


Article

Chainsaw-Carved Cavities Better Mimic the Thermal Properties of Natural Tree Hollows than Nest Boxes and Log Hollows

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Abstract: The creation of supplementary habitats that effectively mimic the physical and thermal characteristics of natural tree hollows should be a key priority for landscape restoration and biodiversity offset programs. Here, we compare the thermal profiles of natural tree hollows with three types of artificial hollows designed for small marsupial gliders and tree-roosting insectivorous bats: (1) ‘chainsaw hollows’ carved directly into the trunks and branches of live trees, (2) ‘log hollows’, and (3) plywood nest boxes. Chainsaw hollows had thermal profiles that were similar to natural tree hollows: they were consistently warmer than ambient conditions at night, while remaining cooler than ambient during the day. In contrast, glider and bat boxes had the opposite pattern of heating and cooling, being slightly cooler than ambient at night and substantially hotter during the day. Glider log hollows had greater variation in internal temperatures compared to natural hollows and chainsaw hollows, but fluctuated less than glider boxes. Our results provide the first empirical evidence that artificial hollows carved directly into live trees can produce thermally stable supplementary habitats that could potentially buffer hollow-dependent fauna from weather extremes; whereas, poorly insulated plywood nest boxes produce lower-quality thermal environments. Together these findings provide positive impetus for stakeholders involved in conservation management and biodiversity offset programs to consider trialing chainsaw hollows in situations where target fauna require well-insulated supplementary habitats.

Keywords: biodiversity offset; hollow-dependent fauna; supplementary habitat; thermal habitat quality

1. Introduction

Hollows, holes and cavities that form in large, old trees are keystone habitat structures used by a broad range of fauna for shelter, refuge from predators, denning, roosting and nesting [1]. However, large hollow-bearing trees continue to be removed from human-impacted landscapes due to land clearing, agricultural intensification, logging and expanding urbanization, resulting in significant negative impacts on native hollow-dependent fauna [2]. Long-term management strategies are urgently required to complement the revegetation and restoration of degraded areas, in conjunction with retaining the large hollow-bearing trees that persist in modified landscapes [3].

One popular management action is the addition of artificial cavities (nest or roost boxes) to provide supplementary habitats for hollow-dependent fauna [4]. A broad range of wildlife has

been recorded using nest boxes worldwide, including invertebrates [5,6], amphibians [7], reptiles [6], birds [8,9], arboreal mammals [9], and insectivorous bats [10,11]. Consequently, nest boxes have long been a popular and productive research tool, facilitating studies into many aspects of the life history and ecology of the species that use them [12]. For example, the use of nest boxes by secondary cavity-nesting birds has been extensively studied, especially in temperate forests of Europe and North America [8,13,14].

Nest box programs employing species-specific box designs and adaptive management plans undertaken over medium- to long-term time scales have been shown to effectively support some populations of endangered species of mammals [15–18] and birds [19,20]. However, the efficacy of nest boxes when used as supplementary habitats in biodiversity offset schemes are less clear [21]. In biodiversity offsetting, development projects that involve the removal of mature, hollow-bearing trees (e.g., the construction of new roads and other civil infrastructure) are often required to compensate for the habitat features that are lost by installing equivalent artificial structures [22–24]. Offsetting the loss of tree hollows is typically undertaken by installing nest boxes on smaller, immature trees (henceforth ‘developing’ trees; [25]). In such scenarios, nest boxes deployed in a given area are usually more uniform in dimensions and height above the ground compared to the wide variety of cavity shapes and sizes that develop over long time scales in large, mature trees [3,26,27], and so offer a comparatively limited variety of supplementary nesting or denning structures for the community of hollow-dependent fauna endemic to that area [8,28]. Further research is required to investigate the efficacy of incorporating novel types of artificial habitats into biodiversity offset programs to provide compensatory habitats for the wide range of biota that rely on tree hollows [25,29].

Artificial hollows may be more structurally similar to natural hollows if mechanically carved directly into the trunk or branches of a tree (e.g., with a chainsaw), rather than attached to the outside of trees as ancillary structures [30–33]. These ‘chainsaw hollows’ have the potential to provide supplementary habitats that mimic the internal physical characteristics of naturally occurring tree hollows that are used by target fauna [34–36]. In addition, cavities carved into trees with chainsaws can be designed to be more similar in external appearance to natural tree hollows (compared to nest boxes) and this may lead to recognition and uptake by target fauna [37,38]. For example, Ruegger [31] presented preliminary evidence that four species of endemic hollow-dependent mammals and one bird investigated and subsequently used chainsaw hollows several days after they were cut into developing trees within a native timber plantation forest. In North America, wood boxes inserted into artificial cavities carved into trees with chainsaws have been used successfully to provide supplementary habitat for red-cockaded woodpeckers [35,36]. Importantly, chainsaw hollows also have the potential to approximate the microclimatic conditions within natural tree hollows used by target fauna [39,40].

For endotherms, the thermal properties of dens used as thermal refuges play a major role in survival and reproductive success [41–43]. When den temperatures are below an endotherm’s thermo-neutral zone (TNZ), animals must use metabolic heat production; conversely, when den temperatures are above the TNZ, water costs rise as evaporative heat-loss is used to avoid overheating [40,44]. Cooler den microclimates may therefore require animals to invest more energy in thermoregulation, at the expense of other processes such as growth [41]. Alternatively, warm den environments may reduce the costs for animals maintaining core body temperature and could therefore promote more rapid growth [45]. The level to which den microclimate influences the fitness of any particular species depends on a range of traits, including morphology, behavior, age and reproductive condition [40]. Given the wide variety of species that use tree hollows, providing artificial hollows with suitable thermal conditions across different seasons for communities of target species in impacted areas is a complex task. For example, among temperate zone insectivorous bats, there are likely to be different roosting requirements at different times of the year. During the breeding season, pregnant or lactating females with dependent young may require warm roosts that minimize the thermoregulatory energy required to maintain gestation or milk production [46,47]; however, social thermoregulation employed by bats roosting in groups may reduce this reliance [48]. Outside of the breeding season,

females may use daily torpor to facilitate significant energy savings when using cooler and more thermally stable roosts [49].

The thermal properties of nest boxes in comparison to those of natural hollows have not been comprehensively studied across the diverse range of fauna that use boxes, or across the range of environments where they are deployed [40]. The majority of studies on this topic have compared microclimates of nest boxes and tree hollows used by secondary cavity-nesting birds, and in some cases linked the differences in microclimate to breeding success [28]. These studies have consistently shown that nest boxes are drier than natural hollows and less well insulated, which results in a larger range in daily cavity temperatures, plus greater maxima and minima occurring in response to periodic extremes in ambient conditions [28,50–53]. Despite these differences in microclimate, studies have shown increased breeding success for some bird species using nest boxes compared to natural tree hollows [13,14,54], while others have found no effect of nest boxes on breeding success [55–58]. However, as factors such as nest predation and parasite infestation can cause variation in the breeding ecology of birds when nesting in boxes compared to natural tree hollows, caution must be taken when using these studies to infer that nest boxes can effectively substitute for the loss of tree hollows [8,28,59–62].

In general, endothermic animals using thermally unsuitable nest boxes may experience non-lethal short-term consequences such as reduced growth and body condition, but may also potentially experience high mortality rates during extremely hot or cold weather events [40,52,63]. For example, during cold weather, tree swallow (*Tachycineta bicolor* (Vieillot, 1808)) chicks in cooler nest boxes were shown to have lower survival, slower growth rates, and smaller body size than those in warmer boxes [41]. Conversely, during heat wave conditions, when daytime ambient temperatures exceeded 39 °C over two consecutive days, juvenile lesser kestrels (*Falco naumanni* Fleischer, 1818) using nest boxes incurred high mortality rates [64]. To date, few studies have examined the influence of cavity temperature on biologically meaningful measures of fitness for hollow-dependent mammals using nest boxes compared to tree hollows [65]. Recently, Rowland et al. [40] showed that the eco-physiological costs of thermoregulation are likely to be considerably higher for arboreal marsupials (adult weight range = 1100–4500 g) in nest boxes compared to tree hollows during summer, but marginally lower during winter. There is also some evidence that free-ranging arboreal marsupials avoid nest boxes that experience temperature extremes during hot weather, presumably to avoid heat-stress [63,65].

Investing in the development and testing of novel supplementary habitats designed to buffer animals from extreme temperatures, particularly during hot and cold weather extremes, is a high priority for stakeholders in biodiversity offset programs to ensure that artificial habitats provide the maximum possible value for wildlife [39,40]. This is particularly relevant across southeastern Australia, which has a diverse endemic hollow-using fauna [66], has experienced extensive and ongoing habitat loss [67], where nest boxes are commonly installed to provide supplementary habitats in impacted landscapes [9,12], and in many regions is characterized by a Mediterranean climate with large variation in weather conditions from day to day and across seasons [40].

In this study, we compare the thermal profiles of natural hollows in large, mature trees (*Eucalyptus* spp.) with three types of artificial hollows designed for small marsupial gliders (*Petaurus* spp.: 100–600 g) and tree-roosting insectivorous bats (Chiroptera: 4–50 g): (1) chainsaw hollows cut directly into live tree trunks or branches, (2) chainsaw hollows cut into felled logs that were subsequently attached to tree trunks (henceforth ‘log hollows’), and (3) nest boxes made from plywood. Our purpose was to investigate whether chainsaw hollows could produce thermal profiles that are more similar to natural tree hollows than traditional plywood nest boxes. If traditional nest box designs provide a different microclimate to that of natural tree hollows, they may not be an effective substitute for those hollows in terms of conserving the community of hollow-dependent fauna that rely on these habitat structures [40]. As nest boxes are frequently used in landscape restoration and biodiversity offset programs to compensate for the loss of natural hollows [4,21], our study provides a timely impetus for policy makers and land managers to consider ways in which novel habitat-creation techniques could

be incorporated into these programs to provide artificial hollows that effectively buffer wildlife from hot or cold weather extremes.

2. Materials and Methods

2.1. Ethics Statement

This research was carried out with approval from La Trobe University's Animal Ethics Committee (project AEC13-30) and the Department of Environment, Land, Water and Planning (research permit 10006790). There was no animal handling or manipulation conducted during the study.

