 80 m north of the northern cave entrance, to minimise the impact of the cave's interior microclimate on the readings, and the logger installed approximately 1.5 m off the ground for accessibility. Two internal roost dataloggers were installed within the cave on the bottom and the top of an approximately 10.5 m tall pole, situated near bat guano deposits approximately 74 m into the cave from the northern entrance. The datalogger at the bottom of the pole was installed ~1 m from the cave floor. The internal cave height at the pole site was approximately 17 m.

Boxes with microclimate dataloggers were checked for occupation approximately fortnightly from installation in March–July until October 2025, excluding the month of August, while natural roost features were checked approximately monthly from March–October 2025. Additionally, boxes at the Sandford Park site were checked occasionally in December 2025 and January 2026. Grand Canyon Cave was not assessed for occupation, but fresh guano was observed near the location of the internal cave dataloggers throughout most of this period.

Figure 2.4 Ambient microclimate dataloggers within solar radiation shields. Image on right shows one installed next to Natural Roost 1.

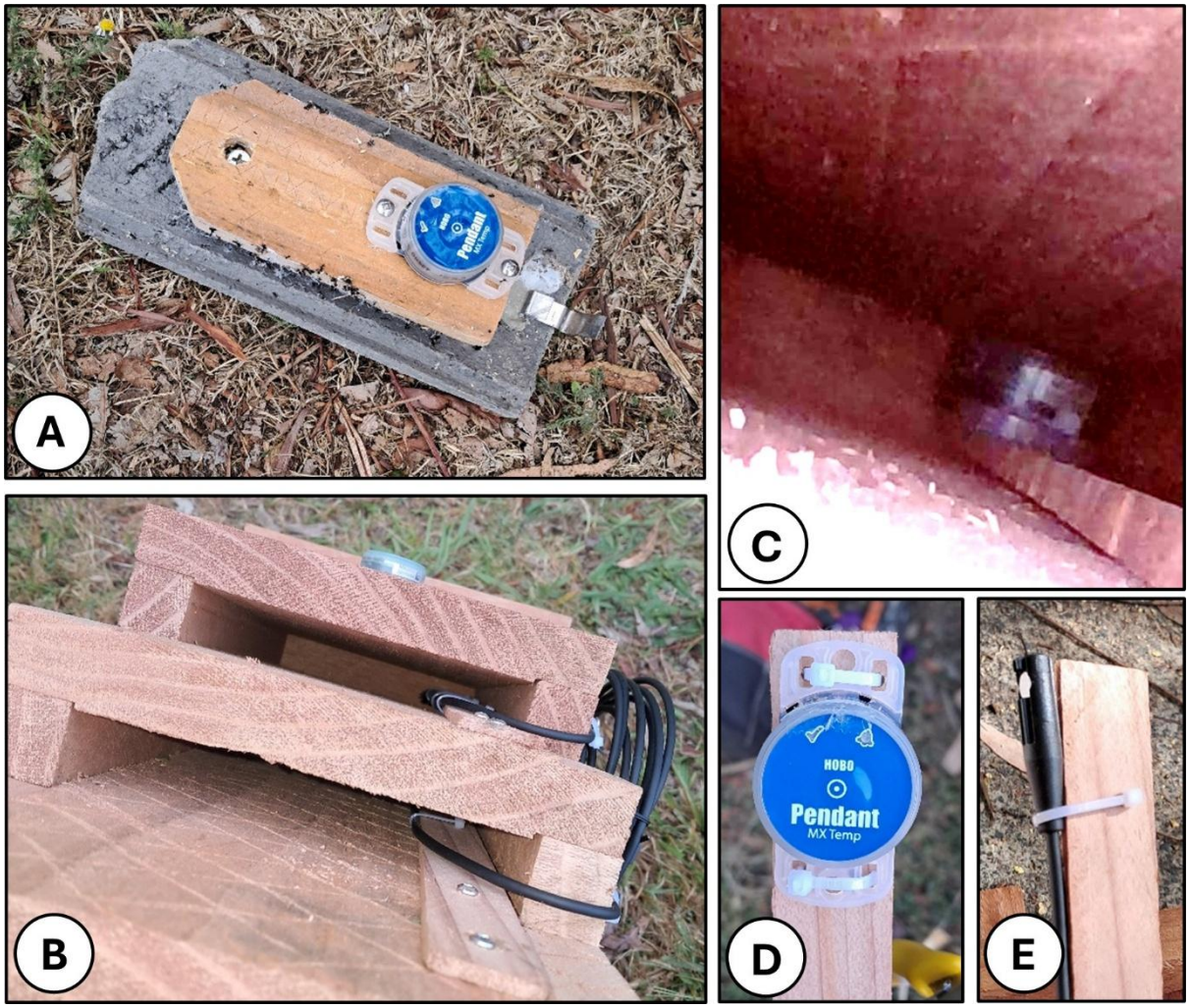

Figure 2.5 Microclimate dataloggers installed in bat boxes. A: A MX2201 logger on the wooden roosting plate attached to the internal face of a Schwegler 2F box, B: External sensors of MX2302A loggers on pieces of wood inserted into both chambers of a Kent bat box, C: A MX2201 logger installed within a Kent box, D: A MX2201 logger attached to a piece of wood prior to being inserted into a Kent box, E: The external sensor of a MX2302A logger attached to a piece of wood prior to insertion into a Kent box.

Occurrences and duration of overheating events in bat boxes were also recorded. Overheating was defined as any record of roost temperature exceeding 40 °C (Crawford & O'Keefe, 2021), with single records recorded as 15-minutes duration.

Statistical analyses of bat box occupation

Box occupation data were filtered to include only the dual-chamber Kent and modified Kent style boxes, as other styles were too dissimilar in chamber number/orientation for the comparison (e.g., Schwegler 2F, triple-chamber Kent boxes) and sample size was too small for statistical comparison.

Generalised linear mixed models (GLMM) with binomial distributions were used to assess the effects of exposure category (sheltered versus exposed) on box occupation and chamber occupation (inner versus outer). Models were fitted using the lme4 package (Bates et al., 2015) with R programming language (version 4.3.2) (R Core Team, 2023). Date and box ID (nested within site) were set as random effects for both models. Both models were assessed for multicollinearity (VIF <3 where applicable) and overdispersion ($P > 0.05$), and residuals assessed for heteroscedasticity and for conformation to model distribution assumptions.

Statistical analyses of bat roost microclimate and occupation

Daily maximum, mean, and range for temperature and relative humidity, along with the daily rate of temperature change, were derived from the differences between the internal roost loggers and ambient loggers. Derived values were used to facilitate direct comparisons between sites and exposures. No statistical analyses were conducted for Schwegler box data as only two of these boxes were measured.

A one-way ANOVA and Tukey HSD post-hoc tests were used to compare differences in temperature variables between sheltered natural tree roosts and Kent boxes. Sheltered Kent boxes were grouped by chamber. Exposed roost data were not used in these comparisons due to a lack of exposed natural tree roosts in the dataset (n = 1). Relative humidity variables were not tested as these sensors experienced saturation in the natural tree roosts (quickly reached 100 % relative humidity and did not deviate).

Generalised linear mixed models (GLMM, Student's t-distribution) were used to test for differences in temperature and relative humidity variables between inner and outer Kent box chambers, and between exposure categories (glmmTMB package [Brooks et al., 2017]). Roost ID (nested within site) and date were included as random effects. All models were assessed for multicollinearity (8> VIF >5 for the interaction term in some models) and overdispersion ($P < 0.05$), and residuals assessed for heteroscedasticity and for conformation to model distribution assumptions. Post-hoc analyses of estimated marginal means values were conducted using the emmeans package (Lenth, 2024).

A paired t-test was used to test for differences in the temperature and relative humidity variables between the top and bottom of Grand Canyon Cave.

Microclimate as a predictor of box occupation

To assess the effect of microclimate on the likelihood of Kent box occupation, a GLMM using a binomial distribution was fitted using the lme4 package. Daily mean temperature and daily temperature range were set as fixed effects, with box ID (nested within site) set as a random effect. Relative humidity variables were not included due to the small sample size (Table 2.2). Date was initially included as a random effect but explained zero variance so was omitted from the final model. Daily maximum temperature and daily rate of temperature change were not included in the model as they were highly correlated with each other and with daily temperature range (Pearson correlation coefficient >0.7) and considered to be less indicative of microclimate conditions than daily mean temperature and daily temperature range. The model was assessed for multicollinearity (VIF <2) and overdispersion ($P < 0.05$), and residuals assessed for heteroscedasticity and for conformation to model distribution assumptions.

Chapter Three: Occupation of Bat Boxes by Long-Tailed Bats (*Chalinolobus tuberculatus*) in Hamilton City

Twenty-nine (63 %) of the 46 monitored bat boxes were used by one or more *Chalinolobus tuberculatus* at least once during the monitoring period. The Schwegler 2F boxes were never observed occupied and thick cobwebs suggested they were not in use, nor was there evidence of historic occupation (e.g., guano, staining). During the study period, 18 boxes were exclusively observed with solo-roosting bats, while three boxes were observed with only communal roosting (one being a maternity roost), with the remaining eight boxes observed occupied communally or by solo bats. Communal roosting behaviour was only observed in boxes at Sandford Park, Peacockes Reserve Esplanade, and Te Anau Park.

Seven of the 10 new boxes installed during this study were observed to be occupied within ≤7 months, with the mean time to uptake of these boxes being approximately four and a half months (136 days). The lowest observed time to uptake was about three months (94 days) (box U10 at Sandford Park). All observed first occupations were by solo-roosting bats.

Box occupation frequency

Across the 46 monitored bat boxes, mean observed occupation per box was 17 % [95 % CI: 15 %, 20 %]. Boxes occupied at least once had a mean observed occupation of 27 % [95 % CI: 24 %, 32 %] (n = 29 boxes). The minimum observed occupancy rate was 5 % (n = 20 checks) at box BB42, Sandford Park, and the maximum was 89 % (n = 9 checks) at box BB20, Te Anau Park.

Mean occupancy for sheltered bat boxes was 22 % [95 % CI: 19 %, 28 %] (n = 27 boxes), compared to 10 % [95 % CI: 9 %, 16 %] (n = 19 boxes) for exposed boxes. The maximum observed occupancy rate for sheltered boxes was 89 % (box BB20 at Te Anau Park, n = 9 checks), compared to 50 % for exposed boxes (box BB08 at Resthills Reserve, n = 14 checks). Exposure was a significant factor for the likelihood of a bat box being occupied (GLMM, $P < 0.05$), with occupancy being more likely in a sheltered box (Figure 3.1). Detailed occupation data for individual boxes is provided in Appendix A, Table A.1.

Chamber occupation frequency

Of the occupied double-chamber Kent boxes (n = 29), the mean occupancy of the outer chamber was 32 % [95 % CI: 29 %, 42 %], while the mean occupancy of the inner chamber was 60 % [95 % CI: 56 %, 69 %]. There was no significant difference in the likelihood of one chamber being occupied over the other (GLMM, $P > 0.05$), nor did box exposure significantly alter this likelihood (GLMM, $P > 0.05$) (Figure 3.1).

