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WILDLIFE RESEARCH

Chainsaw hollows carved into live trees provide well insulated supplementary shelters for wildlife during extreme heat

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ABSTRACT

Context. Supplementary shelters for hollow-dependent fauna, such as timber or plywood nest boxes, have much drier and less thermally insulated cavity microclimates than do natural tree hollows. Hollow-dependent endotherms can experience hyperthermia and dehydration when occupying poorly insulated nest boxes during extreme heat. **Aims.** We investigated the effectiveness of three different types of artificial hollows in buffering hollow-dependent birds and mammals against hyperthermia and dehydration during extremely hot summer weather (ambient air temperatures >40°C). **Methods.** We recorded microclimate (temperature and relative humidity) data inside (1) chainsaw hollows carved into live trees, (2) log hollows, and (3) plywood nest boxes, during extremely hot weather events in Australia in December 2019–January 2020 (austral summer). We quantified temporal variation in microclimates inside the different supplementary shelters relative to ambient conditions and used statistical models to evaluate the effects of different factors (wall thickness and solar exposure) on internal microclimates. **Key results.** Microclimates inside chainsaw hollows were significantly different from those in log hollows and nest boxes, remaining >16°C cooler and 50 percentage points more humid than ambient conditions when daytime air temperatures reached 45°C. In comparison, nest boxes closely tracked ambient conditions throughout the day. Log hollows had an intermediate microclimate profile, getting warmer and drier than chainsaw hollows during the day, but remaining cooler and more humid than nest boxes. **Conclusions.** Our results showed that artificial hollows more effectively mimic the stable microclimates inside naturally occurring hollows if placed inside the tree (e.g. carved into the tree trunk of live trees), rather than attached to the outside. **Implications.** The chainsaw hollow design we tested could provide microclimate refugia that reduce the risks of hollow-dependent wildlife experiencing either hyperthermia in regions with hot summer climates, or hypothermia in areas with cold winters. We encourage managers to consider incorporating chainsaw hollows into existing nest box programs to provide fauna with well insulated microclimate refugia.

Keywords: artificial hollow, cavity microclimate, climate change, conservation biology, environmental stress, nest box, thermoregulation, wildlife management.

Introduction

Hollows that form in the trunk and branches of mature trees are critical habitat features used by a diverse range of invertebrate and vertebrate fauna (Gibbons and Lindenmayer 2002; Remm and Lohmus 2011). Historical land clearing in human-disturbed landscapes has resulted in large-scale reduction of mature hollow-bearing trees worldwide (Lindenmayer *et al.* 2012), and ongoing tree removals in selectively harvested forests, plus in agricultural and urban areas, is continuing these declines (Lindenmayer *et al.* 2014). Management strategies are therefore urgently required to increase the localised availability of hollows (Strain *et al.* 2021), and to ensure that, where possible, mature hollow-bearing trees are retained (Le Roux *et al.* 2014; Treby *et al.* 2014).

Given that formation of tree hollows by natural processes can take decades to centuries (Gibbons *et al.* 2000), artificial hollows (e.g. nest boxes) are widely used to provide supplementary shelters for hollow-dependent fauna in habitat restoration and wildlife management programs (Lambrechts *et al.* 2010; Macak 2020). However, timber or plywood nest boxes have much less thermal insulative capacity than do natural hollows that develop in mature trees (Maziarz *et al.* 2017). As a result, nest box-cavity microclimates can vary much more than those within hollows in live trees in response to day-to-day changes in solar radiation and ambient temperature (Griffiths *et al.* 2017, 2018). This variation is driven by two primary factors, namely: (1) the wood surrounding hollows within tree trunks and branches typically being much thicker than the walls of nest boxes (Strain *et al.* 2021); and (2) water flow and storage in living trees acting to cool the outer layers (i.e. cambium and alburnum) of the trunk and branches (Briscoe *et al.* 2014). During extremely hot weather events (ambient temperatures >40°C), occupying poorly insulated nest boxes may be problematic for endothermic animals because they can experience significant thermal stress and dehydration as boxes overheat (Rowland *et al.* 2017), in some cases causing mortality (Catry *et al.* 2011; Griffiths 2021). This highlights the need for the development and testing of supplementary shelters that have similar levels of insulation as do natural tree hollows, and thereby similar internal microclimates (Griffiths *et al.* 2018), particularly in regions that experience ephemeral hot weather events (Flaquer *et al.* 2014; Goldingay and Thomas 2021).