2.2. Study Sites

This study was conducted at the La Trobe University Zoology Reserve (LTUZR; -37.715949, 145.049104) and the adjacent La Trobe University Wildlife Sanctuary (LTUWS; -37.716604, 145.054991), in the suburb of Bundoora, Melbourne, in southeastern Australia. The region experiences a Mediterranean climate: temperatures range from a mean monthly maximum of 26.9 °C in February to a mean monthly minimum of 5.6 °C in July, but can exceed 40 °C during summer and occasionally falls below 0 °C during winter [68].

The reserves are dominated by regenerating river red gum (*Eucalyptus camaldulensis* Dehnh.) woodland with a grassy understory [69]. Historical agricultural activity in the region resulted in extensive clearing of native river red gum and yellow gum (*Eucalyptus melliodora* Schauer 1843) woodland vegetation prior to the establishment of the reserves in 1967 as part of a corridor network of conservation reserves that are managed by La Trobe University [70]. Consequently, to compensate for the limited number of mature hollow-bearing trees in the reserves, approximately 500 nest boxes of varying designs (targeting a range of arboreal mammals, hollow-nesting birds, and insectivorous bats) were installed from 1988 onwards (G. Parras, pers. comm.). The boxes are used by a range of native fauna, including arboreal mammals (sugar glider *Petaurus breviceps* Waterhouse, 1839, common ringtail possum *Pseudocheirus peregrinus* (Boddaert, 1785), common brushtail possum *Trichosurus vulpecula* (Kerr, 1792)), insectivorous bats (Gould's wattled bat *Chalinolobus gouldii* (Gray, 1841), white-striped free-tailed bat *Austronomus australis* (Gray, 1839) [71]), hollow-nesting birds (musk lorikeet *Glossopsitta concinna* (Shaw, 1791), rainbow lorikeet *Trichoglossus moluccanus* (Gmelin, 1788), Australian wood duck *Chenonetta jubata* (Latham, 1801), striated pardalote *Pardalotus striatus* (Gmelin, 1789)), plus the introduced common myna *Acridotheres tristis* (Linnaeus, 1766) (G. Parras, pers. comm.). The reserves are bordered by La Trobe University's Bundoora Campus and by urban developments.

2.3. Natural and Artificial Hollows

2.3.1. Glider Cavities

We compared ambient temperatures with temperatures inside natural tree hollows and three types of artificial hollows designed for small marsupial gliders (e.g., sugar glider *Petaurus breviceps*): chainsaw hollows, log hollows and nest boxes (henceforth 'glider boxes'). We selected 10 natural tree hollows that were located 5–7 m above the ground (i.e., accessible with a 6 m extension ladder) in the trunks of seven mature trees (*Eucalyptus cladocalyx* F. Muell.). The seven trees were all of comparable size (mean diameter at breast height, DBH = 66.2 cm, range = 62.0–74.0 cm), with canopies providing similar shade profiles (mean canopy shade = 73.5%, range = 70.1–75.6% [39]). From anecdotal observations recorded at the site over the last 11 years (K. Robert, unpub. data), we know that sugar gliders periodically den in five of the natural tree hollows that were selected for this study. For the remaining five natural hollows, we selected those with an entrance wide enough for gliders (entrance width > 3.0 cm; [12]); however, as there were a limited number of tree hollows that were safely accessible with a ladder, we did not place an upper limit on the entrance size. For all ten natural hollows, we recorded the diameter of the trunk at the location of the hollow (five historical glider den hollows: mean diameter = 62.3 cm,

range = 62.0–63.0 cm; extra five hollows: mean diameter = 66.3 cm, range = 62.0–72.0 cm), the width of the entrance (five historical glider den hollows: mean width = 39.8 cm, range = 30.0–55.0 cm; extra five hollows: mean width = 44.0 cm, range = 30–60 cm), and the depth of the hollow (five historical glider den hollows: mean depth = 33.0 cm, range = 25.0–40.0 cm; extra five hollows: mean depth = 31.8 cm, range = 24.0–50.0 cm). Due to the limited number of natural tree hollows that we could safely access with a ladder, the 10 natural hollows selected had entrances facing different orientations (cardinal direction: north = 1; east = 3; south = 4; west = 2). In comparison, all artificial glider hollows were installed facing east to reduce differences in cavity temperatures driven by variation in orientation [40]. No artificial hollows were installed on the seven trees containing natural hollows.

We cut glider chainsaw hollows directly into the trunks of 10 mature trees (nine *E. cladocalyx* and one *Corymbia maculata* (Hook.) K.D. Hill & L.A.S. Johnson). These trees were all of similar size (mean DBH = 61.9 cm, range = 45.0–75.0 cm), with canopies providing similar shade profiles (mean canopy shade = 62.9%, range = 56.7–69.7.6%) [39]. The glider chainsaw hollows had a rectangular cube-shaped internal cavity with dimensions 20 × 20 × 23 cm (width × depth × height), 9200 cm³, and a 3.5 cm diameter entrance hole (Figure 1a and Appendix A). The dimensions and volume of the glider chainsaw hollows were pre-determined based on available data on den selection by small marsupial gliders [72–74]. Using the strength loss formula from Smiley and Fraedrich [75], we calculated that the minimum trunk diameter that could safely incorporate a glider chainsaw hollow was 30 cm. To further reduce the risk of tree failures, we cut hollows in trees with a trunk diameter ≥ 40 cm (mean trunk diameter = 61.9 cm; range = 45.0–75.0 cm).

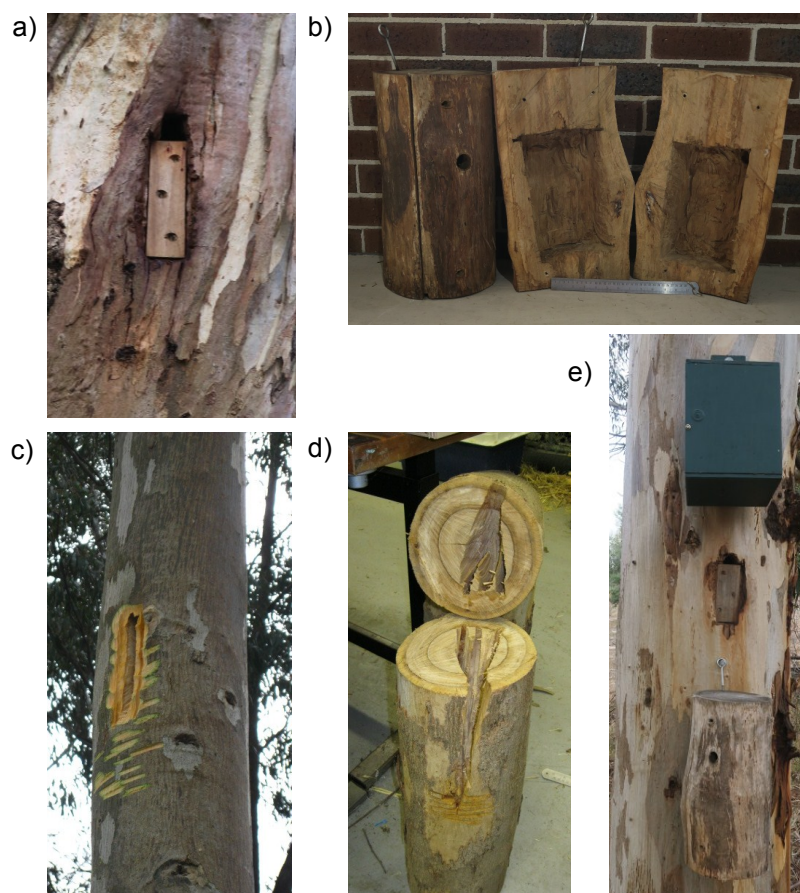


Figure 1. Photographs of the different chainsaw-carved cavities: (a) a glider chainsaw hollow cut into a tree trunk; (b) glider log hollows; (c) a bat chainsaw hollow cut into a tree trunk; (d) an example of a bat chainsaw hollow cut into a felled log to show the wedge-shaped internal cavity; (e) an example of a glider box, log hollow and glider chainsaw hollow installed on a single tree (*C. maculata*).

We created glider log hollows from a live tree (*E. cladocalyx*) that was felled during routine tree management practices at the site. We cut the trunk into lengths with a chainsaw (i.e., logs) with the following mean dimensions: length = 46 cm, range = 44–48 cm; diameter = 26 cm, range = 25–29 cm. We then cut a rectangular cube-shaped internal cavity into each log with similar dimensions as the chainsaw hollows carved into trees: $16 \times 18 \times 28$ cm (width \times depth \times height), 8064 cm^3 , with a 3.5 cm entrance hole (Figure 1b and Appendix A). The mean wall thickness once the cavities had been excavated from the log was 4.7 cm (range = 3.0–7.0 cm).

We built glider boxes from 12 mm marine plywood ($27 \times 28 \times 36$ cm, width \times depth \times height; $20,845 \text{ cm}^3$), with a circular entrance hole (diameter = 3.5 cm) located at the top of the right wall (Figure 2). The glider box dimensions were similar to commercially available nest boxes for small marsupial gliders that are commonly used to supplement natural hollows in management programs and to compensate for the loss of natural hollows in biodiversity offset programs in southeastern Australia [12,16,21]. Glider boxes were painted with three coats of exterior acrylic paint (Wattyl Solagard Low Sheen); we used a dark green colour, consistent with common practice in southeastern Australia [39,40].