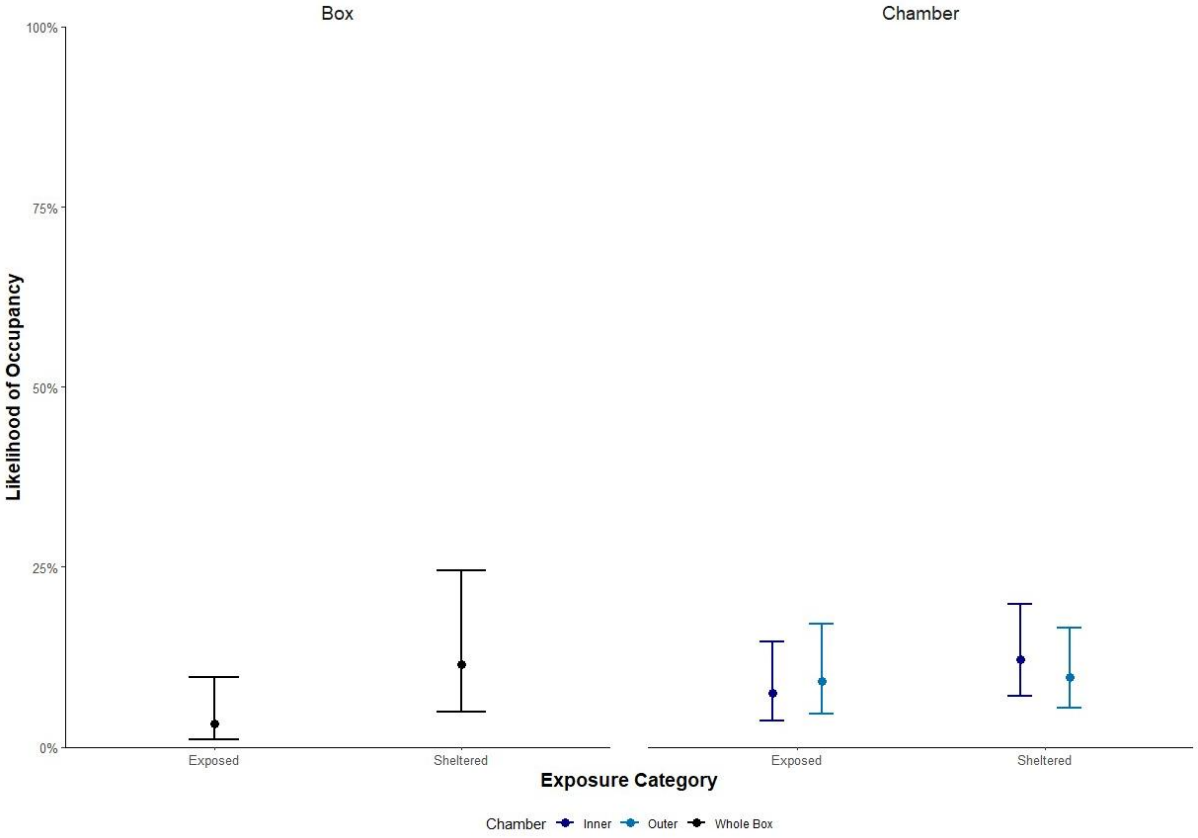

Figure 3.1 Effects plots of GLMM results assessing the main effects of box and chamber, and the interaction between chamber and exposure category, on the likelihood of bat box occupancy (exposure category: P < *0.05, chamber:* P > *0.05, chamber × exposure category:* P > *0.05). Points show predicted probability and bars indicate 95 % confidence intervals.*

The two triple-chamber Kent boxes at Sandford Park (boxes 14 and 15) were excluded from the chamber occupation analyses, but had comparatively high rates of box occupation (occupied on 86 % and 67 % of survey dates, respectively). The inner chamber of each box was the most commonly occupied, 91 % (box 14) and 88 % (box 15). The middle chambers were occupied 73 % and 67 % of the time, respectively. The outer chamber was occupied 45 % (box 14) and 13 % (box 15) of the time.

Sandford Park maternity roost watches

Up to three banded bats were occasionally observed in the known maternity roosts at Sandford Park (boxes 14 and 15), along with pups in box 14. In December 2024, there were approximately 12 pups and 26 adults present. Pups were also observed in this box in February (two pups, 38 adults) and March 2025. On the 11th of March, there were 31 adults and three older pups (one pup likely un-weaned, and all stayed in the roost after the adults had left so were assumed non-volant). On the 18th of March, there was a single adult with an older pup (likely un-weaned and it remained in the roost after the adult had left).

Natural roost occupation monitoring results

Active use of natural roosts by *C. tuberculatus* was not observed during roost emergence monitoring; however, bats were observed commuting/foraging at these sites. At the Franklin site, bats were filmed flying near and landing at the entrance of Natural Roost 4 in November 2025, but no bats entered/emerged from the roost (Figure 3.2).

Figure 3.2 One of multiple instances where Chalinolobus tuberculatus *were observed briefly landing at the entrance to Natural Roost 4 without entering. The cable of the HOBO MX2302A datalogger is visible on the left and extending into the roost. Captured 21 Nov 2025 with a Reflex infrared camera (Reflex Cameras, United Kingdom).*

Chapter Four: Bat Roost Microclimate in the Waikato Region

Microclimate stability

To determine the microclimate conditions in bat boxes and natural roosts in the Waikato region, summary statistics for temperature and relative humidity were calculated. Across all seasons, the range of absolute temperatures recorded in natural roosts (~2–27 °C) indicated that they were generally more thermally stable than both the Kent (~-2.5–46 °C) and the Schwegler (~-0.4–34 °C) bat boxes (Figure 4.1). At exposed sites, the difference was especially noticeable in the Kent boxes, which experienced greater maximum thermal fluctuations than ambient conditions (exposed Kent range: ~-2.5–46 °C vs exposed ambient range: ~-2.5–32 °C). The difference in thermal stability between the Kent boxes and the natural roosts was less pronounced at sheltered sites (sheltered Kent range: ~-1–37 °C vs sheltered natural roost range: ~2–27 °C). The Schwegler boxes were more thermally stable (range: ~-0.4–33 °C) than the Kent boxes (range: ~-2.5–46 °C) at both exposed and sheltered sites. The interior of Grand Canyon Cave was more thermally stable than ambient conditions (ambient: ~-2–28 °C), and this was especially the case towards the top of the cave (top: ~4–20°C vs bottom: ~0.3–20 °C), which was also generally warmer than the bottom of the cave (top median: ~12 °C vs bottom: ~11 °C). Seasonal temperature plots are provided in Appendix B, Figure B.1.

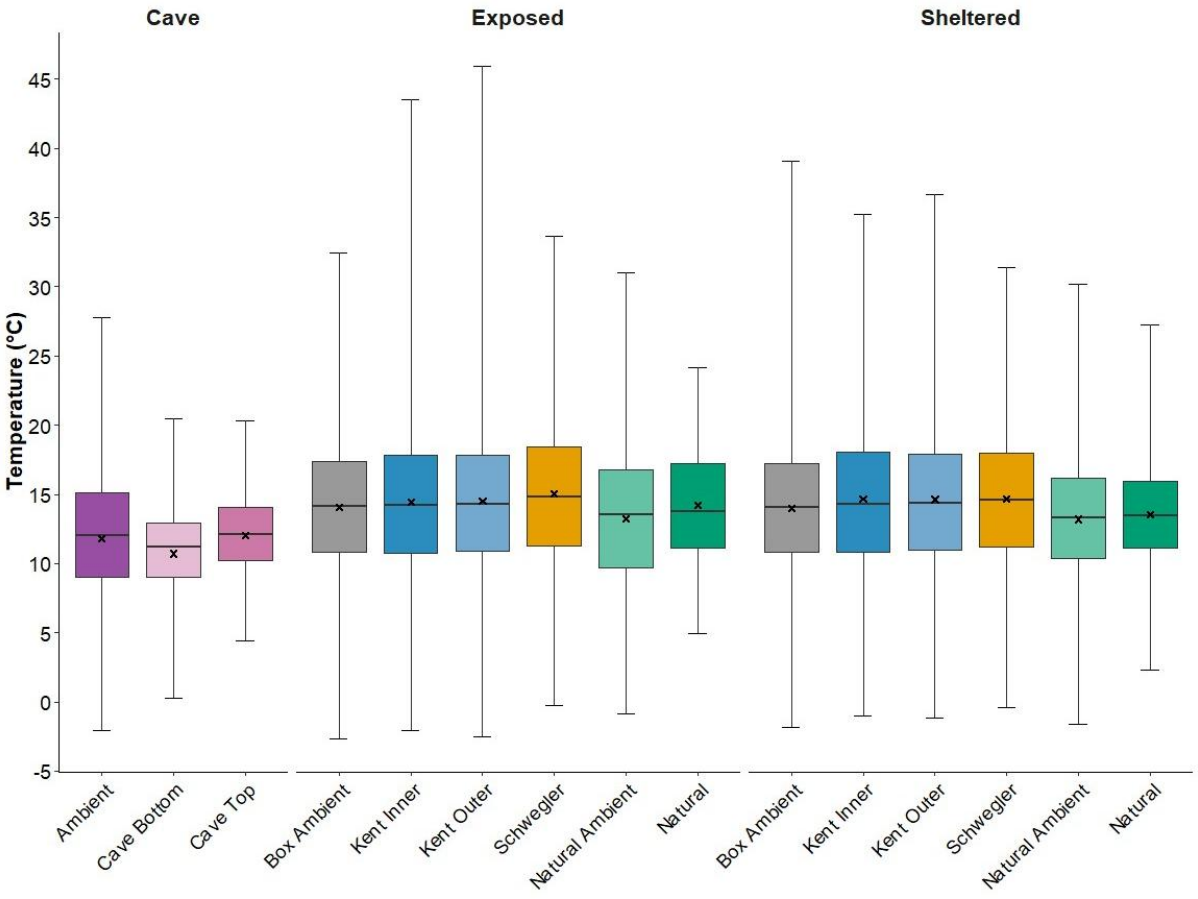

Figure 4.1 Boxplots of temperatures measured in bat boxes, natural roost features, Grand Canyon Cave, and corresponding ambient conditions. Shaded boxes show interquartile range, the thick horizontal line indicates median, the cross is the mean, whiskers indicate maximum and minimum values.

Relative humidity at both sheltered and exposed sites was generally higher than ambient in both chambers of the Kent boxes (5–12 % difference in medians), although the inner chamber was typically more stable than the outer chamber (inner sheltered: 50–100 %, inner exposed: 42–100 % vs outer sheltered: 46–100 %, exposed: 36–100 %), and both chambers at sheltered sites were more stable than those at exposed sites (Figure 4.2). Additionally, the inner chamber experienced higher relative humidity than the outer chamber at exposed sites (inner median: 85 % vs outer: 80 %), but lower at sheltered sites (inner median: 86 % vs outer: 88 %), despite ambient relative humidity being similar at both sites (sheltered median: 76 % vs exposed median: 74 %). Within Grand Canyon Cave, relative humidity was more stable than ambient conditions (ambient range: 34–83 %, median: 78 %) but was generally higher at the bottom of the cave (bottom range: 55–87 %, median: 84 % vs top range: 57–83 %, median: 77 %). Seasonal relative humidity plots are provided in Appendix B, Figure B.2.

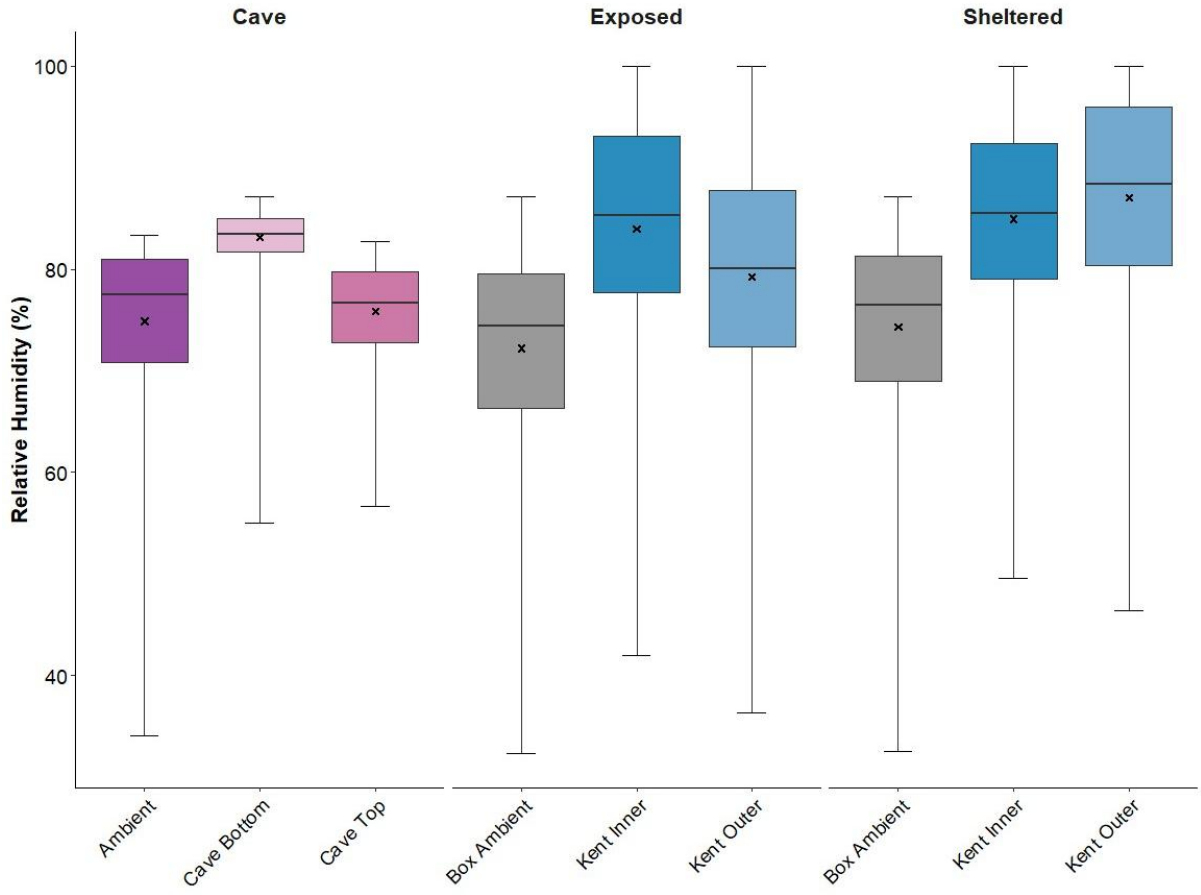

Figure 4.2 Boxplots of relative humidity measured in Kent boxes, Grand Canyon Cave, and corresponding ambient conditions. Shaded boxes show interquartile range, the thick horizontal line indicates median, the cross is the mean, whiskers indicate maximum and minimum values.