Recently, there has been growing interest in developing better-insulated nest boxes (Larson *et al.* 2018; Martin Bideguren *et al.* 2018; Ellis and Rhind 2021; Honey *et al.* 2021). Alternative habitat-creation methods, such as mechanically carving cavities directly into trees with chainsaws (chainsaw hollows, CHs), or re-attaching hollowed-out logs in trees (log hollows, LHs), also offer potential to provide well insulated shelters. For example, CHs carved into live trees have been shown to have a greater insulative capacity than have LHs and (timber or plywood) nest boxes, and, as a result, they can provide stable internal microclimates that are similar to those of natural hollows in large, old trees (Griffiths *et al.* 2018). However, no study has compared internal microclimates in CHs with those in nest boxes or LHs during hot weather events, that is, when ambient temperatures are >40°C. Such data are critical given the increased frequency, intensity and duration of heatwaves recorded over the past ~70 years in many regions globally (Perkins-Kirkpatrick and Lewis 2020). Furthermore, climate models predict that the trend of increasing extreme weather events will intensify in response to future climate warming (Coumou and Rahmstorf 2012; Cowan *et al.* 2014; Australian Bureau of Meteorology and CSIRO 2020).

In this study, we used extremely hot weather that was forecast to occur in December 2019 (austral summer) in Melbourne, south-eastern Australia, as an opportunity to record microclimate (temperature and relative humidity) data inside three different types of supplementary shelters, namely: (1) CHs; (2) LHs; and (3) nest boxes. We conducted a short-term field experiment and recorded ambient and internal-cavity microclimates concurrently over 15 consecutive days, during which time maximum daytime ambient air temperature exceeded 40°C on two separate days. We quantified temporal variation in microclimates inside the different supplementary shelters relative to ambient conditions. We used statistical models to evaluate the effects of different factors (wall thickness, solar exposure) on internal microclimates and to simulate predictions of internal microclimates under hypothetical extreme ambient conditions beyond the study data. We discuss our findings in relation to the capacity of the three types of supplementary shelters to buffer hollow-dependent fauna from exposure to physiologically stressful ambient conditions during extreme heat.

Materials and methods

Study site

We conducted this study at the La Trobe University Zoology Reserve (LTUZR; −37.715949, 145.049104), in the suburb of Bundoora, Melbourne, Victoria, south-eastern Australia (Fig. 1). The Greater Melbourne region experiences a warm temperate climate; temperatures range from a mean monthly maximum of 26.9°C in February (austral summer) to a minimum of 5.6°C in July (austral winter), but can exceed 40°C during summer and occasionally fall below 0°C during winter, with ~660 mL annual mean rainfall (Australian Bureau of Meteorology 2021). Vegetation in the LTUZR is regenerating river red gum (*Eucalyptus camaldulensis*) woodland with a grassy understorey (Griffiths *et al.* 2018).

Artificial hollows

Fieldwork was carried out under permits from La Trobe University Animal Ethics Committee (Ethics Permit AEC17-72) and the Department of Environment, Land, Water and Planning, Victoria, Australia (Research Permit 10008553). There was no animal handling or manipulation conducted during this study.