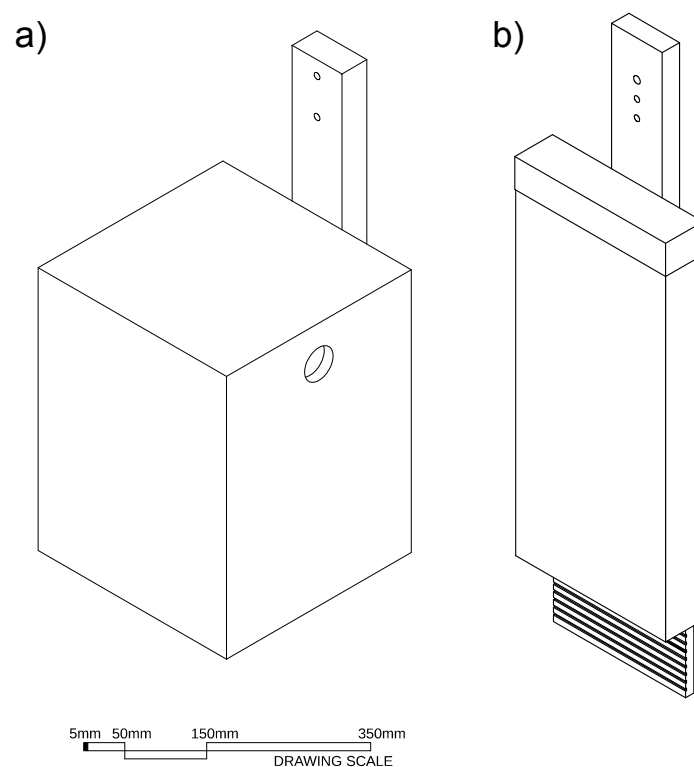


Figure 2. Diagrams of the two nest box designs: (a) glider boxes constructed with 12 mm marine plywood: $27 \times 28 \times 36$ cm (width \times depth \times height); circular entrance diameter, 3.5 cm; internal volume, $20,845 \text{ cm}^3$; (b) bat boxes constructed with 12 mm marine plywood with a narrow, single-chamber, open-bottomed design: $43 \times 7.5 \times 50$ cm (width \times depth \times height); bottom entrance width, 1.5 cm; internal volume, 9555 cm^3 .

On each of the ten trees in which chainsaw hollows were constructed, we attached a log hollow and a glider box (Figure 1e), resulting in a total of 10 chainsaw hollows, 10 log hollows and 10 glider boxes to compare with the 10 natural hollows. The artificial hollows were installed at heights ranging from 1.5–2.0 m above the ground to facilitate ease of access for recording internal temperatures. All chainsaw hollows, log hollows and glider boxes were aligned facing east (either cut into, or attached to, the east side of the tree trunk) to ensure they received the same temporal pattern of exposure to solar radiation.

2.3.2. Bat Cavities

We also compared ambient temperatures with temperatures inside natural tree hollows and two types of artificial hollows designed for insectivorous bats: chainsaw hollows and bat roost boxes (henceforth ‘bat boxes’). We selected 23 natural tree hollows in 11 trees as a representative sample of the hollows available to bats at the site; these were different to the 10 hollows used for the ‘glider hollows’ comparison. As we did not have any data on specific tree hollows used by bats at the study site, we considered any hollow with an entrance wide enough for bats to enter as suitable. Bats often select tree roosts with entrances small enough to exclude larger predators [76]; however, as there were a limited number of naturally occurring tree hollows that we could safely access, we did not place an upper limit on the entrance size. All tree hollows were 5–7 m above the ground, and were in the trunk (13 hollows) or branches (10 hollows) of live trees (*E. cladocalyx*). We recorded the width (mean entrance width = 6.8 cm, range = 0.6–18.0 cm) and orientation (cardinal direction: north = 2; east = 2; south = 5; west = 14) of the entrance to each hollow, the diameter of the trunk or branch at the location of the hollow (mean trunk diameter = 67.9 cm, range = 58.0–87.0 cm; mean branch diameter = 39.0 cm, range = 16.0–60.0 cm), and the depth of the hollow (mean depth = 25.8 cm, range = 15.0–30.0 cm).

We cut 35 chainsaw hollows designed for bats directly into the trunks (14 hollows) and branches (21 hollows) of 20 live trees (*E. cladocalyx*). Bat chainsaw hollows had a vertical slit entrance 2×15 cm (width \times height); plunge cuts angled upwards at approximately 60° were then used to create a wedge-shaped internal cavity (maximum depth = 25–30 cm) with a volume of approximately 500 cm^3 (Figure 1c,d and Appendix A). This design was intended to simulate natural tree roosts used by bats that have ‘vertical fissure’ type entrances [76]. A single arborist (M. Cashmore, Tretec Arboriculture and Ecology) cut all the bat chainsaw hollows using a systematic procedure to ensure consistency in the dimensions of the entrance slit and internal cavity. The selection of candidate trees, and the locations within trees where chainsaw hollows were cut, were determined using the International Society of Arboriculture Tree Risk Assessment Method [77], which incorporates empirical assessment of a range of factors that may influence the risk that any particular tree poses to the public (i.e., recording a range of data to assess the overall health and structural integrity of a tree), the risk and potential consequences that any work action taken may pose (e.g., pruning or not pruning a specific limb), plus the risks that the tree poses to anyone working within it (e.g., an arborist using the single rope climbing technique to access the canopy [78]). Using the strength loss formula from Smiley and Fraedrich [75], we calculated that the minimum stem diameter that could safely incorporate a bat chainsaw hollow was 10 cm. The mean diameter of the trunks and branches that we cut bat chainsaw hollows in were 39 cm (range = 19–63 cm) and 23 cm (range = 16–35 cm), respectively. As there were a limited number of trees with suitable stems that we could safely access, we installed bat chainsaw hollows with the entrances facing different orientations (hollows cut into trunks: north = 5; east = 1; south = 6; west = 2; hollows cut into branches: north = 10; east = 1; south = 2; west = 8).

We made bat boxes from 12 mm marine plywood, using a design based on the Bat Conservation International single-chamber box [79]. The dimensions of the boxes were $43 \times 7.5 \times 50$ cm (width \times depth \times height), with an internal volume of 9555 cm^3 and an open-bottom entrance with a width of 1.5 cm (Figure 2). Bat boxes were installed on the same trees as the bat chainsaw hollows, positioned 15–20 cm below the entrance of each hollow, so that every box was paired with a chainsaw hollow on a trunk (14 boxes) or branch (21 boxes). Bat boxes were painted the same dark-green colour as the glider boxes (see Figure 1e).

To estimate variation in canopy cover (to assess how much solar radiation reached the natural and artificial bat hollows), we used the method described by Griffiths et al. [39] to quantify the ‘percent canopy shade’ above each bat chainsaw hollow, bat box and natural tree hollow (mean \pm SE canopy openness = $31.0 \pm 0.7\%$, range = 12.5–47.4%; see Appendix A for details).

2.4. Monitoring Thermal Profiles of Natural and Artificial Hollows

We used temperature data loggers (Thermochron iButton model DS1922L, Maxim Integrated Products, San Jose, CA, USA; operating range $-10\text{ }^{\circ}\text{C}$ to $+65\text{ }^{\circ}\text{C}$, precision $\pm 0.5\text{ }^{\circ}\text{C}$ [80]) to simultaneously record temperatures within natural hollows and artificial hollows, plus ambient conditions. Temperature data were recorded hourly within glider boxes, glider chainsaw hollows, log hollows and natural hollows (i.e., those used for the glider cavity temperature comparisons) for a total of 110 days: 50 consecutive days in spring (2 October to 20 November 2016) and 60 days in summer (23 December 2016 to 20 February 2017). Data loggers were suspended from a hook attached to the inside of the lid of each glider box (loggers hung 15 cm below the lid, just above the approximate location where gliders typically roost within boxes; S. Griffiths, unpub. data). For natural hollows and chainsaw hollows, the data loggers were attached to wire and suspended in the center of the internal cavity, approximately 15 cm from the entrance hole. Data loggers were also attached to seven trees (suspended behind a glider box between the back of the box and the tree trunk, to ensure loggers were not exposed directly to sunlight or wind) in spring, and eight trees in summer, to record hourly ambient temperatures. We installed loggers in each replicate glider cavity (40 loggers in total); however, due to logger failures, we only recorded complete temperature data from 36 loggers during the spring survey and 36 loggers during the summer survey (Table 1).

Table 1. Summary of the number of cavities monitored. Temperatures were recorded hourly in bat cavities over 63 consecutive days in autumn (5 March to 6 May 2015), plus in glider cavities hourly over 50 consecutive days in spring (2 October to 20 November 2016) and 60 consecutive days in summer (23 December 2016 to 20 February 2017). Surveys of glider and bat cavities were conducted at different times of the year due to logistic constraints.

Cavity Type	Survey Period	
Bat cavities	Autumn	
Bat box	35	
Chainsaw hollow	35	
Natural tree hollow	23	
Glider cavities	Spring	Summer
Glider box	10	10
Chainsaw hollow	10	9
Log hollow	9	7
Natural tree hollow	7	10

Temperature data were recorded hourly within bat chainsaw hollows, bat boxes and natural hollows (i.e., those used for the bat cavity temperature comparisons) over 63 consecutive days in autumn (5 March to 6 May 2015; Table 1). Data loggers were suspended from a hook attached to the inside of the lid of each bat box (loggers hung 10 cm below the lid, below the location where bats typically roost within boxes; S. Griffiths, unpub. data). Data loggers were placed inside natural hollows and bat chainsaw hollows using the same methods described above. We also attached data loggers to nine trees (suspended behind a bat box using the same method described above) to record hourly ambient temperatures.

In this study, we focused only on cavity temperatures, not on the effect of temperature on the use of cavities by animals. Consequently, during temperature recordings, the entrances to all bat and glider boxes, chainsaw hollows and log hollows were blocked with wire mesh, enabling natural airflow, while excluding animals from occupying the artificial hollows, and thus altering internal temperature profiles. We did not block the entrance to natural tree hollows during temperature recordings to avoid excluding hollow-dependent wildlife that rely on these habitat resources. Therefore, it is possible that animals may have occupied some natural hollows during the survey. The placement of loggers within

the natural hollows eliminated the chance of animals resting directly against loggers; however, it is possible that body heat produced by animals may have influenced cavity temperatures.

2.5. Statistical Analyses

We conducted all analyses in R, version 3.3.3 [81] and analysed glider and bat cavity data separately since they were undertaken at different times of the year. For ambient temperature measures, we took the mean measurement across all ambient data loggers at any one point in time.

As a first step to compare patterns of warming and cooling over the course of the day, we pooled all of the raw data for each of the cavity types (e.g., nest box, chainsaw hollow) and calculated the mean internal temperature and 95% confidence interval (CI) for each hour (12 am to 11 pm).