Daily microclimate profiles

The mean daily range of roost temperature and relative humidity conditions in bat boxes and natural roosts over a 24-hour period were assessed. The internal microclimate conditions of Kent boxes varied in response to ambient fluctuations depending on exposure and season. Across all seasons, sheltered Kent boxes were approximately 1 °C warmer than ambient at night, up to 0.5 °C cooler than ambient in the mornings, and up to 0.5 °C warmer than ambient in the afternoons – although in summer these warmer temperatures were maintained throughout the entire day, with temperatures between 0.2–2 °C warmer than ambient. Exposed Kent boxes were up to 1 °C cooler than ambient in the morning, and up to 2 °C warmer than ambient in the afternoon, with night temperatures 0.6 °C warmer than ambient (Figure 4.3). The two Schwegler 2F boxes maintained internal temperatures ~0.4–1.5 °C higher than ambient, although the exposed box experienced up to 1 °C greater warming than the sheltered box, and the severity and timing of temperature peaks depended on season with

spring and summer producing approximately three-hour earlier peaks 2 °C warmer than other seasons. In a similar pattern to the sheltered Kent boxes, the natural tree roosts were warmer than ambient at night and cooler during the day, but the magnitude of difference was greater in the natural roosts – typically being 2–4 °C warmer than ambient at night and 1–2 °C cooler than ambient during the day, compared with the approximately -0.5–2 °C difference from ambient observed in the Kent boxes. The top of Grand Canyon Cave (closer to where bats would roost) followed a very similar pattern to the natural tree roosts. Where the boxes generally warmed above, or were close to, ambient conditions during the day, the cave and natural roosts remained cooler, and they were more insulated from ambient fluctuations at night. Typically, the top of the cave was approximately 1.6 °C warmer than ambient at night and 1.2 °C cooler during the day.

Rate of temperature change within the Kent boxes was similar to ambient, especially in the sheltered Kent boxes (sheltered: mean derived difference -0.01–0.01 °C/15-minutes, exposed: -0.04–0.04 °C/15-min); although there was more diel variation during the summer (sheltered Kent summer range: -0.37–0.3 °C/15-min vs typical range: -0.16–0.15 °C/15-min; exposed Kent summer range: -0.3–0.7 °C/15-min vs typical range: -0.16–0.3 °C/15-min) and temperature changes were generally slower than ambient in the morning (derived difference -0.16 °C/15-min) and faster in the mid-afternoon (derived difference 0.15 °C/15-min) (Figure 4.4). The rate of temperature change in the Schwegler boxes was also similar to ambient changes (derived difference typically -0.01–0.01 °C/15-min), but warming was faster in the mornings than for other roost types (derived difference 0.26 °C/15-min), and was more variable in spring and summer (derived range difference up to -0.9–1.5 °C/15-min). In natural tree roosts, temperature changes were generally slower than ambient in the morning (derived difference -0.3 °C/15-min), and faster in the evening (derived difference 0.31 °C/15-min) – although this pattern was more pronounced in summer. At the top of Grand Canyon cave, the rate of temperature change was similar to ambient (mean derived difference -0.05–0.05 °C/15-min), although more variable in summer (derived difference summer range: -0.34–0.47 °C/15-min vs all data range: -0.28–0.35 °C/15-min).

Relative humidity of Kent boxes was generally maintained above ambient throughout a 24-hour period (2–16 % above ambient); although in summer, exposed boxes experienced relative humidity below ambient at night (4 % below) (Figure 4.5). Additionally, measurements were comparatively higher than ambient during daytime hours (9–16 % above ambient), while at night they were much closer to ambient (2–9 % above). At the top of

Grand Canyon Cave, relative humidity was 4 % higher than ambient during the day, and 2 % lower at night. However, in spring and summer the lower relative humidity only occurred for a brief time (three hours) in the early morning, and the higher relative humidity occurred for longer and was more pronounced throughout the whole day. Similar to the Kent boxes, relative humidity was higher than ambient in the afternoons (up to 13 % higher).

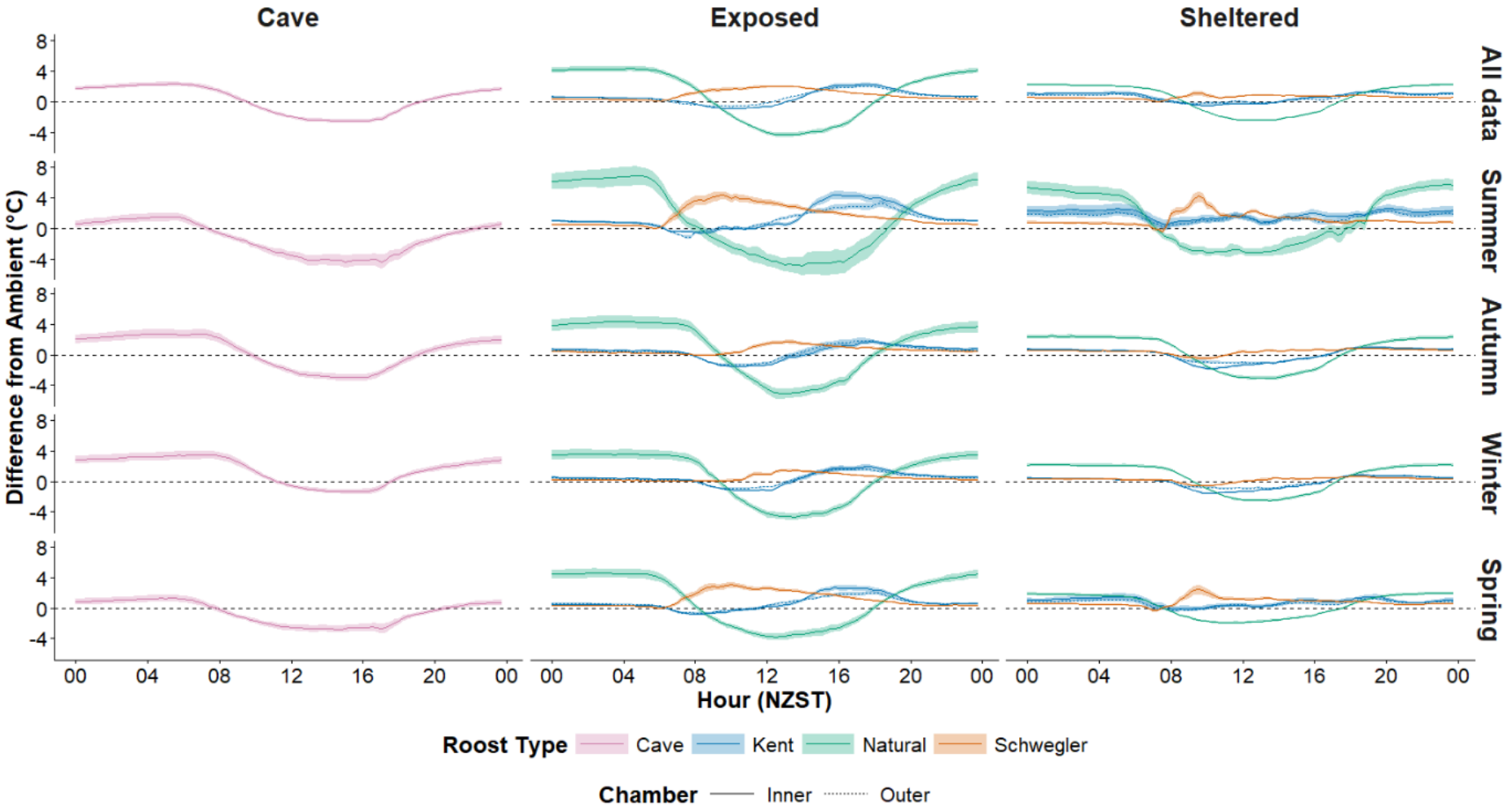

Figure 4.3 Derived daily mean temperatures, separated by exposure category and data collection period/season. Line colours indicative of the mean conditions recorded in the type of bat roost measured, with Kent boxes separated into inner and outer chambers. Cave data reflect conditions recorded by the logger near the top of the cave. Shading indicates 95 % confidence intervals. Mean ambient temperatures are indicated by the dotted lines at y = 0.

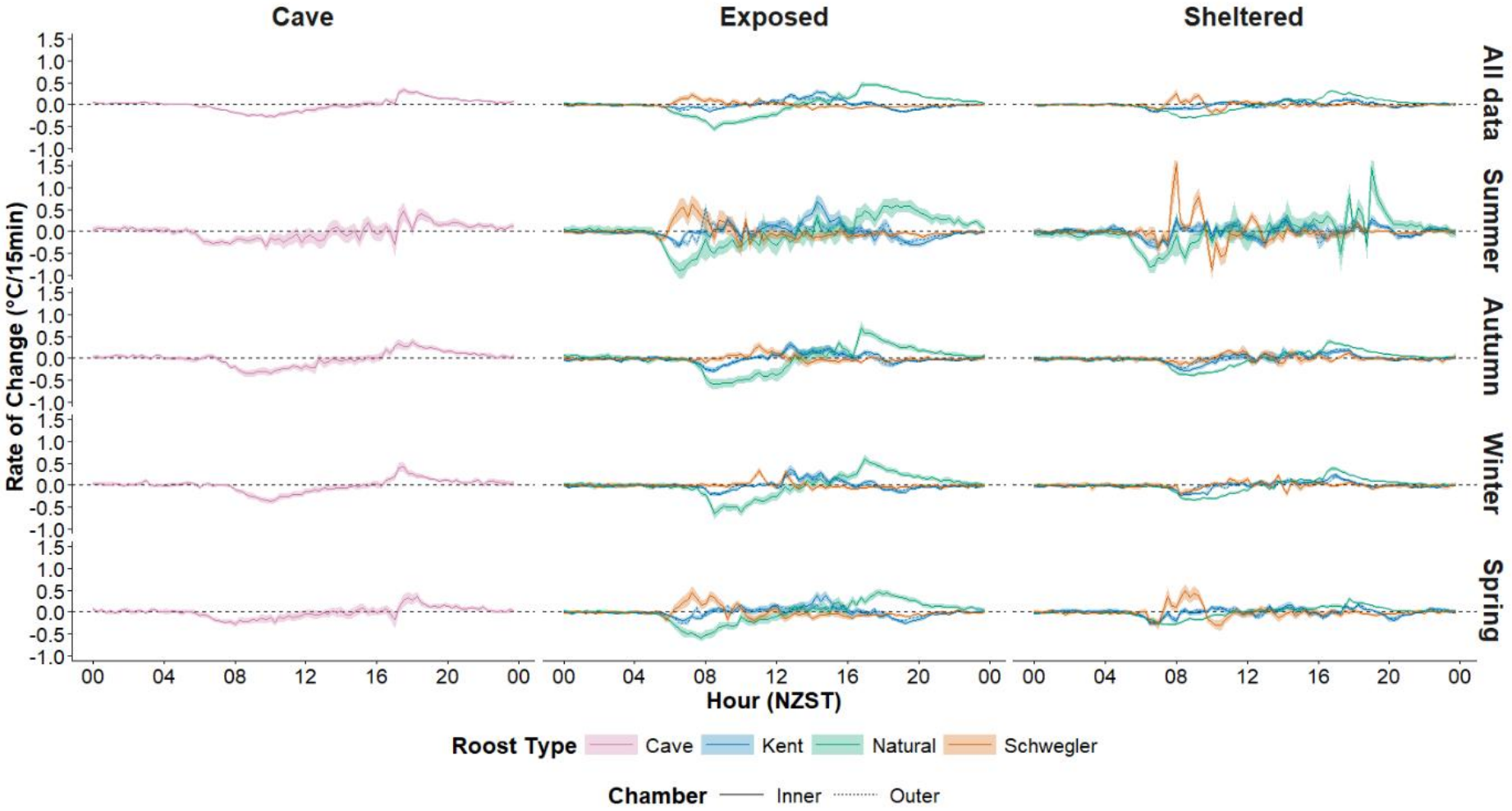

Figure 4.4 Derived daily mean temperature rate of change, separated by exposure category and data collection period/season. Line colours indicative of the mean conditions recorded in the type of bat roost measured, with Kent boxes separated into inner and outer chambers. Cave data reflect conditions recorded by the logger near the top of the cave. Shading indicates 95 % confidence intervals. Mean ambient temperatures are indicated by the dotted lines at y = 0.