We compared ambient temperature and humidity with microclimates inside the following three types of artificial hollows designed for small hollow-dependent birds (e.g. musk lorikeet, *Glossopsitta concinna*; body mass ~70 g) and mammals (e.g. sugar glider, *Petaurus breviceps*; 100–150 g): (1) CHs; (2) LHs; and (3) nest boxes. In November 2016, we contracted arborists to carve CHs directly into the trunks of eight mature trees (sugar gum, *Eucalyptus cladocalyx*; mean diameter at breast height = 65.7 ± 15.8 cm, ±s.d.). The CHs were designed to replicate 'knot hole' cavities that form naturally at locations in tree trunks where branches break off (Mattheck and Breloer 1994). Knot holes are common structural features of many tree species and, consequently, are used by a wide range of hollow-dependent fauna,

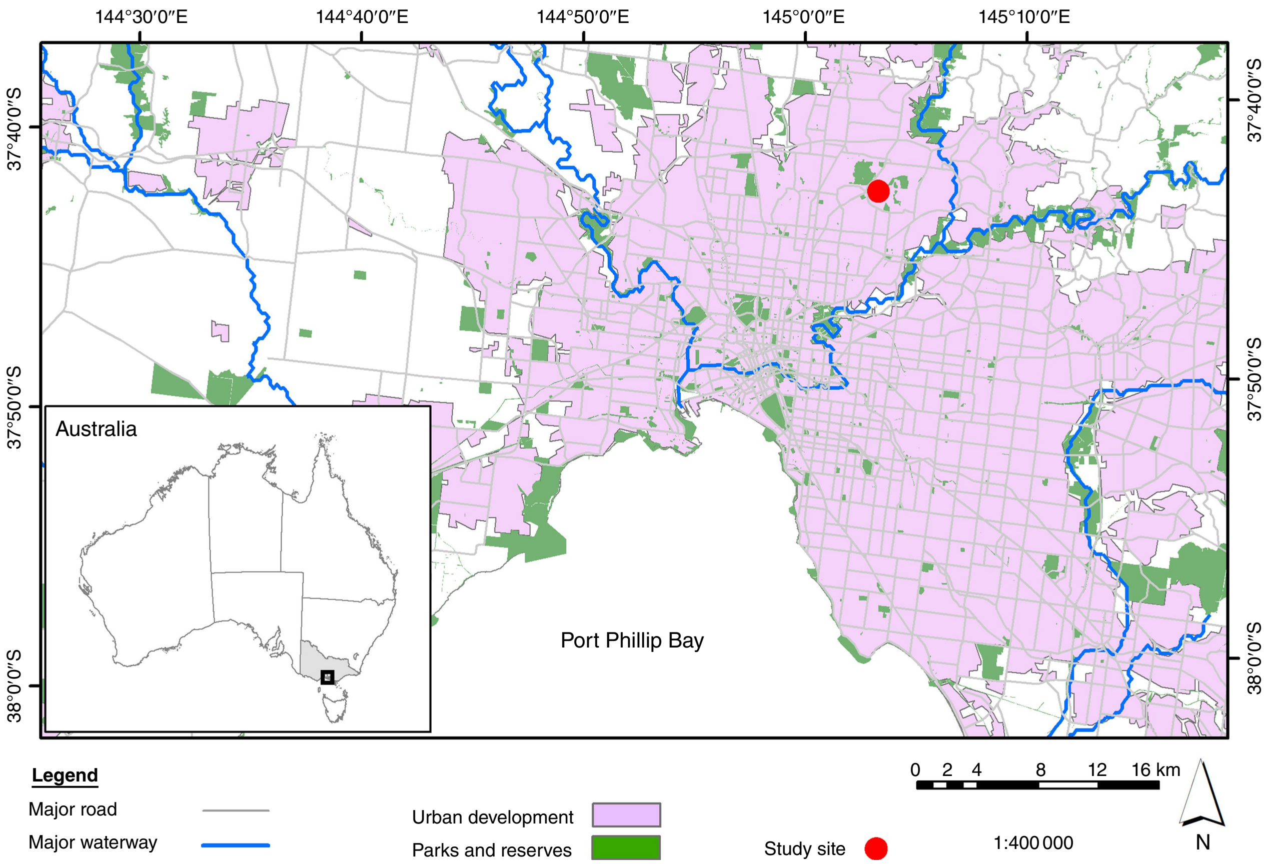

Fig. 1. Location of the La Trobe University Zoology Reserve (red circle) in the suburb of Bundoora, Melbourne, Victoria, south-eastern Australia.