We then constructed linear mixed-effect models (LMMs) of internal cavity temperatures against a range of covariates using the 'lme' function in the 'nlme' package. For the glider cavities, internal temperature was modelled against an interaction between the structure type (natural hollow, chainsaw hollow, log hollow, glider box) and ambient temperature. For the bat cavities, we again used an interaction between the structure type (natural hollow, chainsaw hollow, bat box) and ambient temperature, but, because there was greater variation in the placement of the bat structures, we also included terms for structure orientation (cardinal direction: north, east, south, west), location (trunk or branch) and the percent shade from the canopy as covariates. Because more than one of the bat model covariates was continuous (i.e., both ambient temperature and shade), these were standardized (mean subtracted, then divided by the standard deviation) to allow for direct comparison across coefficient estimates.

We then split the dataset into day and night. Hourly daytime records were those that occurred between sunrise and sunset, hourly nighttime records occurred between sunset and sunrise, based on sunrise and sunset times during each survey period [68]. For each day or night period, we calculated the maximum and minimum temperature recorded in each cavity, as well as the difference between these two measures (i.e., cavity maximum–minimum). These responses were again modelled using LMMs against the same covariates used for each group (gliders and bats) as the raw cavity temperature data, with the exception that we did not include an interaction term between cavity type and the ambient temperature variable. The ambient temperature covariate was different for each response: for cavity maximum, it was ambient maximum; for cavity minimum, it was ambient minimum, and, for the difference between cavity maximum and minimum, it was the difference ambient maximum and minimum. Continuous covariates were again standardized for the bat models (mean subtracted, then divided by the standard deviation).

All LMMs were fitted to correct for heterogeneity in variance and potential spatial- and temporal-correlation resulting from our repeated measures, nested study design. For gliders, each individual cavity nested within each study tree, nested within each study season, was fitted as having a random effect on the intercept; however, for the bats, use of the cavity identification alone as a random effect was found to result in best model fit. Models were also fitted using either a corARMA or corCompSymm correlation structure to account for temporal correlation between records across hours or days [82]. We used the 'constant plus power of the variance covariate' function (varConstPower) to account for heterogeneity in the variance of the model's residuals, which changed for different cavity types according to ambient temperature [83].

3. Results

3.1. Ambient Conditions

Ambient conditions during the autumn bat box survey ranged from a minimum of 7.1 °C to a maximum of 31.7 °C, with mean (\pm SD) daily temperatures of 17.4 ± 3.4 °C (Appendix B). Conditions during the spring glider survey were comparable to the bat survey, ranging from 4.1 °C to 33.8 °C, with a daily mean of 16.3 ± 3.7 °C (Appendix B). During the summer, glider conditions were warmer,

daily temperatures ranged from a minimum of 26.8 °C to a maximum of 37.4 °C, with a daily mean of 27.3 ± 6.0 °C (Appendix B).

3.2. Cavity Thermal Profiles

Over the daily 24-h cycle, mean hourly temperatures (calculated from the raw data) in chainsaw hollows were comparable to natural hollows. For example, during the day by 3 p.m. (the time of day when ambient conditions were at their warmest and the greatest difference occurred between cavity and ambient temperatures), the glider chainsaw hollows and natural hollows were both cooler than ambient (glider chainsaw hollow 19.6 ± 4.3 , natural hollow 19.7 ± 5.0 , ambient 22.1 ± 6.1), while at night by 3 a.m. both were warmer (glider chainsaw hollow 17.8 ± 4.5 , natural hollow 17.8 ± 4.7 , ambient 15.2 ± 5.0 , Figure 3a). Similarly, the bat chainsaw hollows and natural hollows were cooler than ambient at 3 p.m. (bat chainsaw hollow 18.0 ± 3.3 , natural hollow 18.1 ± 3.6 , ambient 19.8 ± 4.1) and warmer than ambient at 3 a.m. (bat chainsaw hollow 15.4 ± 3.3 , natural hollow 14.3 ± 3.2 , ambient 13.5 ± 2.7 , Figure 3b). Mean hourly temperatures in log hollows were also cooler than ambient during the day at 3 p.m. (log hollow 20.2 ± 6.7) and warmer than ambient at night by 3 a.m. (log hollow 16.7 ± 5.1), but fluctuated more than temperatures in chainsaw hollows and natural hollows (Figure 3a). In contrast, the boxes exhibited the opposite pattern: both glider and bat boxes began warming rapidly in the morning and by 3 p.m. were much warmer than ambient (glider box 17.8 ± 4.5 , bat box 17.8 ± 4.7); at night, the box temperatures dropped rapidly and by 3 a.m. were either closely tracking (glider box 15.1 ± 5.23 , Figure 3a) or below (bat box 12.5 ± 3.0 , Figure 3b) ambient temperatures. Temporal patterns of cavity temperatures in natural hollows, chainsaw hollows and log hollows also followed ambient conditions but had a slower rate of heating and cooling than nest boxes, whereby daily cavity maxima and minima lagged 1–2 h behind the ambient (Figure 3).

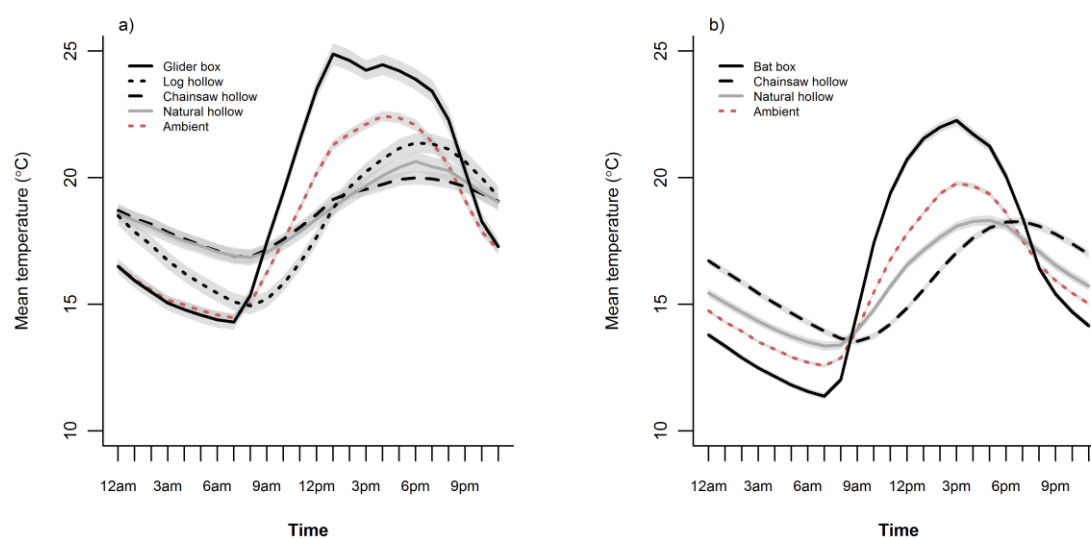


Figure 3. Mean temperature (°C, calculated from raw data) over 24 h inside natural and artificial hollows compared to external ambient conditions. (a) temperatures were recorded hourly in glider boxes, log hollows, natural hollows, chainsaw hollows, and outside under shaded ambient conditions over 50 days in spring (2 October to 20 November 2016) and 60 days in summer (23 December 2016 to 20 February 2017); (b) hourly temperatures were recorded in bat boxes, natural hollows, chainsaw hollows, and outside under shaded ambient conditions over 63 days in autumn (5 March to 6 May 2015). Shaded areas represent 95% confidence intervals.

Across the range of ambient conditions experienced during the study, both the hottest and coldest predicted mean temperatures were in glider boxes (max 38.7 CI 1.4, min −1.7 CI 1.4) and bat boxes (max 40.3 CI 0.7, min −3.6 CI 0.7), while log hollow cavity temperatures (max 32.1 CI 1.4, min 3.83 CI 1.4)

were intermediate between the extremes recorded in nest boxes and the more stable conditions within natural hollows (glider max 28.8 CI 1.4, min 7.2 CI 1.4, bat max 28.4 CI 0.7, min 5.3 CI 0.7) and chainsaw hollows (glider max 27.3 CI 1.4, min 9.0 CI 1.4, bat max 29.2 CI 0.7, min 4.9 CI 0.7, Figure 4 and Appendix C).

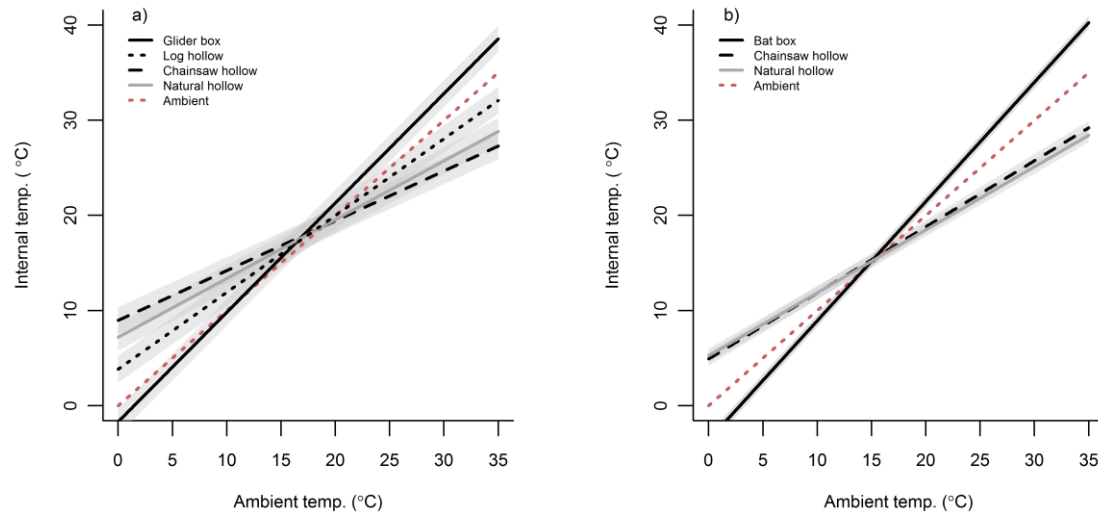


Figure 4. Modelled data showing predicted mean internal cavity temperatures (°C) across all ambient temperatures experienced during the study. (a) temperatures were recorded hourly in glider boxes, log hollows, natural hollows, chainsaw hollows, and outside under shaded ambient conditions over 50 days in spring (2 October to 20 November 2016) and 60 days in summer (23 December 2016 to 20 February 2017); (b) temperatures were recorded hourly in bat boxes, natural hollows, chainsaw hollows, and outside under shaded ambient conditions over 63 days in autumn (5 March to 6 May 2015). Shaded areas represent 95% confidence intervals. See Appendix C for Table of modelled parameter estimates.