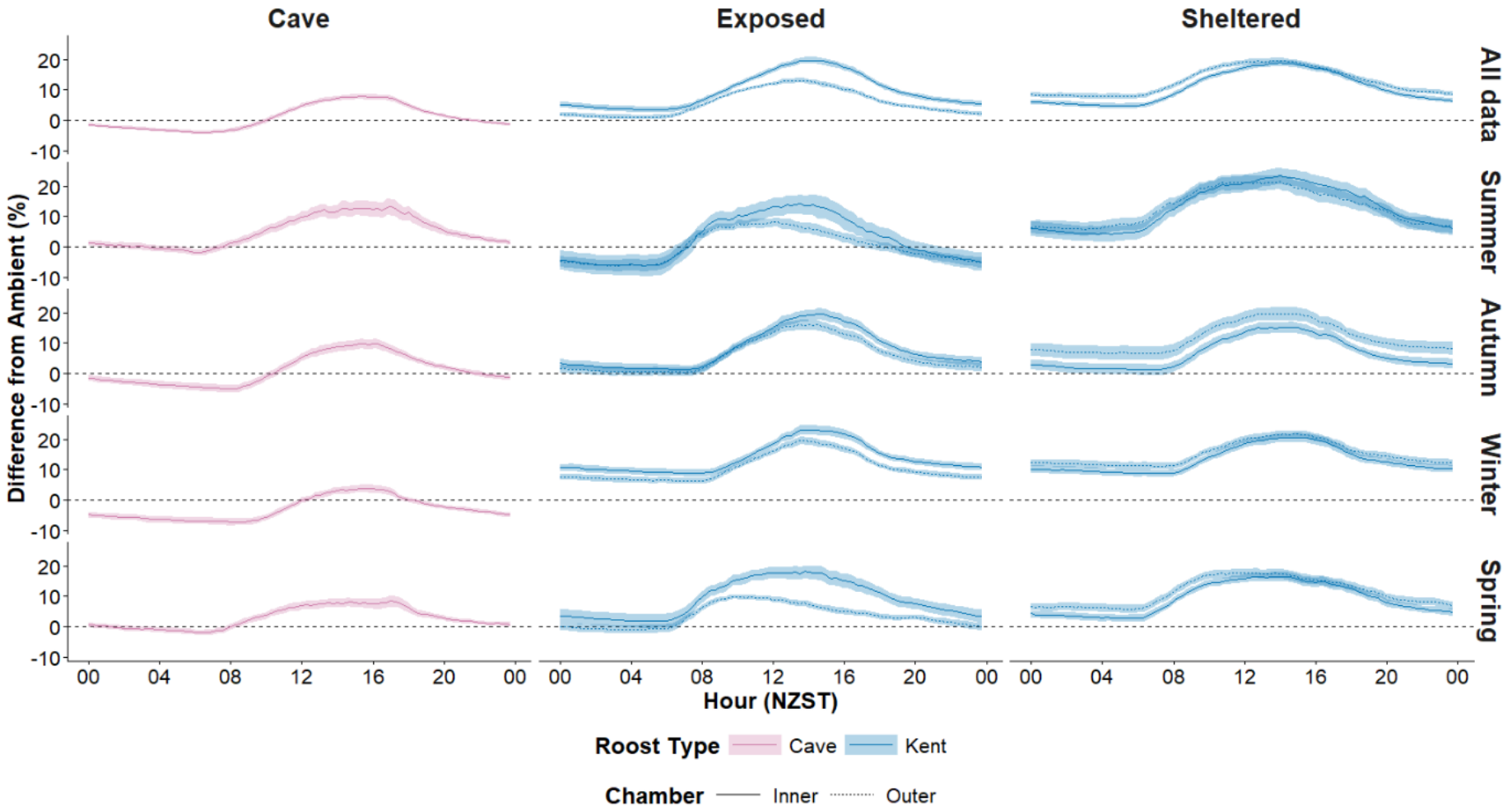

Figure 4.5 Derived daily mean relative humidity, separated by exposure category and data collection period/season. Line colours indicative of the mean conditions recorded in the type of bat roost measured, with Kent boxes separated into inner and outer chambers. Cave data reflect conditions recorded by the logger near the top of the cave. Shading indicates 95 % confidence intervals. Mean ambient relative humidity is indicated by the dotted lines at y = 0.

Natural roosts versus Kent boxes

To assess the difference between microclimate conditions of natural roosts and bat boxes, derived daily temperature variables of sheltered roosts were compared. Sheltered natural tree roost cavities had significantly lower derived daily temperature maximums, ranges, and rates of change than both the inner and outer chambers of Kent boxes (one-way ANOVA, $P < 0.001$) (Figure 4.6). The derived daily temperature means were significantly higher in the sheltered natural tree roosts than in both the inner and outer chambers of Kent boxes. The post-hoc table from the ANOVA is provided in Appendix B, Table B.1.

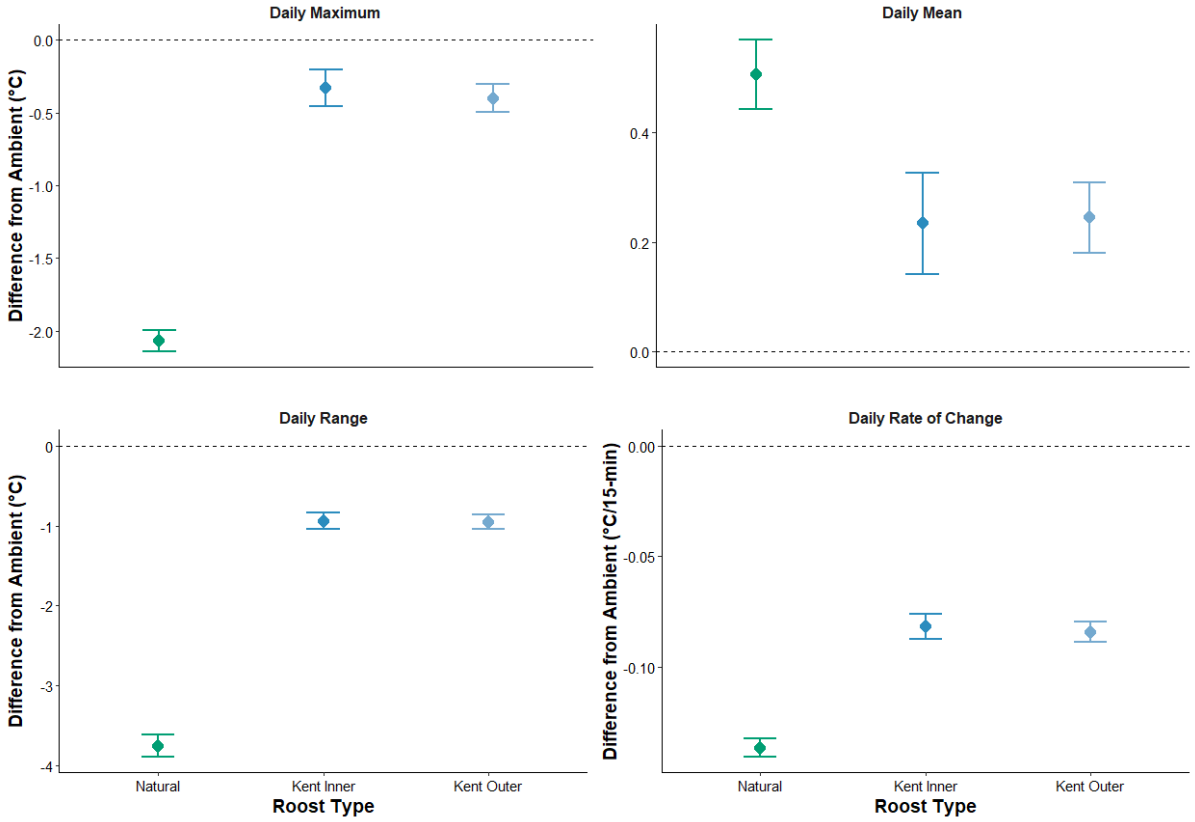

Figure 4.6 Mean derived daily temperature variables and 95 % confidence intervals of sheltered natural roosts and the outer and inner chambers of sheltered Kent boxes. Ambient conditions represented by black dashed lines at y = 0. All differences between natural roosts and Kent boxes were significant (one-way ANOVA, P < *0.001).*

Effect of chamber on Kent box microclimate

GLMMs were fitted to determine the potential microclimate conditions experienced by *C. tuberculatus* roosting in Kent boxes in Hamilton City, in relation to chamber and season. Overall, the derived daily temperature maximums, ranges, and rates of change were significantly lower in the inner chamber compared to the outer chamber of Kent boxes, while

the derived daily temperature means were significantly higher in the inner chamber than in the outer chamber (GLMM, $P < 0.05$) (Table 4.1). However, these differences did vary seasonally. In summer, the derived daily temperature maximums were significantly warmer in the inner chamber than the outer chamber (GLMM, $P < 0.05$), while differences in the derived daily rate of temperature change were not significant (GLMM, $P > 0.05$) (Table 4.1). The difference in derived daily mean temperatures of the inner chamber compared to the outer chamber was not significant in autumn and winter (GLMM, $P > 0.05$) (Table 4.1).

Derived daily relative humidity maximums and ranges of the inner chambers were significantly lower than the outer chambers (GLMM, $P < 0.01$) (Table 4.1).

Table 4.1 Results of the Generalised Linear Mixed Models (GLMM) and post-hoc tests assessing the effect of chamber on derived daily temperature and relative humidity variables, and the interaction with season, in Kent bat boxes. Negative estimated difference values reflect lower inner chamber values in relation to outer chambers.

Measurement	Season	Derived daily variable	Estimated difference (inner vs outer chambers) ± std. dev.	*P*-value
Temperature	Autumn	Maximum	-0.14 ± 0.06 °C	< 0.05
		Mean	n.s.	n.s.
		Range	-0.33 ± 0.08 °C	< 0.001
		Rate of change	-0.01 ± 0.003 °C/15-minutes	< 0.001
	Winter	Maximum	-0.29 ± 0.05 °C	< 0.001
		Mean	n.s.	n.s.
		Range	-0.52 ± 0.06 °C	< 0.001
		Rate of change	-0.02 ± 0.002 °C/15-minutes	< 0.001
	Spring	Maximum	-0.22 ± 0.06 °C	< 0.001
		Mean	0.05 ± 0.02 °C	< 0.05
		Range	-0.36 ± 0.07 °C	< 0.001
		Rate of change	-0.01 ± 0.002 °C/15-minutes	< 0.001
	Summer	Maximum	0.27 ± 0.12 °C	< 0.05
		Mean	0.27 ± 0.04 °C	< 0.001
		Range	n.s.	n.s.
		Rate of change	n.s.	n.s.
	Whole dataset	Maximum	-0.1 ± 0.04 °C	< 0.05
		Mean	0.08 ± 0.01 °C	< 0.001
		Range	-0.3 ± 0.05 °C	< 0.001
		Rate of change	-0.01 ± 0.001 °C/15-minutes	< 0.001
Relative humidity	NA	Maximum	-0.75 ± 0.21 %	< 0.001
		Mean	n.s.	n.s.
		Range	-2.94 ± 0.2 %	< 0.001

Effect of exposure on Kent box microclimate

GLMMs were also fitted to determine the effect of exposure on the microclimate conditions experienced by *C. tuberculatus* roosting in Kent boxes in Hamilton City. Exposed Kent boxes had significantly higher derived daily temperature maximums, means, ranges, and rates of change than sheltered Kent boxes (GLMM, $P < 0.05$) (Table 4.2). Exposed boxes also had significantly lower derived daily relative humidity maximums than sheltered boxes (GLMM, $P < 0.05$), but all other results were not significant (GLMM, $P > 0.05$) (Table 4.2).

Table 4.2 Results of the Generalised Linear Mixed Models (GLMM) and post-hoc tests assessing the effect of exposure on derived daily temperature and relative humidity variables in Kent bat boxes. Negative estimated difference values reflect lower exposed box values in relation to sheltered boxes.

Measurement	Derived daily variable	Estimated difference (exposed vs sheltered Kent boxes) ± std. dev.	*P*-value
Temperature	Maximum	0.97 ± 0.27 °C	< 0.01
	Mean	0.33 ± 0.07 °C	< 0.01
	Range	0.86 ± 0.43 °C	< 0.05
	Rate of change	0.02 ± 0.008 °C/15-minutes	< 0.01
Relative humidity	Maximum	-2.88 ± 1.25 %	< 0.05
	Mean	n.s.	n.s.
	Range	n.s.	n.s.