including invertebrates, reptiles, amphibians, birds, terrestrial and arboreal mammals and tree-roosting bats (Gibbons and Lindenmayer 2002; Wesołowski and Martin 2018). The arborists carved a trapezoid prism-shaped cavity into the heartwood through a rectangular opening (8 × 20 cm, width × height) cut into the outer bark and vascular (cambium and sapwood) tissue (Fig. 2*a*, *b*). Internal volume of the eight CH cavities ranged from 4940 to 7644 cm^3 (mean = 6258 ± 892 cm^3; Fig. 2*a*, *b*). The cavities were sealed with a pre-made hardwood faceplate (10 × 20 × 3 cm, width × height × depth), and a 3.5 cm diameter entrance hole was drilled above the faceplate (Fig. 2*c*). Because of the irregular shape of the CH cavities, we could not accurately measure wall thickness. To estimate the amount of wood tissue surrounding each CH (i.e. wall volume), we calculated the volume of the section of the trunk where the CH was carved and then subtracted the volume of the CH cavity. The mean (±s.d.) wall volume across the eight CHs was 76 145 ± 37 427 cm^3. Note that this metric underestimates the total volume of wood surrounding each CH because it does not include tissue in the trunk above or below the cavity.

In May 2018, we created LHs by felling a live tree (*E. cladocalyx*) and then cutting the trunk into lengths with a chainsaw (i.e. logs). The mean (±s.d.) dimensions of the eight logs were as follows: length = 60 ± 3 cm; diameter = 31 ± 2 cm; total log volume = 45 632 ± 5822 cm^3. We then carved a cylindrical-shaped internal cavity (Fig. 2*e*) with similar volume (mean = 6343 ± 675 cm^3) as the CH cavities carved into trees, and drilled a 3.5 cm diameter entrance hole at the top of the cavity (Fig. 2*d*). We sealed the top and bottom of each log with 2 cm thick recycled plastic (high-density polyurethane) sheet (Fig. 2*f*). We calculated the wall volume of the eight LHs by subtracting the cavity volume from the total volume of each log (mean wall volume = 39 288 ± 5914 cm^3).

We purchased 'off-the-shelf' nest boxes designed for small marsupial gliders (Fig. 2*c*, *d*). The boxes were made from 1.5 cm thick marine plywood (15 × 35 × 16 cm, width × height × depth; cavity volume = 8400 cm^3), with a circular entrance hole (diameter = 3.5 cm) located at the top of the back panel of the box (i.e. entrance facing the tree trunk when installed). We did not paint the boxes. We calculated the wall volume of the nest boxes by adding the volume of the six plywood panels that comprised each box (i.e. front, back, sides, lid and floor; wall volume = 5582 cm^3).

On 19 December 2019, we attached a LH and a nest box to each of the eight trees with existing CHs, resulting in a total of eight of each type of artificial hollow (24 hollows in

Fig. 2. Diagram of a trapezoid prism-shaped chainsaw hollow cavity showing (*a*) cross-section and (*b*) side views of the trunk (cavity dimensions shown are in mm); grey-shaded rectangles represent the pre-made hardwood faceplate (100 × 200 × 30 mm, width × height × depth; adapted from Best *et al.* 2022). (*c*, *d*) An example of a nest box (1.5 cm thick marine plywood; internal cavity dimensions 15 × 35 × 16 cm, width × height × depth; cavity volume = 8400 cm^3), log hollow (mean ± s.d. dimensions of the eight logs: length = 60 ± 3 cm; diameter = 31 ± 2 cm; cavity volume = 6343 ± 675 cm^3) and chainsaw hollow (mean volume of the eight cavities = 6258 ± 892 cm^3) installed on a single tree (sugar gum, *E. cladocalyx*); all artificial hollows had a 3.5 cm diameter entrance hole; the nest box and (e) LH entrances faced the trunk. (*f*) Internal view of a cylindrical cavity carved into a log hollow.