For the glider cavities, the predicted temperatures in chainsaw hollows showed similar daytime maxima (0.2 ± 0.3) and nighttime minima (0.6 ± 0.3) relative to natural hollows (Figure 5 and Appendix D). In comparison, the glider boxes experienced far greater extremes (daytime max 6.2 ± 0.3 , nighttime min -3.1 ± 0.3), while log hollows (daytime max 1.0 ± 0.3 , nighttime min 2.3 ± 0.5) were intermediate between the box extremes and the more stable conditions within natural hollows and chainsaw hollows (Figure 5 and Appendix D). For example, based on the fitted models, when the daytime ambient temperature reached 37.2°C , the predicted maxima in chainsaw hollows (32.3°C) and log hollows (33.2°C) were 0.2°C and 1.0°C warmer than natural hollows (32.1°C), respectively, while glider boxes (38.3°C) were 6.2°C warmer than natural hollows (Figure 5a). When nighttime ambient conditions dropped to 4.4°C , the predicted minima inside chainsaw hollows (7.4°C) was 0.6°C warmer than natural hollows (6.8°C), while log hollows (5.8°C) and glider boxes (3.7°C) were 1.0°C and 3.1°C cooler, respectively (Figure 5d).

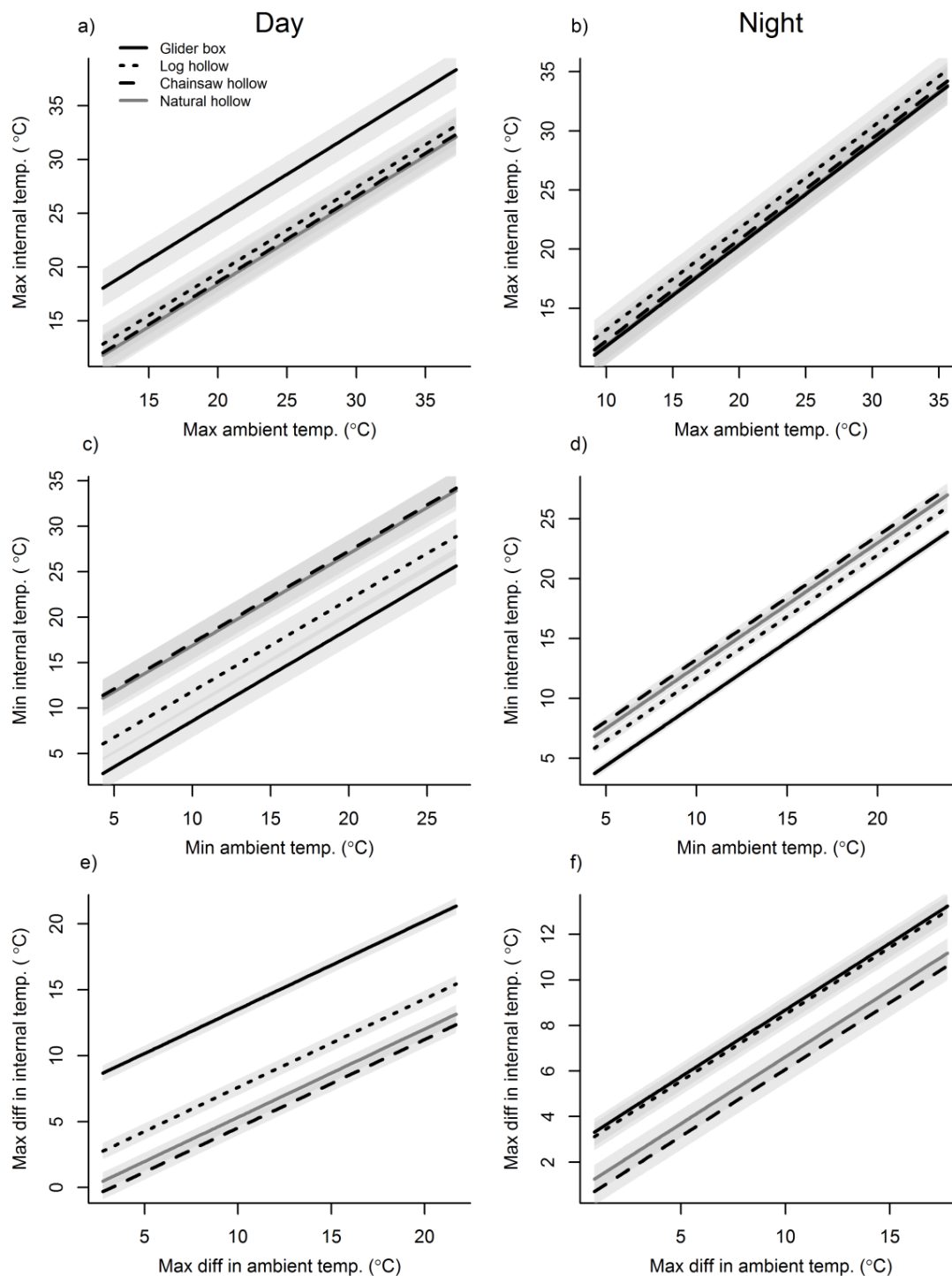


Figure 5. Modelled data showing predicted temperature (°C) response variables in glider nest boxes, log hollows, chainsaw hollows and natural hollows across the range of ambient temperatures recorded during the study. Data were combined across the two survey periods (spring, 2 October to 20 November 2016; summer, 23 December 2016 to 20 February 2017). Panels on the left show modelled averages recorded during the day ((a), daytime maximum; (c), daytime minimum; (e), difference between daytime maximum and minimum), and panels on the right for night ((b), nighttime maximum; (d), nighttime minimum; (f), difference between nighttime maximum and minimum). Shaded areas represent 95% confidence intervals. See Appendix D for Table of modelled parameter estimates.

For the bat cavities, when the chainsaw hollows were compared to natural hollows, they again had similar predicted daytime maxima (-0.6 ± 0.4) and nighttime minima (0.4 ± 0.4), while bat boxes had much greater extremes in daytime maxima (6.44 ± 0.51) and nighttime minima (2.0 ± 0.4 , Figure 6 and Appendix D). For example, when daytime ambient temperature reached 31.8°C , the predicted maxima in chainsaw hollows (26.3°C) was 0.6°C cooler than natural hollows (26.9°C), while bat boxes (33.3°C) were 6.4°C warmer than natural hollows (Figure 6a). At a nighttime ambient minimum of 7.1°C , the predicted minima inside chainsaw hollows (8.4°C) was 0.4°C warmer than natural hollows (8.0°C), while bat boxes (6.0°C) were 2.0°C cooler (Figure 6d).

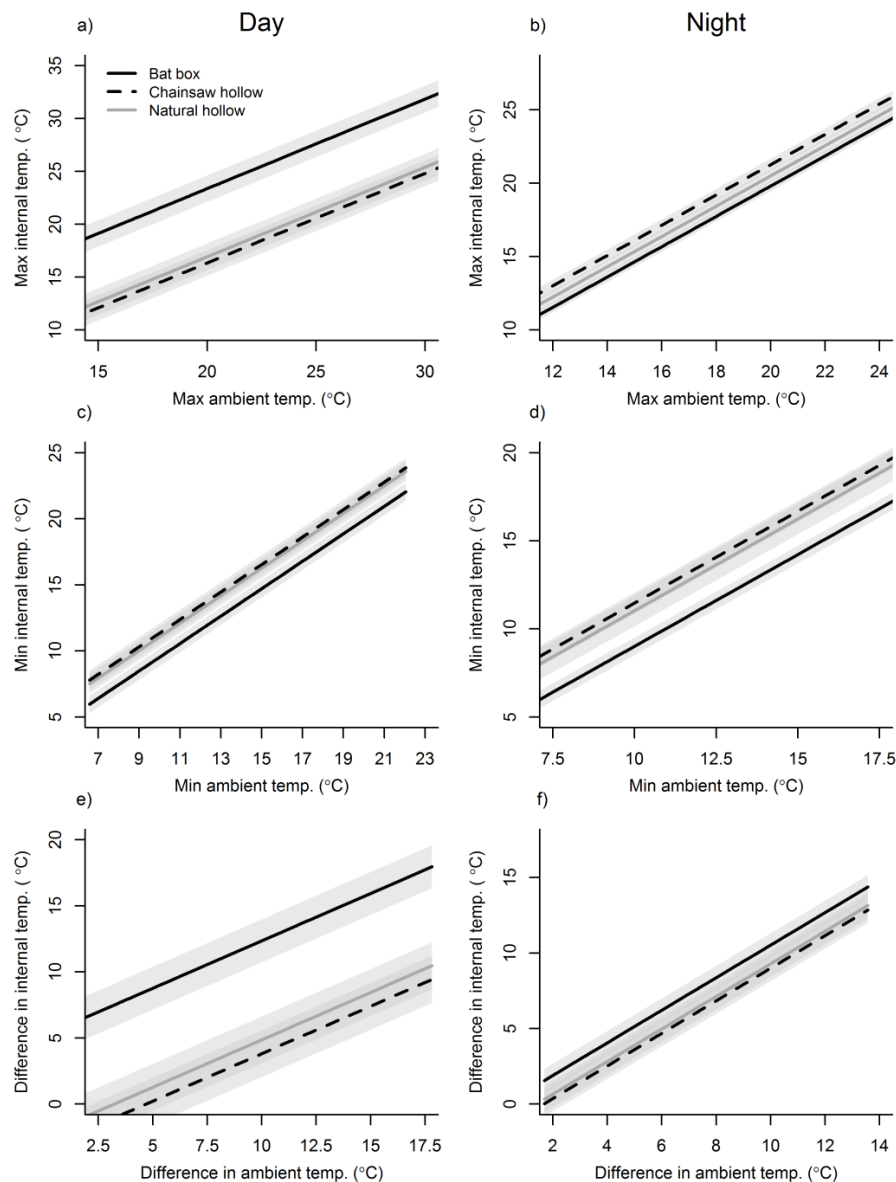


Figure 6. Modelled data showing predicted temperature ($^\circ\text{C}$) response variables in bat nest boxes, chainsaw hollows and natural hollows across the range of ambient temperatures recorded during the autumn survey period (5 March to 6 May 2015). Panels on the left show modelled averages recorded during the day ((a), daytime maximum; (c), daytime minimum; (e), difference between daytime maximum and minimum), and panels on the right for night ((b), nighttime maximum; (d), nighttime minimum; (f), difference between nighttime maximum and minimum). Shaded areas represent 95% confidence intervals. See Appendix D for Table of modelled parameter estimates.