Microclimate stratification at Grand Canyon Cave

To provide context regarding the microclimate conditions available to *C. tuberculatus* occupying a cave roost site, derived daily temperature and relative humidity variables were assessed. The top of the cave had significantly higher derived daily temperature maximums, means, and lower ranges, rates of change, daily relative humidity maximums, means, and ranges compared to the bottom of the cave (paired t-test, $P < 0.01$) (Figure 4.7, Figure 4.8). The paired t-test table is provided in Appendix B, Table B.2.

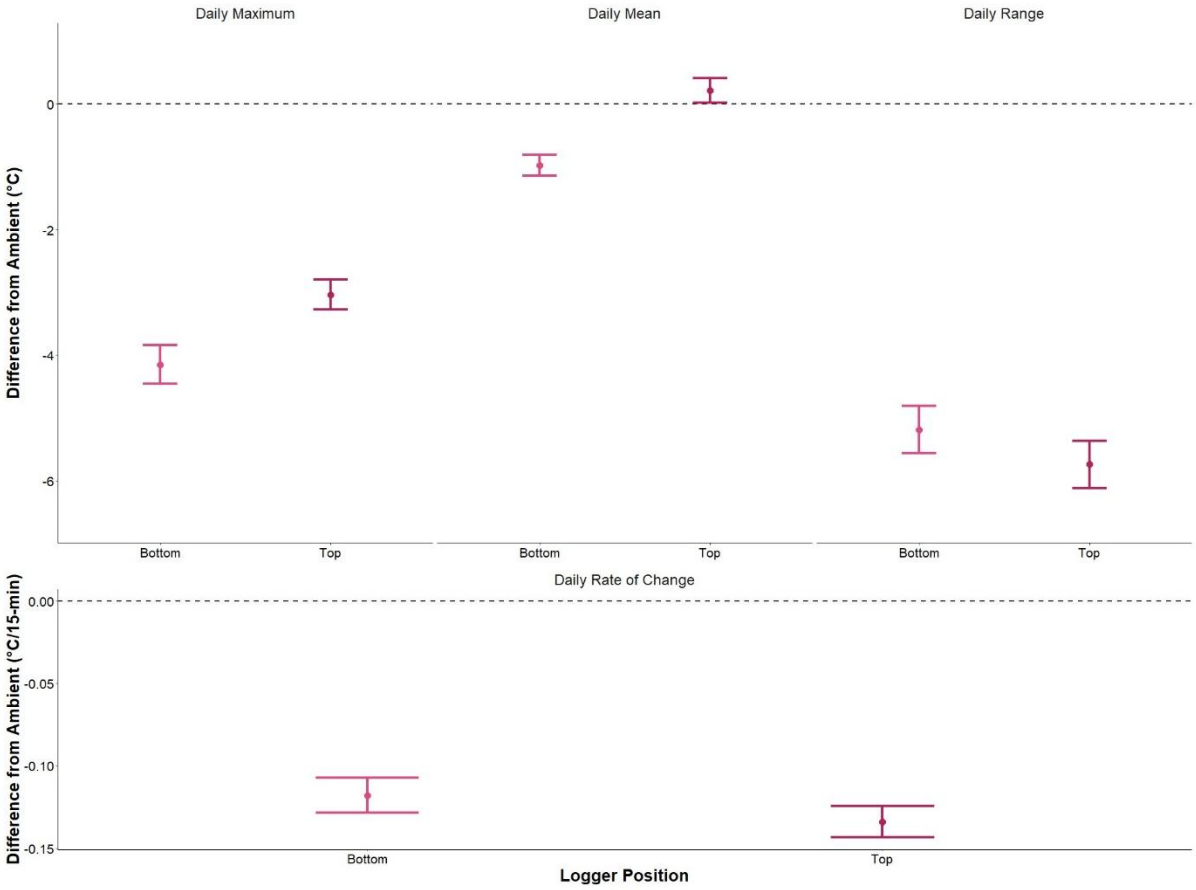

*Figure 4.7 Mean derived daily temperature variables and 95 % confidence intervals of both loggers within Grand Canyon Cave. Ambient conditions represented by black dashed lines at y = 0. All differences were significant (*P < *0.01).*

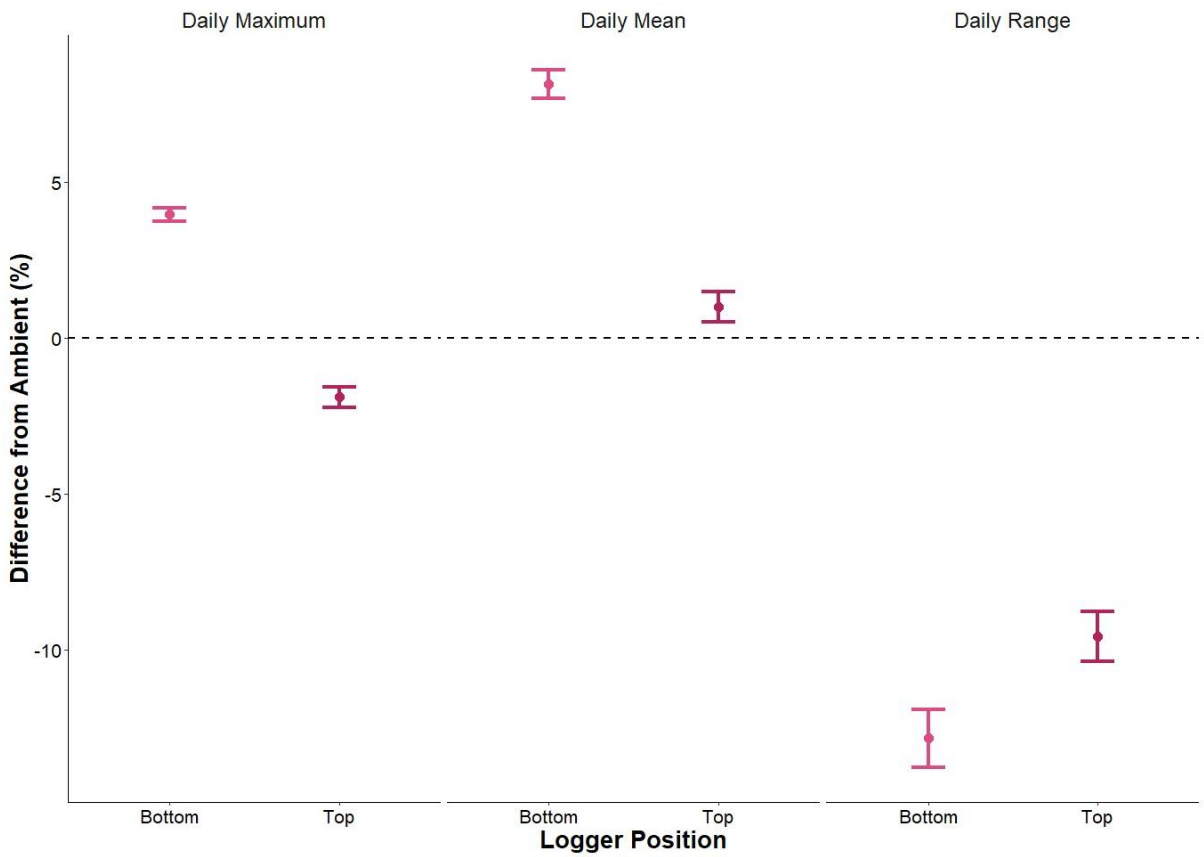

*Figure 4.8 Mean derived daily relative humidity variables and 95 % confidence intervals of both loggers within Grand Canyon Cave. Ambient conditions represented by black dashed lines at y = 0. All differences were significant (*P < *0.01).*

Detailed information regarding sample sizes used for all above microclimate analyses are provided in Appendix A, Table A.2.

Box overheating events

Data were assessed for potential overheating (>40 °C) events within all roost types. Two exposed Kent boxes were recorded overheating: box U1 at Resthills Reserve (outer chamber only), and box U5 at Te Anau Park (both chambers). No natural tree, cave, or Schwegler box roosts experienced overheating events, and there were no ambient temperatures recorded above the overheating threshold. The roost overheating events occurred on the 8th, 9th, 10th, and 14th of December 2025, and high (>40 °C) temperatures lasted between 0.25–4 hours. These events began between 14:45–16:45 NZST and roost chambers had cooled below the threshold by between 17:00–18:30 NZST. It should be noted that, in December, local time is NZDT i.e., one hour later than NZST.

Microclimate of occupied bat boxes

To determine the effect of Kent box microclimate on occupation by *C. tuberculatus*, a GLMM was fitted using derived daily temperature variables. Derived daily temperature mean and range were not significant predictors of Kent box occupation (GLMM, $P > 0.05$) (Figure 4.9). Detailed information regarding sample sizes used for these analyses are provided in Appendix A, Table A.3.

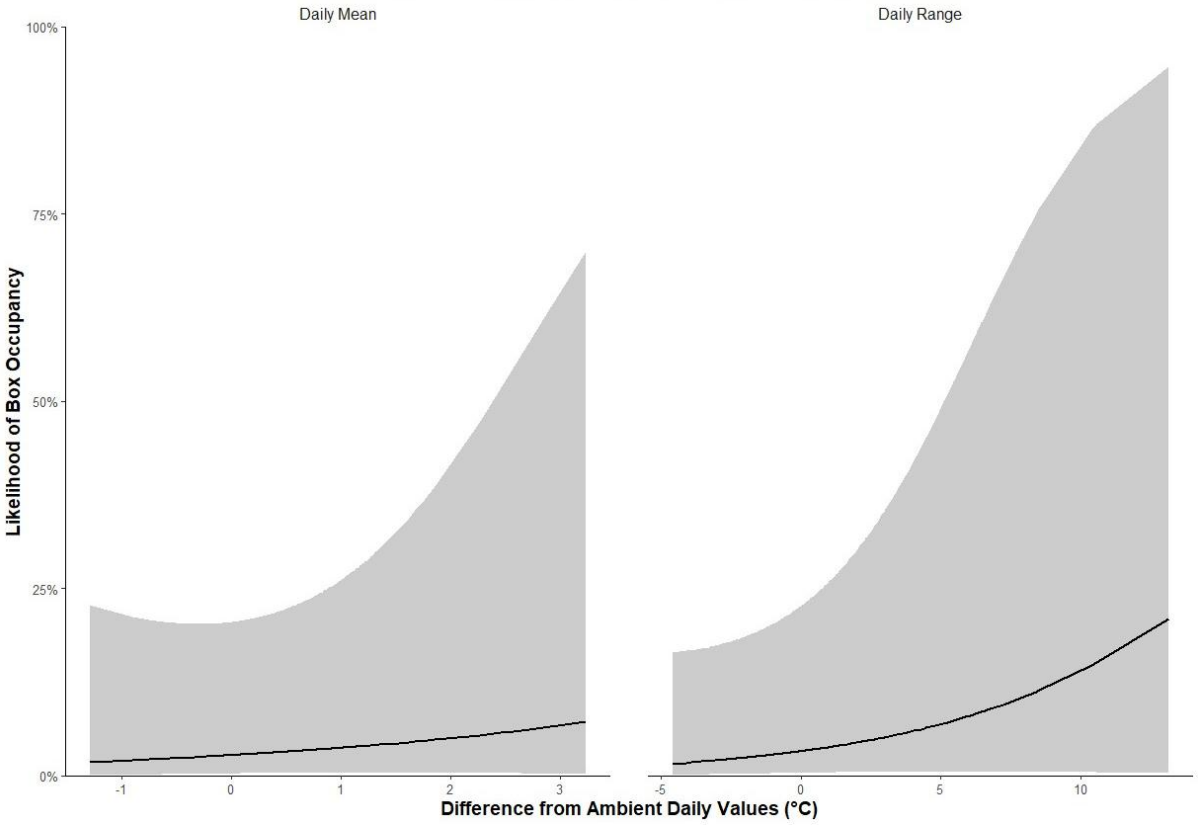

*Figure 4.9 Effects plot of GLMM results assessing the main effects of derived daily mean temperature and range on the likelihood of occupation of Kent boxes (*P *> 0.05). Ambient conditions x = 0.*

Chapter Five: Discussion

Land clearance has led to a reduction in available tree cavities for cavity-roosting animals such as bats (Eyre et al., 2010). In many parts of the world, bat boxes are used to mitigate such losses; however, their suitability is rarely assessed against species-specific roost requirements such as microclimate (Rueegger, 2016). In Hamilton City, bat boxes have been installed to mitigate losses of potential roosts due to urban expansion and roading development (Jonker et al., 2024; Robinson et al., 2023). However, the internal microclimates of these boxes have never been assessed. This research aimed to understand the microclimate conditions of bat boxes in Hamilton City by collecting temperature and relative humidity data from a selection of boxes. These data were then used to determine the effect of box chamber, season, and exposure on the internal conditions of the boxes. In addition, occupancy rates were assessed over a period of 8 months to determine the effect of box microclimate on occupation, along with the effect of box chamber and exposure. Microclimate data were also collected from natural roost sites to compare with box microclimates.