total; Fig. 2*c*, *d*). The artificial hollows were installed at heights ranging from 1.5 to 2.5 m above the ground to facilitate ease of access for recording internal microclimate data (see configuration of artificial hollows shown in Fig. 2). All artificial hollows were aligned facing east (either cut into, or attached to, the eastern side of the tree trunk, as is considered best-practice in Australia; Roads and Traffic Authority 2011) to ensure they received the same temporal pattern of exposure to solar radiation (Griffiths *et al.* 2017, 2018).

Monitoring cavity microclimates

We used data loggers (Hygrochron iButton model DS1923, Maxim Integrated Products Inc., USA) to simultaneously record temperature and humidity within artificial hollows and ambient conditions. The operating range for DS1923 Hygrochron iButtons is from −20 to +85°C and 0% to 100% relative humidity; measurement precision for temperature is ±0.5°C and for humidity ±5% (Maxim Integrated Products Inc. 2015). Saturation drift is a known potential problem for humidity data recorded using DS1923 Hygrochron iButtons, where the measurements become less accurate through time. To account for this, a saturation drift correction was applied to the humidity data in this study, using the manufacturer's equations (Maxim Integrated Products Inc. 2015, pp. 53–54).

We attached data loggers (that were held within a plastic fob) to wire and suspended them inside each artificial hollow about 5 cm below the entrance hole, toward the middle of the cavity. We also attached data loggers to the southern side of the trunk of three trees (2 m above the ground) to record ambient conditions; these loggers were housed within a white plastic funnel, to ensure that they were not exposed directly to sunlight or wind. We programmed all loggers to record microclimate data every 10 min over 15 consecutive days during austral summer, from 20 December 2019 to 3 January 2020. During data recording, the entrances to the artificial hollows were blocked with wire mesh, facilitating natural airflow while excluding animals from occupying boxes and thus altering cavity microclimates (Griffiths *et al.* 2017).

Measuring canopy cover and solar exposure

We used the method described by Griffiths *et al.* (2017) to calculate the 'percentage canopy openness' above each grouping of a CH, LH and nest box on a tree. Using a digital SLR camera (EOS 5D Mark II, Canon, Japan) with a circular (180° field of view) fisheye lens (8 mm 1:4.6 EX DG Lens, Sigma, Japan), we took hemispherical photographs directly above each group of artificial hollows (i.e. one photo per tree). Variation in the exposure of photographs was standardised in the field using the method described by Beckschafer *et al.* (2013). Digital photos were analysed for percentage canopy openness using Gap Light Analyzer version 2.0.4 (https://www.sfu.ca/rem/forestry/downloads/gap-light-analyzer.html) image-processing software (Frazer *et al.* 1999). The mean ± s.d. canopy openness across the eight trees was 69.8 ± 5.8%. We then used solar-radiation data (W m^{-2}) recorded every minute at Melbourne Airport (Australian Bureau of Meteorology 2021), approximately 20 km from the study site, to calculate an index of solar exposure (to assess how much solar radiation reached the artificial hollows) by multiplying the total amount solar radiation recorded every 10 min (to match times when data loggers took records) by percentage canopy openness for each tree.