Daily fluctuations in cavity temperatures were much greater in nest boxes than natural hollows, chainsaw hollows and log hollows (Figures 5 and 6 and Appendix D). For the glider cavities, the difference between daytime cavity maxima and minima in log hollows (predicted mean diff 7.9 °C, parameter estimate 2.3 ± 0.5) was intermediate between the large fluctuation that occurred in glider boxes (predicted mean diff 13.8 °C, parameter estimate 8.2 ± 0.5) and the more stable conditions within chainsaw hollows (predicted mean diff 4.8 °C, parameter estimate -0.8 ± 0.4), which were comparable to natural hollows (predicted mean diff = 5.6 °C, Figure 5e and Appendix D). While at night, differences within glider boxes (predicted mean diff 7.2 °C, parameter estimate 2.1 ± 0.2) and log hollows (predicted mean diff 7.1 °C, parameter estimate 1.9 ± 0.2) were similar, with both experiencing greater variation in cavity temperatures than chainsaw hollows (predicted mean diff 4.6 °C, parameter estimate -0.6 ± 0.2), which were again comparable to natural hollows (predicted mean diff = 5.2 °C, Figure 5f and Appendix D). For the bat cavities, bat boxes also had considerably greater difference in daytime cavity temperatures (predicted mean diff 10.6 °C, parameter estimate 7.5 ± 0.7) than in natural hollows (predicted mean diff = 3.1 °C), while the difference in chainsaw hollow temperatures (predicted mean diff = 2.0 °C, parameter estimate -1.1 ± 0.7) was comparable to natural hollows (Figure 6e and Appendix D). At night, the mean differences in cavity temperatures within chainsaw hollows (predicted mean diff = 4.1 °C, parameter estimate -0.3 ± 0.3) and natural hollows (predicted mean diff = 4.4 °C) were similar, while slightly larger variation occurred in bat boxes (predicted mean diff = 5.6 °C, parameter estimate 1.2 ± 0.3 , Figure 6f and Appendix D).

4. Discussion

Nest boxes are a popular tool for providing supplementary habitat for hollow-dependent fauna in disturbed landscapes where natural hollows are limited [4,21]. However, traditional plywood or timber nest boxes are not effective at replicating the thermal conditions that occur within natural tree hollows [28]. Consequently, nest boxes may provide thermal habitats that are sub-optimal for target fauna, particularly during extremely hot or cold weather [39,40]. We conducted a study to investigate whether artificial hollows cut with chainsaws into live trees and felled logs could better approximate the thermal properties of naturally occurring hollows in mature trees. Our results revealed that chainsaw hollows had thermal profiles that were similar to tree hollows, being consistently warmer than ambient conditions at night, while remaining cooler than ambient during the day. This daily pattern of heating and cooling could provide ecophysiological benefits to nocturnal mammals using cool chainsaw hollows (relative to external ambient conditions) during warm summer days by decreasing the amount of evaporative heat-loss required to maintain constant body temperature [39,40]. It could also benefit diurnal hollow-nesting birds using warm (compared to ambient) chainsaw hollows at night by decreasing the amount of metabolic heat production required to maintain core body temperature [41,84]. In contrast, glider and bat boxes had the opposite pattern of heating and cooling, being slightly colder than ambient at night and substantially hotter during the day. These findings provide the first empirical evidence that chainsaw hollows designed for target species could be used to deliver supplementary habitats with thermal conditions that closely mimic those in well-insulated natural tree hollows, thereby addressing a significant shortcoming of nest boxes [40].

Our data showed that natural hollows and chainsaw hollows had similarly low thermal inertia [85], both effectively buffering internal cavity temperatures from large daily variation in external ambient conditions. Conversely, the plywood glider and bat boxes had little thermal insulation, resulting in daily cavity temperature fluctuations that were considerably greater than ambient. Thermal profiles of log hollows were intermediate to these: they experienced greater variation in internal temperatures than natural hollows and chainsaw hollows, but were more stable than glider boxes. The difference in thermal stability of natural hollows and chainsaw hollows in live trees versus nest boxes and log hollows was likely driven by two factors. First, the wood surrounding hollows within the live tree trunks and branches would be much thicker than the 1.2 cm plywood nest boxes, and the approximately 4.7 cm timber walls of the log hollows [40,86]. Second, water flow within the

tree's living vascular tissue (i.e., cambium) was probably acting to cool the outer layers of the trunk and branches [87].

The thermal buffering capacity of natural hollows and glider chainsaw hollows, and the lack of thermal insulation provided by the plywood glider boxes, was particularly evident on hot summer days. For example, when ambient temperatures reached 37.0 °C (on 25 December 2016), maxima recorded in natural hollows and chainsaw hollows were 29.9 °C and 28.1 °C, which was 19.2% and 24.1% cooler than ambient, respectively, while glider boxes reached 46.6 °C (25.9% hotter than ambient). Previous studies have shown that endothermic animals using nest boxes on extremely hot days are likely to experience significant thermal stress as their capacity to lose body heat via evaporative heat-loss is reduced when den temperatures exceed 40 °C [40,64]. As a result, animals must trade-off between remaining in nest boxes and experiencing potentially lethal levels of hyperthermia [39,40,64,88], or vacating boxes and thereby increasing predation risk [89,90]. Furthermore, in secondary-cavity nesting passerines, even short exposure to nest temperatures exceeding 40.5 °C during egg incubation is lethal to developing embryos [91]. Therefore, the fact that our data show that chainsaw hollows remained much cooler than daily ambient maxima, and slightly cooler than natural tree hollows, indicates that these novel artificial habitats could provide more suitable thermal refuges than nest boxes during extremely hot weather events, which are predicted to increase in frequency and severity with anthropogenic climate change [92].

Our data show that the negligible insulative capacity of nest boxes made from 12 mm plywood results in temporal patterns of heating and cooling that are far more extreme than the daily temperature variation occurring within tree hollows. Nest boxes constructed from thicker timber, or from materials with greater insulation (e.g., a mixture of sawdust and concrete), are likely to produce more stable thermal profiles than the plywood boxes used in this study [28,40]. While these types of boxes are becoming more common in the Northern Hemisphere, the nest boxes used in this study were similar to designs that are widely used in southeastern Australia. Furthermore, better-insulated nest boxes may still be used predominantly by common, abundant species. For example, long-term monitoring of bat boxes in Melbourne, Australia has shown that, despite the provision of boxes constructed from materials with a range of insulative properties (ranging from 12 mm plywood to 90 mm pine), box use was dominated by one widespread, urban-adapted species, Gould's wattled bat *Chalinolobus gouldii* (Gray, 1841) [71]. Further research is required to investigate whether there is a link between the thermal profiles in nest boxes (compared to tree hollows) deployed in disturbed landscapes and their disproportionate level of use by widespread, highly adaptable species of birds [29,93,94] and mammals [21,71,95,96]. Field-based studies examining rates of occupation of chainsaw hollows and log hollows by target species versus undesirable exotic species would be of great interest, particularly in urban and peri-urban landscapes where nest box programs are often undertaken by land managers and conservation-focused community groups [4,97].

We found that glider log hollows were not as thermally stable as natural hollows or chainsaw hollows, but they were more effective at buffering extremes in daily ambient conditions than nest boxes. To date, log hollows have not been commonly used; however, there are several reported examples of fauna using salvaged log hollows attached to trees and other artificial structures, including torquise parrots *Neophema pulchella* (Shaw, 1792) [98], red-tailed black-cockatoos *Calyptorhynchus banksii graptogyne* (Latham, 1790) [99], and sugar gliders [100,101]. Combined with our data showing that log hollows can provide relatively stable thermal profiles, these findings suggest that, for developments where the removal of mature trees is unavoidable (e.g., road developments), using salvaged log hollows, or hollows carved into felled sections of solid timber, could be an effective method of supplementing the loss of tree hollows [102]. However, further research is required to investigate how variation in the moisture content of dead wood tissue influences the thermal buffering capacity of log hollows as they age. Furthermore, long-term studies are required to examine rates of weathering and attrition of log hollows compared to traditional plywood or timber nest boxes.

Despite initial trials investigating mechanical excavation of hollows in trees being conducted several decades ago in North America [32,103,104], these techniques have not been widely adopted (but see [31,105]). The lack of uptake has likely been due in part to such techniques being contradictory to widely adopted prescriptive guidelines for pruning amenity trees (i.e., trees with recreational, functional, environmental, ecological, social, health or aesthetic value, rather than for production purposes [106]). In this study, we addressed this by employing a two-stage systematic risk assessment procedure to reduce the probability of tree failures occurring. First, we used an empirical strength loss formula [75] to calculate the minimum stem diameter required to safely accommodate bat and glider chainsaw hollows (with pre-determined dimensions) into trunks and branches. Second, we consulted specialised arborists and the managers of the two study sites to select trees located in areas within the reserves that, in the event of trunk or branch failures, posed a negligible risk to the public. At the time of publication (approximately one and three years post installation for glider and bat hollows, respectively), no failures had occurred in any of the tree trunks or branches in which we cut chainsaw hollows. This provides preliminary evidence that, with careful planning incorporating site-specific risk assessments and candidate tree evaluation protocols, chainsaw hollows could potentially be safely carved into developing trees as novel supplementary habitats in management programs and in biodiversity offset programs. In relation to sourcing felled timber to make log hollows, pruning of amenity trees in a variety of landscapes is a widespread and ongoing management practice that provides ample opportunities for stakeholders to source timber (that would otherwise typically be chipped) that could be used for the creation of log hollows.