Box occupation

Comparison with previous local studies

The rate of box occupation observed in this study (63 %) was 24–31 % higher than the occupancy rates recorded in two previous studies of box occupation in Hamilton City (AECOM New Zealand Limited, 2022; Robinson et al., 2023), and higher than the 10 % occupancy rate of Schwegler bat boxes by *C. tuberculatus* recorded in south Canterbury by O'Donnell (2024). Although, the selection of boxes assessed in this study and by Robinson et al. (2023) were biased towards those with signs of use and/or previously confirmed occupation. AECOM New Zealand Limited (2022) reported an occupation rate of 39 % occupancy from the 80 Kent and Schwegler 2F boxes installed in the city since 2019, through one-off box checks via thermal imaging, endoscope surveys, and environmental DNA (eDNA).

The higher box occupation rates by *C. tuberculatus* observed in the current study may reflect a general increase in occupation since the studies by Robinson et al. (2023) and AECOM New Zealand Limited (2022) undertaken approximately four years ago. Increasing occupation rates over time have also been reported for bats in other studies (Agnelli et al., 2011). For example, Pschonny et al. (2022) determined that older boxes, and boxes in an area

with older boxes, had higher occupancy by *Myotis nattereri*, with modelling predicting one box type to increase in occupancy rate from ~5 % in the initial year following installation to ~40 % after nine years. Continued occupancy monitoring would determine whether this is the case in Hamilton City.

During this study there were no confirmed occupation events of the monitored natural tree roosts, although *C. tuberculatus* were confirmed to be present in the areas. This may be due to low roost fidelity and roost reuse of *C. tuberculatus* (O'Donnell & Sedgeley, 1999), coupled with infrequent (monthly) monitoring.

Effect of Kent box exposure and chamber on occupancy

Generalised linear mixed modelling indicated that, within the sample group, Kent boxes located in sheltered areas had a significantly higher chance of being occupied compared to those in exposed locations. This supported previous work by Robinson et al. (2023), who found that boxes further within a stand of trees or located in gullies had higher occupation rates than those in open locations, which the authors proposed was due to sheltered roosts providing more stable microclimates. Some overseas studies of bat box occupancy have shown exposed boxes to be preferred depending on season. For example, Kerth et al. (2001) found that *Myotis bechsteinii* favoured sheltered boxes during the pre-natal period but moved to exposed boxes after pups were weaned. This change was thought to occur due to exposed boxes being cooler at night and less suitable for the development of non-volant pups (Zahn, 1999). Additionally, Crawford et al. (2026) reported that *Myotis sodalis* favoured sheltered boxes in the cooler months, and exposed boxes in the warmer months. Therefore, it is possible that *C. tuberculatus* may at times favour exposed Kent boxes, but box monitoring in the current study largely occurred over autumn–winter and seasonal comparisons were not conducted.

Although there was an observed difference between the occupation rate of the outer Kent box chambers and the inner chambers (32 % vs 60 %), the effect of chamber on occupancy, when accounting for existing variation between individual boxes, sites, and dates, was not statistically significant.

Schwegler boxes

Results from this study supported previous findings of no confirmed use of the Schwegler bat boxes by *C. tuberculatus* in Hamilton City (AECOM New Zealand Limited, 2022). However, *C. tuberculatus* have been recorded using Schwegler 2F and similar woodcement box types in south Canterbury, where 10 % of boxes installed in forest and farmland were occupied (O'Donnell, 2024). Boxes made from woodcement are commonly used by bats in Europe but are undertested in the southern hemisphere (Rueegger, 2016). It is possible that *C. tuberculatus* occasionally occupy Schwegler boxes in Hamilton City, but the low number of boxes (10) and the challenges in determining occupation have resulted in infrequent occupation checks. In addition, Kent boxes have been present in the city since 2011, while Schwegler 2F boxes have been present since 2019. *Chalinolobus tuberculatus* were not found using the Kent boxes until seven years after installation, suggesting that box discovery may take some time, a notion supported by other studies which have found box age to be a significant predictor of occupancy (Agnelli et al., 2011; Pschonny et al., 2022). Although, signs of *C. tuberculatus* roosting in Schwegler bat boxes were confirmed within two years of installation by O'Donnell (2024) in south Canterbury, but in that study there were 72 Schwegler boxes of similar design installed in the area; the greater number of boxes may have facilitated more rapid discovery.

Incidence of communal and maternity roosting

Communal roosting behaviour was relatively uncommon, occurring in 38 % of the 29 occupied boxes and only at three of the six sites with box occupation (compared to solo roosting which was observed in 90 % of the 29 boxes, and at all six sites).

The use of bat boxes as maternity roosts is generally rare (Rueegger, 2016). In the current study, maternity roosting was only observed in one box at Sandford Park, confirming its ongoing use as a maternity roost (Robinson et al., 2023). A second Sandford Park box has previously been used as a maternity roost (Robinson et al., 2023), although no pups were observed in this box during the current study. Both boxes were part of the original 27 installed by Project Echo in 2011, and experience consistent occupation throughout most of the year, with numbers of >50 observed during the summer (this study; Robinson et al., 2023). It is uncertain why the two Sandford Park boxes have been consistently occupied. It is possibly the result of social learning as pups, with the boxes subsequently representing

familiar, secure roost sites outside the maternity season for young-of-the-year and non-breeding females. Mark-recapture and radio-tracking studies may assist in determining why the two Sandford Park boxes are used as maternity roosts, and if their consistent occupation is related to social learning.

Non-volant pups were observed in Box 14 in December 2024, again in February 2025, with the final observation occurring on 18 March 2025. This represents an extended breeding period compared to those previously reported for *C. tuberculatus*, as pups are typically born from mid-November to mid-December and fledge at about 5–6 weeks (i.e., typically by February) (O'Donnell et al., 2021). The existence of an extended breeding period should be considered when developing management protocols such as regarding roost tree felling, as non-volant pups are inherently more vulnerable to the clearance of roosts since they cannot fly without their mothers.

Rapid uptake of new boxes and a new box monitoring method

The period of 94 days from installation to first recorded box occupation was notably shorter than the 18 months previously recorded by Robinson et al. (2023) in Hamilton City, and an overall mean uptake time of 136 days for the seven new boxes which experienced occupation. Uptake times of less than five months have been reported for other bat species, and time to uptake decreases where bats are already familiar with the roost type (Rueegger, 2016). The comparatively rapid uptake of the newly installed boxes in this study was likely due to increasing familiarity with Kent boxes by the local *C. tuberculatus* population and the proximity of these boxes to regularly occupied ones. Additionally, observations of first occupations were likely due to the higher frequency of monitoring compared to previous studies.

The telescopic pole and endoscope camera used in this study for assessing box occupancy was highly effective, allowing >40 boxes across southern Hamilton to be assessed in approximately four hours, including both Kent and Schwegler boxes, the approximate number of bats, and which chambers were occupied. In comparison, methods such as roost emergence watches, thermal imaging cameras, tree-climbing endoscope surveys, and eDNA are relatively time-consuming, costly, and may not provide the same level of detail.

Roost microclimate

The microclimate conditions (temperature and relative humidity) of bat boxes were assessed and compared to both a cave roost and natural tree cavity roosts at daily to seasonal timescales. In addition, comparisons were made between Kent boxes in exposed and sheltered locations, between inner and outer Kent box chambers, and between Schwegler 2F and Kent bat box types.

Comparisons of box and natural tree cavity roost microclimates

Exposed Kent boxes exhibited the greatest fluctuations in temperature and relative humidity, especially the outer chamber (range: -2.5–46 °C, 36–100 %; median: 14 °C), while natural tree cavities were more thermally stable and experienced lower temperature maximums (range: 2–27 °C; median: 13 °C). Generalised linear mixed modelling indicated that sheltered Kent boxes, especially the inner chamber, were significantly more thermally stable than exposed Kent boxes (derived daily temperature range and rate of change were higher in exposed Kent boxes, and lower in the inner chambers). This aligns with findings by Sudyka et al. (2022) showing that natural tree cavities used by nesting birds were more thermally stable, insulated from external fluctuations, and had lower temperature maximums than wooden and woodcement artificial nest boxes. Additionally, tree cavities have been reported to be more thermally stable than Schwegler 2FN woodcement bat boxes, with exposed bat boxes less stable than sheltered ones (Kerth et al., 2001). Notably, solo-roosting male *Nyctophilus gouldi* bats may take advantage of thermally unstable roosts via passive rewarming as roosts heated in the afternoon, therefore reducing their energy expenditure (Turbill, 2006). However, thermally unstable roosts are unlikely to be preferred by female bats during maternity roosting, as they have been shown to generally select warmer, thermally stable roosts and do not undertake torpor as extensively, instead utilising social thermoregulation through communal roosting (Besler & Broders, 2019; Johnson & Lacki, 2013; Lausen & Barclay, 2003; Sedgeley, 2001; Solick & Barclay, 2006). Therefore, solo-roosting male bats may favour less thermally stable exposed Kent boxes to better facilitate torpor, while communally roosting bats, especially during maternity roosting, may favour the more thermally stable sheltered Kent or natural roosts.

The Schwegler 2F boxes were generally warmer (median: 15 °C) and more thermally stable (range: -0.4–34 °C) than both the exposed (median: 14 °C; range: -2.5–46 °C) and sheltered

(median: 14 °C; range: -1–37 °C) Kent boxes, but less-so than the natural tree roosts (median: 13.5 °C; range: 2–27 °C), and cooler at night than the Kent boxes (0.4–0.5 °C warmer than ambient vs 0.6–1 °C warmer than ambient). Additionally, they tended to warm quicker in the mornings, although this is likely due to the limited number of monitored boxes (i.e., two) and the easterly aspect of their placement leading to direct sun exposure in the morning. Warmer temperatures have also been reported for Schwegler 2F boxes compared to other box types, although they were less thermally stable compared to wooden board bat boxes, which are similar to the Kent boxes in this study (Martin Bideguren et al., 2018). Warm, thermally stable roosts which warm quickly and provide space for communal roosting have been shown to be favoured by reproductive females, including *C. tuberculatus* (Sedgeley, 2001; Solick & Barclay, 2006). Therefore, it is unlikely that the reason for a lack of occupation of Schwegler boxes in Hamilton City is due to an unsuitable microclimate. However, as social roosting is an important factor for bat thermoregulation (Russo et al., 2017), the smaller roosting area available in this box type may not be preferred. Schwegler 2F boxes may, therefore, be more favourable to smaller groups of pre-natal females which do not require warm overnight temperatures for non-volant pups.

Relative humidity

Inferences regarding the relative humidity of bat boxes are limited, as data were not obtained on natural tree cavity humidity due to the saturation of sensors. Relative humidity can be compared to that measured at the Grand Canyon Cave roost site. The relative humidity of Kent boxes was generally 5–12 % higher than ambient conditions and less stable compared to Grand Canyon Cave (range: 36–100 % vs 55–87 %), while nearer the cave ceiling (the roosting area of the cave), humidity was similar to the ambient readings outside the cave (median: 77 % vs 78 %). This was not surprising, as caves generally have stable humidity, and well-ventilated caves like Grand Canyon may not become saturated, although areas with different microclimates may occur within the cave (Lauritzen, 2019).

Generalised linear mixed modelling indicated that exposed Kent boxes had significantly lower derived daily relative humidity maximums than sheltered boxes (-2.88 %), and the inner chambers at both exposures had significantly lower derived daily relative humidity maximums (-0.75 %) and ranges (-2.94 %), indicating improved stability in the inner chambers. Sedgeley (2001) found that, over a 24-hour period, unoccupied known *C.*

tuberculatus roost cavities were more humid (mean: 95 % vs 93 %) and stable (varied by: 4 % vs 11 %) than available non-roost cavities and ambient conditions (mean: 77 %; varied by: 39 %). The author proposed that this was important for *C. tuberculatus* roost selection as it would reduce dehydration caused by evaporative water loss. The relative humidity of Kent boxes in this study was generally closer to ambient (5–12 % above) than the tree roost cavities in Sedgeley (2001).

The effect of chamber

Overall, the results of the GLMMs indicated that the inner chambers of Kent boxes were significantly more thermally stable (derived daily range 0.3 °C less), and on average warmer (derived daily mean 0.08 °C higher) but with lower temperature maximums (derived daily maximum 0.1 °C lower), than the outer chambers of Kent boxes. Although, season did affect the direction and magnitude of these differences, with the most notable change being in derived daily summer maximums which were 0.27 °C warmer in the inner chamber. These differences were possibly due to the inner chamber being 10 cm longer than the outer chamber as it has been reported that temperatures further from the opening of a bat box were generally higher than those closer to the opening, with this difference especially pronounced on warmer, sunnier days, and temperatures near the open bottom of a bat box more closely following ambient fluctuations (Bakken & O'Keefe, 2025). The unstable outer chambers may be more favourable for solo-roosting male bats compared to the inner chambers, as these thermal fluctuations can facilitate passive rewarming from torpor and therefore greater energy savings (Turbill, 2006). In summer, the warmer inner chambers could be avoided by bats during particularly warm weather. Although the estimated derived differences between the chambers were largely under 0.5 °C and 3 % relative humidity. Sedgeley (2001) measured mean hourly temperatures of known *C. tuberculatus* cavities that were 0.5 °C higher than non-roost cavities and proposed that this would lead to a 1.1 % reduction in energy expenditure. This may not be physiologically relevant to *C. tuberculatus*.

Box overheating

The two exposed Kent boxes where overheating was recorded were either northwest-facing or south-facing. The events occurred alongside ambient temperatures close to the absolute

maximums recorded (i.e., approximately 30 °C; absolute maximum temperatures at these sites were recorded at about 32 °C), apart from the 15-minute overheating event on the 14th of December. This event occurred at 16:00 NZST alongside an ambient temperature of 24.8 °C, however, the site maximum ambient temperature for that day was recorded as 27.3 °C and occurred at 15:30 NZST, before air temperatures cooled, therefore, the box was likely still warming while ambient temperatures had reduced. Ambient temperatures never rose above the 40 °C threshold, indicating that boxes were warming above ambient conditions; at times >10 °C above ambient peaks. Summer temperatures in Hamilton City range between 10 °C to >25 °C, with occasional peaks above 30 °C (Chappell, 2013) (also observed in this current study). Therefore, a few exposed Kent bat boxes in the city may experience a limited number of overheating events each summer. The longest of the overheating events recorded in this study was four hours, and peaked at 45.9 °C. *Myotis yumanensis*, *Tadarida brasiliensis*, and *Antrozous pallidus* bats have been recorded suffering heat stress at temperatures above 40 °C and mortality within less than an hour of near 45 °C temperatures (Licht & Leitner, 1967). This suggests the conditions in the Hamilton City boxes were likely outside the tolerance range for *C. tuberculatus*. The specific boxes which experienced these overheating events were not observed to be occupied by *C. tuberculatus* during this study and it is unknown whether these potentially overheating boxes were selected as roosts. However, a box adjacent to one of the overheating boxes with a similar exposure and northeast-facing aspect did contain roosting *C. tuberculatus* on more than one occasion (37 % occupancy), with occupation observations occurring during February-April and October. Therefore, these boxes may be selected as roosts outside of these warmer days and even be preferred during cooler weather.

Interestingly, no overheating events were recorded in the two Schwegler 2F boxes measured in Hamilton City, despite Martin Bideguren et al. (2018) showing that these boxes were warmest and most prone to >40 °C temperatures. This may be explained by the fact that one box was a sheltered box, and the other was exposed but east-facing, likely reducing solar exposure and therefore maximum internal temperatures during the afternoon, when the potential overheating events were recorded.

Statistical vs physiological significance of roost microclimate

It is important to note that the derived differences between chambers and exposure categories of Kent boxes in Hamilton City were generally in the range of 1–2 °C and less than 5 % for relative humidity. Such small differences between chambers and exposure categories are unlikely to be physiologically relevant for *C. tuberculatus* in terms of roost microclimatic preferences. This is supported by the observation that there was no significant effect of Kent box thermal conditions on observed occupation. Although microclimate is generally regarded as important for roost selection (Rueegger, 2016), other studies have found factors such as microclimate to be specific to species or even individuals (Lausen & Barclay, 2003; Rueegger et al., 2020). For example, Rueegger et al. (2020) found that box selection by *Chalinolobus gouldii* did not depend on temperatures, although, *Nyctophilus geoffroyi* did favour warmer boxes.

Comparisons of the sheltered natural and Kent box roosts revealed that the estimated derived differences were generally less than 3 °C, although differences in overall stability and timing of warming patterns were clearer. However, no bats were observed using the natural roosts on any of the survey nights, so it is possible they were not active roosts for *C. tuberculatus*.

Grand Canyon Cave

Temperature stability of Grand Canyon Cave was relatively similar to tree cavities, suggesting that thermal stability is a factor in roost selection by *C. tuberculatus* (O'Donnell, 2002). Conditions towards the top of the cave were more thermally stable and warmer, but with lower and less stable relative humidity, than the conditions measured near the cave floor. This indicates that the cave provides a wide range of microclimates, although estimated derived differences were less than 2 °C and 10 % relative humidity, so their ecological significance may be limited. Reproductive female *C. tuberculatus* have been recorded favouring stable microclimates (Sedgeley, 2001), however, only pre-natal females have been captured at Grand Canyon Cave and post-natal females with pups are assumed to roost elsewhere (O'Donnell, 2002). The data from the current study suggests tree cavities may be warmer than ambient at night compared to Grand Canyon Cave, especially in summer when breeding occurs. Lactating females have been shown to favour roosts with warmer nighttime temperatures (Lausen & Barclay, 2003) as these better support the development of non-volant

pups (Zahn, 1999), therefore, post-natal female *C. tuberculatus* may move out of the cave and into tree cavities providing warmer nighttime temperatures.

Future research

Kent box exposure was found to have a significant effect on occupancy rates. However, there are likely other factors contributing to individual box occupancy, especially as some individual exposed boxes had higher occupancy rates than some sheltered boxes. This could include the abundance of natural cavities and other boxes in the immediate area (Rueegger, 2016). Future studies could seek to determine this by quantifying the availability of roost features (boxes and natural features) and comparing box occupancy rates in these areas.

The current study lacked comparisons between Kent box and natural roost humidity as humidity sensors became saturated. Future research could seek to fill this gap e.g., by re-attempting measurements of relative humidity in tree cavities. A different type of sensor could be trialled. Also, additional research into the importance of relative humidity for *C. tuberculatus* in natural roosts would be valuable as current knowledge is lacking. This study was also unable to compare the effect of microclimate on occupancy of natural tree roosts versus Kent bat boxes, as no natural roost occupancy events were observed, so future studies could utilise radio-tracking to locate actively used roosts for comparison.

Further research regarding the thermal preferences and limits e.g., thermal maxima of *C. tuberculatus*, would be valuable. This work could help determine the level of significance the measured microclimatic differences would have on physiological responses and roost selection and inform the development of appropriate bat box designs and installation guidelines. Further to this, additional research should trial different box designs and measure microclimate to assess suitability for *C. tuberculatus*. One such trial could be regarding longer Kent-style boxes, as Bakken and O'Keefe (2025) found that on sunny days, 1.4 m long rocket bat boxes could support a vertical temperature gradient of approximately 10 °C, while shorter boxes offered a smaller range of temperatures. Providing longer boxes of a similar design to existing Kent boxes may increase the range of microclimatic conditions available for *C. tuberculatus* while also maximising quick uptake due to a familiar box design. Trialling boxes with different internal volumes, colours, and construction materials could also be valuable, as these factors have been shown to impact box microclimates (Martin Bideguren et al., 2018).

Conclusions

The new box monitoring method with a telescopic pole and endoscope camera allowed for more frequent roost checks with minimal disturbance to roosting bats. This technique required minimal training and was less costly than tree-climbing endoscope assessments and eDNA, while also allowing a greater number of boxes to be surveyed in a day compared to roost emergence watches. Additionally, it provided direct observations of roost occupation and information on the number of bats present and chambers occupied.

Bat box occupancy recorded in this study was higher than rates previously reported in similar occupation surveys of Hamilton bat boxes. This may be due to *C. tuberculatus* using more Kent boxes since the previous studies, as time since box installation can increase occupancy. However, it should be noted that the current study monitored a subset of boxes which were initially selected based on signs of occupation. Also of note, non-volant pups were observed in mid-March, indicating that breeding may extend for longer than previously reported, which should be considered when developing management protocols such as for roost tree felling to ensure that disturbance is reduced while young are unable to escape via flight.

Occupancy rates of individual boxes varied considerably. Sheltered boxes were more likely to be occupied than exposed boxes, supporting findings by Robinson et al. (2023). This may be due to greater microclimatic stability of boxes located in sheltered areas compared to the exposed boxes. However, the differences are unlikely to have physiological relevance to *C. tuberculatus*. This is supported by the observation that although there was a significant difference in derived microclimatic differences between the outer and inner chambers of Kent boxes, there was no significant effect of chamber on occupancy. Additionally, modelling indicated no significant effect of temperature on box occupancy. It is likely that other factors contributed to the observed variability in individual box occupancy rates, such as local availability of additional roosts (boxes and natural features), familiarity, and social learning. Box installation should, however, favour sheltered sites if the aim is to maximise occupancy.

Kent box microclimates were less stable than the natural tree cavity roosts and Grand Canyon Cave, with exposed Kent box microclimates being the least stable, especially the outer chamber. Microclimate stability has been shown to be important for *C. tuberculatus* and other bat species' roost choice (Lausen & Barclay, 2003; Sedgeley, 2001), although temperate-zone solo-roosting male and non-reproductive female bats likely favour roosts with less stable microclimates to facilitate passive rewarming out of torpor to benefit from energy savings.

These individuals may favour the exposed Kent boxes, but further research would be required to confirm this hypothesis. Two exposed Kent boxes did experience a limited number of overheating events, which could pose a heat stress or even mortality risk for *C. tuberculatus*. Although it is unknown whether *C. tuberculatus* avoid these boxes during warm weather and they may still utilise these boxes during cooler conditions. Bat box installations at exposed, north-facing sites should therefore be minimised but not entirely avoided, as providing a range of roost microclimate choices is likely beneficial for *C. tuberculatus*. To increase this range of microclimate conditions in roosts for *C. tuberculatus* and to facilitate better within-roost behavioural thermoregulation, future studies should trial different box types, especially those similar to Kent boxes but with a longer chamber.

Generalised linear mixed modelling revealed that thermal conditions did not have a significant effect on Kent box occupancy rates, despite these being significantly different between sheltered and exposed sites. It is possible that the estimated derived differences were not physiologically significant for *C. tuberculatus*, and that other factors, such as roost availability and social learning, may drive the observed differences in box occupancy. However, the number of occupation events for which microclimate data was available was limited, and further monitoring would be required to improve confidence in the model. Future research could also quantify absolute temperature and relative humidity variables, rather than derived differences, as these may have a greater bearing on box selection due to physiological constraints.

Overall, this study represents a significant contribution to the knowledge of New Zealand bat box microclimates and associated *C. tuberculatus* ecology. The findings will be valuable to inform the use of bat boxes specifically for *C. tuberculatus* and their conservation.

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Appendices

Appendix A

Table A.1 All 46 monitored bat boxes in Hamilton City, box information, total occupation checks, and the results of occupancy checks. S: solo roosting, C: communal roosting, M: maternity roost.