When assessing the efficacy of providing supplementary habitats for hollow-dependent fauna, consideration should be given to both the ecological value and the financial costs involved in making and maintaining the artificial habitats [21]. In our study, the primary expense was for highly skilled arborists, with the appropriate training and safety accreditation, and precision chainsaw work, to create the structures: it took approximately one hour to carve a glider chainsaw hollow (estimated cost = \$238 AUD), 20 min to carve a bat chainsaw hollow (estimated cost = \$79 AUD), and 30 min to carve a log hollow (estimated cost = \$120 AUD). Compared to the estimated cost of installing premium quality ‘off the shelf’ glider boxes (AUD \$225 per box, including purchase and installation), glider chainsaw hollows represent a similar expense, while log hollows were approximately half the cost. Installing bat chainsaw hollows would be significantly cheaper than premium quality two-chamber bat boxes (AUD \$198 per box, including purchase and installation). For these price comparisons, we intentionally chose high quality, and therefore relatively expensive, premade nest boxes, as we advocate for the use of boxes designed to last for a minimum of 20 years. The artificial hollows created during this project are part of a larger, ongoing study investigating temporal patterns in use of the different types of hollows by wildlife, along with documenting changes in tree health and any required maintenance. We anticipate that the expenses involved in ongoing monitoring of cavity use by wildlife will be the same for the different types of artificial hollows. One component of the ongoing monitoring that will be of particular interest are the costs associated with repairs, maintenance and replacement as the different types of artificial hollows weather and degrade. For the chainsaw hollows, cutting back wound-wood produced as trees callous over holes is likely to be required as an ongoing maintenance action [31,103,107]; however, the rate at which this may occur in the hollow host tree species used in this study is unknown.

5. Conclusions

In this study, we have shown that cavity temperatures within chainsaw hollows cut into live trees, and to a lesser extent felled logs, are more effective than nest boxes at mimicking the thermal profiles of natural tree hollows. Our results provide the first evidence that chainsaw hollows can potentially produce well-insulated, thermally stable supplementary habitats for hollow-dependent fauna in modified landscapes. However, it is still critical for mature hollow-bearing trees to be retained

where possible, as they contain a broad range of cavity types and sizes, along with many other ecological benefits beyond the provision of habitat for hollow-dependent fauna [67,108,109].

We have also presented further evidence that poorly insulated plywood nest boxes produce low-quality thermal habitats that are unlikely to adequately compensate for the loss of large hollow-bearing trees, particularly in regions that experience periodic extremes of hot or cold weather. There is a growing body of evidence questioning the general efficacy of traditional timber or plywood nest boxes as a conservation tool for communities of hollow-dependent fauna in disturbed landscapes [4,21,25,71,110]. Combined with the preliminary evidence of the uptake and use of chainsaw hollows by wildlife [31,37,38], this provides a positive impetus for collaboration between policy makers, conservation practitioners, the arboriculture industry, and managers of biodiversity offset programs, to empirically test the effectiveness of mechanically creating artificial hollows to provide well-insulated permanent structures within trees for hollow-dependent fauna.

Author Contributions: S.R.G., K.S. and P.E.L. conceived and designed the experiments; S.R.G., K.S. and P.E.L. performed the experiments; S.R.G. and P.E.L. analyzed the data; S.R.G. and P.E.L. contributed reagents/materials/analysis tools; S.R.G. wrote the paper; P.E.L., K.S., S.J.W., L.F.L. and K.A.R. revised the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest and also declare that the funding sponsors had no role in the design of the study, either in the collection, analyses, or interpretation of the data or in the writing of the manuscript, or in the decision to publish the results.

Appendix A. Detailed Description of Chainsaw Hollows and Log Hollows

Appendix A.1. Glider Chainsaw Hollows

To create the glider chainsaw hollows, we first cut a rectangular-shaped opening (8×20 cm; width \times height) through the bark (periderm) and into the sapwood layer of the tree trunk (i.e., the outer layers of living tissue involved in vascular transport). Using angled cuts with the chainsaw, we then carved out a rectangular-shaped cube from the central heartwood of the trunk (i.e., non-living solid inner tissue which no longer conducts vascular fluids) to form an internal cavity with dimensions $20 \times 20 \times 23$ cm (width \times depth \times height), 9200 cm^3 . Once the internal cavity was completed, we used a faceplate (8×20 cm, 3 cm thick) made from kiln-dried hardwood to block the opening. The faceplate was placed within the sapwood tissue layer, internal to the outer bark layer, to facilitate the formation of scar tissue over the faceplate (i.e., callusing), which in time will increase the structural integrity of the affected area of trunk [111]. An entrance hole (diameter = 3.5 cm) was cut directly above the faceplate to allow animals to access the internal cavity (Figure A1).



Figure A1. Photo sequence showing the process of cutting a glider chainsaw hollow into a tree trunk: (a) the trunk prior to cutting; (b) a rectangular opening (8×20 cm; width \times height) is cut through the bark and into the cambium layer, an internal rectangular cube-shaped cavity is then carved out (dimensions = $20 \times 20 \times 23$ cm (width \times depth \times height), 9200 cm^3); (c) a pre-made hardwood faceplate is screwed into place, leaving a 3.5 cm wide entrance above the faceplate; (d) the same chainsaw hollow 18-months post installation; note the tree has begun callusing over the faceplate.

Appendix A.2. Chainsaw-Carved Glider Log Hollows

We created glider log hollows by felling a live tree (*E. cladocalyx*) at the LTUZR and then cutting the trunk into 46 cm sections (i.e., logs) with a chainsaw. We selected logs with a diameter ranging from 25–29 cm and cut them in half, carved out a rectangular box with similar dimensions as the chainsaw hollows carved into trees: $16 \times 18 \times 28$ cm (width \times depth \times height), 8064 cm^3 . The two halves of

the log were then re-attached using galvanised screws and an entrance hole (diameter = 3.5 cm) was drilled into the side of the log hollow (Figure A2).



Figure A2. Chainsaw-carved log hollows designed for small marsupial gliders (*Petaurus* spp.).

Appendix A.3. Bat Chainsaw Hollows

To create bat chainsaw hollows, we first made a single plunge cut into the trunk or branch with the chainsaw blade angled upward at approximately 60° , resulting in a vertical slit entrance 2.5×15 cm (width \times height). We then made three further plunge cuts (to a depth of 25–30 cm) through the same entrance slit with the chainsaw blade at slightly different lateral angles. The bark and cambium tissue layers around the entrance slit were then scored with the chainsaw to reduce the tree's ability to callous over the entrance, plus to create a rough surface for bats to land on and grip when alighting to the entrance (Figure A3). Due to the design of the bat chainsaw hollows, it was not possible to accurately measure the dimensions of the internal 'wedge-shaped' cavity. Therefore, to obtain an estimate of the internal volume of the bat chainsaw hollows cut into trees, we used the same process described above to make three bat chainsaw hollows in felled logs. We then recorded the volume of water it took to fill the cavity within each of the logs, resulting in a mean (\pm SE) internal volume of 498.3 ± 7.3 cm³.

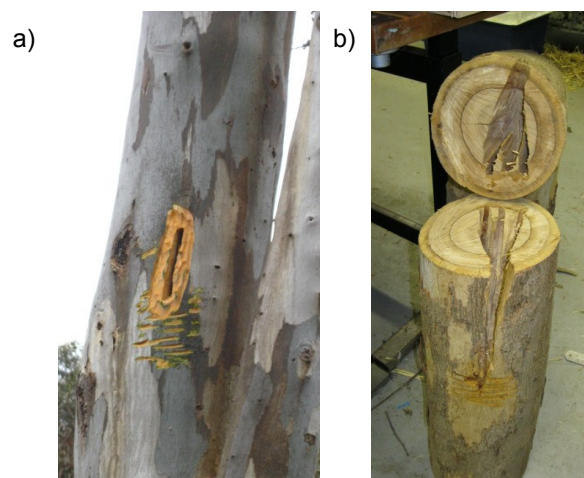


Figure A3. (a) bat chainsaw hollow cut into a tree trunk with a vertical entrance slit (2.5×15 cm; width \times height) designed to simulate the entrance to a natural fissure or crack in the trunk. (b) example of a bat chainsaw hollow cut into a felled log, with the same internal dimensions as those cut into trees, used to estimate the internal volume of the wedge-shaped cavity (mean \pm SE = 498.3 ± 7.3 cm³).

Appendix A.4. Measuring Canopy Cover

To estimate variation in canopy cover (to assess how much solar radiation reached natural hollows, bat chainsaw hollows and bat boxes), we quantified the ‘percent canopy cover’ above each natural and artificial bat cavity. Using a digital SLR camera (EOS 5D Mark II, Canon, Tokyo, Japan) with a circular (180° field of view) fisheye lens (8 mm 1:4.6 EX DG Lens, Sigma, Kanagawa, Japan) we took hemispherical photographs directly above each cavity. Variation in the exposure of photographs taken at different times, and on different days, was standardized in the field using the method described by Beckschafer et al. [112]. Digital photos were analyzed for percentage canopy shade using Gap Light Analyzer version 2.0.4 image processing software [113].