Box	Site	Chambers	Number of checks	Occupancy (% of checks)	Occupancy (chambers)	Occupancy (type)
3	Hamilton Gardens	3	13	0 %	NA	NA
3B	Hamilton Gardens	2 (left & right)	9	0 %	NA	NA
BB68	Hamilton Gardens	2	15	0 %	NA	NA
BB69	Hamilton Gardens	2	20	10 %	Inner, outer	S
U6	Hamilton Gardens	2	13	23 %	Outer	S
BB70	Hamilton Gardens	2	16	38 %	Outer	S
BB66	Dillicar Park	2	16	0 %	NA	NA
BB67	Dillicar Park	2	15	0 %	NA	NA
BB41	Sandford Park	2	13	8 %	Inner	S
BB42	Sandford Park	2	20	5 %	Inner	S
U7	Sandford Park	2	12	8 %	Outer	S
BB45	Sandford Park	2	21	29 %	Inner, outer	S + C
U4	Sandford Park	2	15	33 %	Inner	S
BB46	Sandford Park	2	16	6 %	Outer	S
BB47	Sandford Park	2	21	10 %	Inner, outer	S + C
U8	Sandford Park	2	12	8 %	Inner	S
BS09	Sandford Park	1	10	0 %	NA	NA
14	Sandford Park	3	14	86 %	Inner, middle, outer	C + M
U9	Sandford Park	2	6	17 %	Inner	S
15	Sandford Park	3	15	67 %	Inner, middle, outer	S + C
U10	Sandford Park	2	6	33 %	Inner	S
BB53	Peacockes Reserve Esplanade	2	12	0 %	NA	NA
BB54	Peacockes Reserve Esplanade	2	12	0 %	NA	NA
BBS1	Peacockes Reserve Esplanade	2	13	8 %	Inner	C
BBS3A	Peacockes Reserve Esplanade	2	10	0 %	NA	NA
BBS3B	Peacockes Reserve Esplanade	2	12	50 %	Inner	S + C
BBS5	Peacockes Reserve Esplanade	2	13	15 %	Inner	S + C
BB34	Fitzroy Park	2	17	0 %	NA	NA
BB35	Fitzroy Park	2	16	0 %	NA	NA
BB36	Fitzroy Park	2	16	6 %	Inner	S
BBF5B	Fitzroy Park	2	13	7 %	Inner	S
BBF6B	Fitzroy Park	2	14	27 %	Inner	S
BS01	Fitzroy Park	1	9	0 %	NA	NA
17	Te Anau Park	2	18	22 %	Unknown	C*
U3	Te Anau Park	2	12	8 %	Inner	S
BB20	Te Anau Park	2	9	89 %	Inner, outer	S + C
BB22	Te Anau Park	2	11	9 %	Inner	S
BB27	Te Anau Park	2	11	69 %	Outer	S + C
BB28	Te Anau Park	2	19	37 %	Inner, outer	S + C

U5	Te Anau Park	2	12	0 %	NA	NA
BB08	Resthills Reserve	2	14	50 %	Outer	S
BB09	Resthills Reserve	2	17	0 %	NA	NA
U1	Resthills Reserve	2	12	0 %	NA	NA
BB10	Resthills Reserve	2	14	14 %	Outer	S
BB11	Resthills Reserve	2	14	0 %	NA	NA
U2	Resthills Reserve	2	13	0 %	NA	NA

**Communal roosting behaviour was not directly observed in Box 17, but due to other evidence (audible social vocalisations and the quantity of guano beneath the box), communal roosting was assumed, as where similar evidence at other boxes was followed up with roost emergence counts, >10 bats were observed.*

Table A.2 Number of sample days included for analyses of bat roost microclimate for each roost, separated by season.

	Days sampled				
Roost ID	Autumn	Winter	Spring	Summer	Total
U1	67	93	92	46	298
U2	67	93	92	46	298
U3	67	93	92	46	298
U4*	67	93 (Inner: 55)	92 (Inner: 0)	46 (Inner: 0)	298 (Inner: 122)
U5	67	93	92	46	298
U6	67	93	92	46	298
U7	20	93	92	46	251
U8	20	93	92	46	251
U9	0	48	92	46	186
U10	0	48	92	46	186
BS01	67	93	92	46	298
BS09	67	93	92	46	298
NaturalRoost1	52	93	92	18	255
NaturalRoost2	67	93	92	18	270
NaturalRoost3	67	91	0	0	158
NaturalRoost4	65	93	81	0	239
NaturalRoost5	65	93	81	0	239
NaturalRoost6	65	93	81	0	239
Grand Canyon Cave*	80	93	92	46 (Bottom: 40)	311 (Bottom: 305)

**one of a pair of loggers failed early. Individual day count specified where this differs.*

Table A.3 Number of occupation survey dates included for analyses of the effect of box microclimate on occupation for each box used in the analysis.

	Number of survey dates		
Box ID	Occupied	Unoccupied	Total
U1	0	24	24
U2	0	26	26
U3	1	23	24
U4	2	37	39
U5	0	24	24
U6	3	10	13
U7	1	25	26
U8	1	25	26
U9	11	29	40
U10	3	17	20
14	17	0	17
15	3	0	3
17	2	10	12
BB09	0	12	12
BB11	0	12	12
BB28	4	9	13
BB42	0	11	11
BB45	4	11	15
BB47	2	11	13
BB69	0	14	14
Total	54	330	384

Appendix B

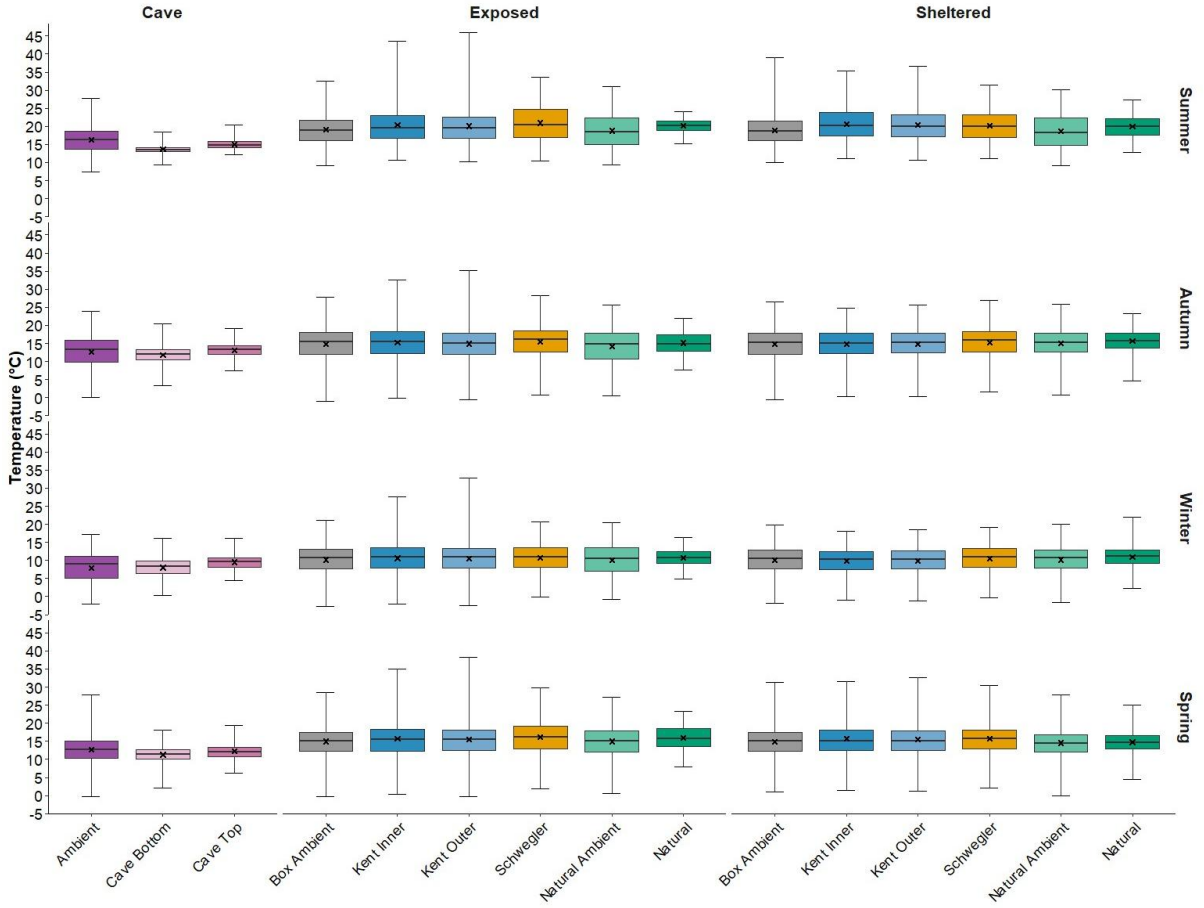

Figure B.1 Boxplots of temperatures measured in bat boxes, natural roost features, Grand Canyon Cave, and corresponding ambient conditions, separated by season. Shaded boxes show interquartile range, the thick horizontal line indicates median, the cross is the mean, whiskers indicate maximum and minimum values.

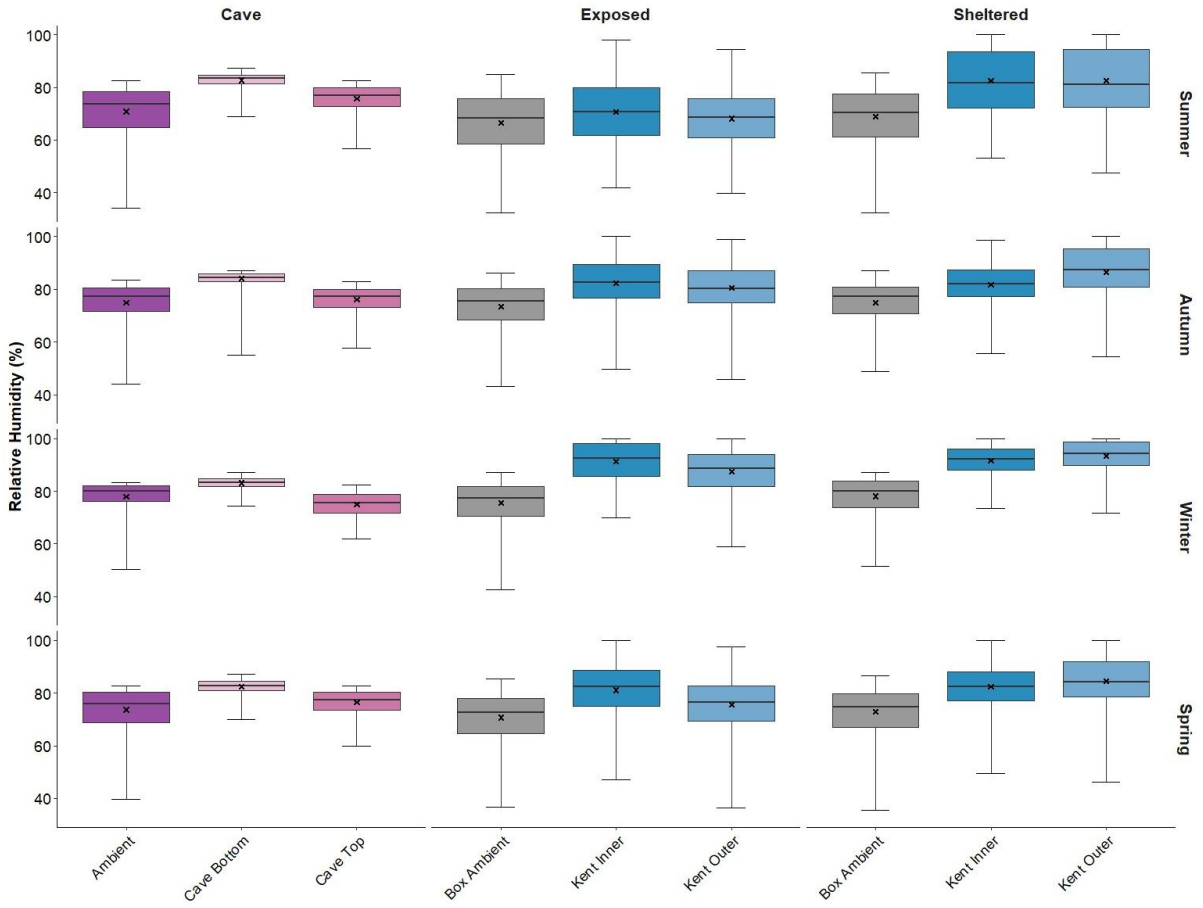

Figure B.2 Boxplots of relative humidity measured in Kent boxes, Grand Canyon Cave, and corresponding ambient conditions, separated by season. Shaded boxes show interquartile range, the thick horizontal line indicates median, the cross is the mean, whiskers indicate maximum and minimum values.

Table B.1 Results of the one-way ANOVA and Tukey's HSD post-hoc tests assessing the difference of derived daily temperature variables between sheltered natural roosts and Kent boxes, separated by chamber. Negative difference values indicate lower natural values in relation to Kent boxes.

Measurement	Derived daily variable	Estimated difference [95 % confidence interval: lower, upper]		*P*-value
		Natural vs Kent inner	Natural vs Kent outer	
Temperature	Maximum	-1.7 °C [-1.9 °C, -1.6 °C]	-1.7 °C [-1.8 °C, -1.5 °C]	< 0.001
	Mean	0.27 °C [0.14 °C, 0.39 °C]	0.26 °C [0.15 °C, 0.37 °C]	< 0.001
	Range	-2.8 °C [-3.03 °C, -2.6 °C]	-2.8 °C [-2.9 °C, -2.6 °C]	< 0.001
	Rate of change	-0.055 °C/15-minutes [-0.063 °C/15-min, -0.046 °C/15-min]	-0.052 °C/15-minutes [-0.059 °C/15-min, -0.045 °C/15-min]	< 0.001

Table B.2 Results of the paired t-test assessing the difference between derived daily temperature and relative humidity variables at the top and bottom of Grand Canyon Cave. Negative differences indicate lower top values in relation to bottom values.

Measurement	Derived daily variable	Mean difference (top vs bottom of cave)	*P*-value
Temperature	Maximum	1.131 °C	< 0.01
	Mean	1.236 °C	< 0.01
	Range	-0.576 °C	< 0.01
	Rate of change	-0.018 °C/15-minutes	< 0.01
Relative humidity	Maximum	-5.920 %	< 0.01
	Mean	-7.238 %	< 0.01
	Range	3.277 %	< 0.01