Appendix B. Summary of Ambient Conditions during the Study

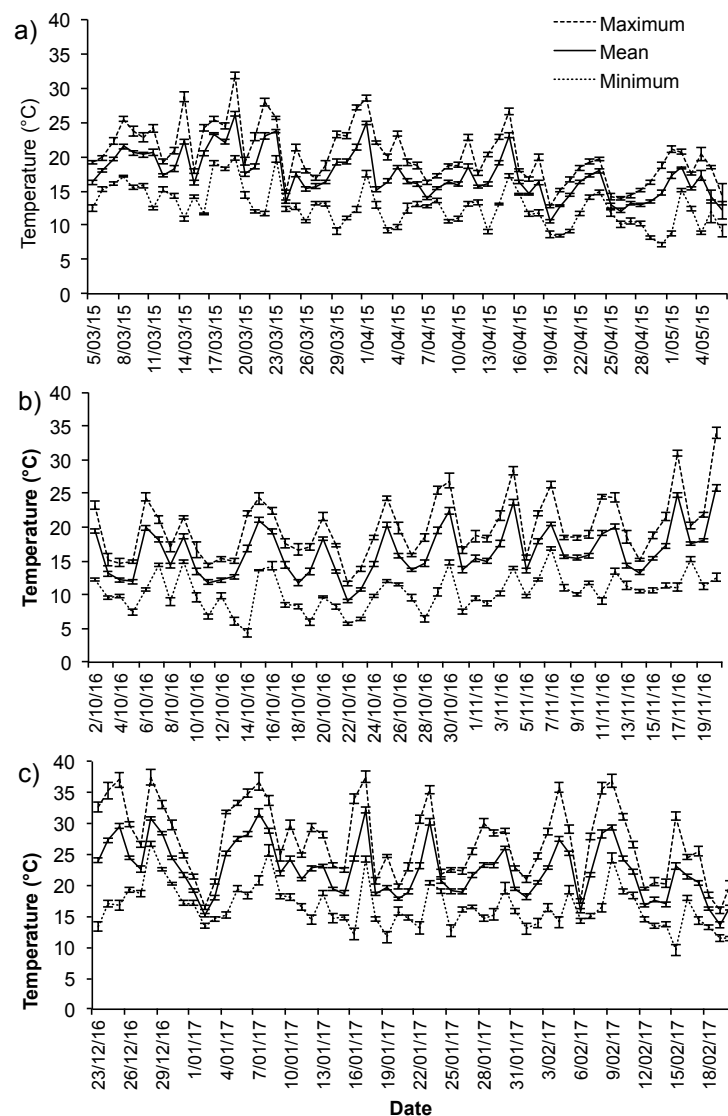


Figure A4. Daily minimum, mean and maximum (\pm SD) ambient temperature ($^{\circ}$ C) recorded during (a) the bat cavity monitoring in autumn (5 March to 6 May 2015), and during the glider cavity monitoring in (b) spring (2 October to 20 November 2016) and (c) summer (23 December 2016 to 20 February 2017).

Appendix C. Table of LMM Parameter Estimates for Mean Cavity Temperatures

Table A1. Parameter estimates (\pm SE) for model predictions of mean cavity temperatures ($^{\circ}$ C) across the entire range of ambient temperatures recorded: glider and bat cavities were modelled separately. For the glider cavities, internal temperature was modelled against an interaction between the structure type (natural hollow, chainsaw hollow, log hollow, glider box) and ambient temperature. For the bat cavities, internal temperature was modelled against an interaction between the structure type (natural hollow, chainsaw hollow, bat box), ambient temperature, plus covariates for structure orientation (cardinal direction: north, east, south, west), location (trunk or branch) and the percent shade from the canopy. The predictors for the bat models were standardized (mean subtracted, then divided by the standard deviation). “*” indicates the effect size relative to the intercept was significant at $p < 0.01$; “^” indicates a significant difference at $p < 0.05$.

Explanatory Variables	Estimate (\pm SE)
Glider cavities	
Intercept: Natural hollow	7.19 (± 0.70) *
Type: Chainsaw hollow	1.77 (± 0.31) *
Type: Log hollow	−3.36 (± 0.32) *
Type: Glider box	−8.89 (± 0.31) *
Ambient temperature	0.62 (± 0.00) *
Chainsaw hollow \times Ambient temperature	−0.09 (± 0.00) *
Log hollow \times Ambient temperature	0.19 (± 0.00) *
Glider box \times Ambient temperature	0.53 (± 0.00) *
Bat cavities	
Intercept: Natural hollow, Trunk, East	15.75 (± 0.17) *
Type: Chainsaw hollow	0.18 (± 0.13)
Type: Bat box	0.52 (± 0.13) *
Ambient temperature ¹	2.76 (± 0.01) *
Location: Branch	−0.25 (± 0.1) ^
Aspect: North	0.38 (± 0.17) ^
Aspect: South	0.02 (± 0.18)
Aspect: West	0.16 (± 0.17)
Shade ²	0.07 (± 0.05)
Chainsaw hollow \times Ambient temperature	0.14 (± 0.02) *
Bat box \times Ambient temperature	2.47 (± 0.02) *

¹ Mean (\pm SD) ambient temperature = 15.86 ± 4.17 . ² Mean (\pm SD) percent shade = 69.02 ± 7.24 .

Appendix D. Table of LMM Parameter Estimates for the Maximum, Minimum and Difference in Cavity Temperatures

Table A2. Parameter estimates (\pm SE) for model predictions of the effect of cavity type and ambient conditions on the maximum, minimum and difference (i.e., maximum—minimum) in cavity temperatures ($^{\circ}$ C) recorded during the day (from sunrise to sunset) and night (from sunset to sunrise). For the glider cavities, each internal temperature response variable was modelled against structure type (natural hollow, chainsaw hollow, log hollow, glider box) and an ambient temperature covariate (ambient maximum, ambient minimum, or the difference between ambient maximum and minimum). For the bat cavities, each internal temperature response variable (difference) was modeled against the following covariates: structure type (natural hollow, chainsaw hollow, bat box), an ambient temperature covariate (ambient maximum, ambient minimum, or the difference between ambient maximum and minimum), structure orientation (cardinal direction: north, east, south, west), location (trunk or branch) and the percent shade from the canopy. The predictors for the bat models were standardized (mean subtracted, then divided by the standard deviation). “*” indicates the effect size relative to the intercept was significant at $p < 0.01$; “^” indicates a significant difference at $p < 0.05$.

Explanatory Variable	Maximum (\pm SE)	Minimum (\pm SE)	Difference (\pm SE)
Glider cavities: day			
Intercept: Natural hollow	2.53 (\pm 0.88) *	6.78 (\pm 0.99) *	−1.38 (\pm 0.34) *
Type: Chainsaw hollow	0.23 (\pm 0.30)	0.30 (\pm 0.96)	−0.79 (\pm 0.44)
Type: Log hollow	1.04 (\pm 0.30) *	−5.03 (\pm 0.97) *	2.28 (\pm 0.45) *
Type: Glider box	6.24 (\pm 0.31) *	−8.28 (\pm 0.94) *	8.20 (\pm 0.45) *
Ambient temp variable	0.79 (\pm 0.01) *	1.01 (\pm 0.01) *	0.67 (\pm 0.01) *
Glider cavities: night			
Intercept: Natural hollow	3.33 (\pm 0.80) *	2.34 (\pm 0.25) *	0.75 (\pm 0.31) ^
Type: Chainsaw hollow	0.36 (\pm 0.19)	0.59 (\pm 0.32)	−0.55 (\pm 0.23) ^
Type: Log hollow	1.31 (\pm 0.20) *	−1.01 (\pm 0.32) *	1.87 (\pm 0.24) *
Type: Glider box	−0.09 (\pm 0.18)	−3.10 (\pm 0.31) *	2.06 (\pm 0.23) *
Ambient temp variable	0.86 (\pm 0.01) *	1.03 (\pm 0.00) *	0.59 (\pm 0.01) *
Bat cavities: day			
Intercept: Natural hollow, Trunk, East	17.08 (\pm 0.63) *	13.79 (\pm 0.36) *	3.12 (\pm 0.88) *
Type: Chainsaw hollow	−0.58 (\pm 0.42)	0.28 (\pm 0.28)	−1.05 (\pm 0.66)
Type: Bat box	6.44 (\pm 0.51) *	−1.54 (\pm 0.27) *	7.49 (\pm 0.65) *
Location: Branch	0.68 (\pm 0.35)	−0.80 (\pm 0.21) *	1.23 (\pm 0.51) ^
Aspect: North	2.03 (\pm 0.61) *	−0.30 (\pm 0.34)	3.34 (\pm 0.86) *
Aspect: South	0.93 (\pm 0.64)	−0.17 (\pm 0.36)	1.58 (\pm 0.90)
Aspect: West	1.77 (\pm 0.62) *	−0.26 (\pm 0.35)	2.61 (\pm 0.87) *
Ambient temp variable ¹	3.50 (\pm 0.03) *	3.27 (\pm 0.01) *	2.65 (\pm 0.03) *
Percent shade ²	−0.11 (\pm 0.17)	0.23 (\pm 0.10) ^	−0.37 (\pm 0.25)
Bat cavities: night			
Intercept: Natural hollow, Trunk, East	18.09 (\pm 0.22) *	13.26 (\pm 0.44) *	4.47 (\pm 0.43) *
Type: Chainsaw hollow	0.76 (\pm 0.20) *	0.44 (\pm 0.41)	−0.29 (\pm 0.33)
Type: Bat box	−0.70 (\pm 0.18) *	−2.02 (\pm 0.39) *	1.24 (\pm 0.31) *
Location: Branch	0.14 (\pm 0.12)	−0.30 (\pm 0.17)	1.07 (\pm 0.25) *
Aspect: North	0.18 (\pm 0.18)	−0.16 (\pm 0.25)	0.49 (\pm 0.41)
Aspect: South	0.17 (\pm 0.19)	−0.14 (\pm 0.27)	0.39 (\pm 0.43)
Aspect: West	0.18 (\pm 0.19)	−0.30 (\pm 0.27)	0.53 (\pm 0.41)
Ambient temp variable ³	3.37 (\pm 0.01) *	2.80 (\pm 0.01) *	3.12 (\pm 0.02) *
Percent shade ²	0.05 (\pm 0.06)	0.14 (\pm 0.09)	−0.23 (\pm 0.12)

¹ Mean (\pm SD) ambient temperature measures: maximum = 20.19 ± 4.14 ; minimum = 12.62 ± 3.15 ; difference = 7.57 ± 3.69 .

² Mean (\pm SD) percent shade = 69.02 ± 7.24 . ³ Mean (\pm SD) nighttime ambient temperature measures: maximum = 17.67 ± 3.27 ; minimum = 12.14 ± 2.69 ; difference = 5.53 ± 2.89 .

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