Historical and future climate data

To understand and evaluate the observed data within the context of historical and future climates, we extracted historical climate data from the study area (Australian Bureau of Meteorology 2021) and hypothetical maximum future climate scenarios based on Coupled Model Intercomparison Project Phase 5 [CMIP5] predictions (Australian Bureau of Meteorology and CSIRO 2020). Data were available only for temperature, not humidity, for historical and future scenarios. We identified the highest maximum temperature recorded within the study area historically (all years since 1979 from Bundoora station 86351), to indicate the upper limit of historical extremes, with a highest recorded temperature of 46.5°C in February 2009 (Australian Bureau of Meteorology 2021). Future climate model predictions from the 'Climate Change in Australia' website (CSIRO and Bureau of Meteorology 2021) indicated that maximum temperatures in the Melbourne region in 2070 would be approximately 3°C hotter than current conditions (mean: 2.9, 10–90%, range: 2.4–4.2), with more than twice the number of days >40°C and approximately 30% more days >35°C (ACCESS1-0 model), under high emission scenarios (RCP 8.5).

Data analysis

All data compilation and analyses were conducted using R version 4.0.3 (R Core Team 2020, R: a language and environment for statistical computing; R Foundation for Statistical Computing, Vienna, Austria). Data analyses were conducted for cavity microclimates (temperature and relative humidity) to determine how the effect of cavity type (CH, LH and nest box) and cavity wall thickness resulted in departures from ambient conditions. We then conducted simulations on the basis of these models to predict cavity microclimates under potential ambient climates within and beyond the range of the study data.

Linear mixed-effects models (LMM) were used for microclimate models. We initially evaluated the effect of cavity wall thickness on the microclimates of CHs only, to isolate an effect separate from cavity type. We restricted the data to daytime only, indicated by non-zero solar radiation index values, so that the effect of buffering against heating could be determined as per the focus of the study. We did not conduct a separate model to examine the effect of buffering against cooling because of the mild night temperatures of the study period. Separate models were run for temperature and humidity. Ambient temperature and relative humidity (mean values across relevant loggers for each 10-min interval) and cavity wall thickness were included as fixed effects, and tree identity was included as a random effect to allow for minor variation in data relationships among trees owing to variation in immediate environmental or unmeasured factors. Ambient climate variables and cavity wall thickness were scaled (mean subtracted, then divided by the standard deviation) prior to analysis to enable direct comparison of effects.

We then constructed LMMs to evaluate the effects of cavity type on microclimates and to make simulated predictions for temperatures within and above the range recorded in the study data. Ambient temperature and relative humidity throughout the study period (day and night to compare microclimates over the full range of observed data), cavity type and cavity wall thickness were included as fixed effects, whereas tree identity was included as a random effect. Continuous variables were scaled as above. An interaction term was added between ambient temperature and cavity type to account for the differing impacts of cavity types at different temperatures.

We ran the LMMs using the *lmer* function in the *lme4* package (Bates *et al.* 2015). Model fits were estimated using the *r.squaredGLMM* function within the *MuMIn* package (Barton 2020, MuMIn: Multi-Model Inference; R package version 1.43.17), providing the marginal and conditional R^2 values for each model. Visual inspection of model outputs was also conducted by reviewing residual plots and quantile–quantile regressions. Significance was defined by the threshold of $P < 0.05$. We investigated the use of corCompSymm correlation structure to account for temporal correlation between records (Zuur *et al.* 2009) but found that this did not improve model performance because the ambient temperature covariate adequately accounted for temporal patterns and correlations.

LMM simulations were then used to predict cavity microclimate values using the variance components in the fitted model. Predictions spanned the range of values recorded within the study and extended into more extreme unobserved ambient conditions matching historical extremes (46.5°C in 2009) or hypothetical maximum future scenarios (49.5°C in 2070) outlined above. These models assumed an approximate linear relationship between cavity and ambient temperatures, which corresponded with recorded data during heating and cooling phases and replicated approaches used by Griffiths *et al.* (2017, 2018). Cavity wall thickness was input as the mean wall thickness within each cavity type across the study.

Results

Ambient temperatures varied considerably over the study period, with daily maxima ranging from 23°C to 45°C (daily minima 10–20°C; Fig. 3*a*). Ambient humidity was variable at the daily minimum level (8–50%) but had stable daily maximum values (71–97%; Fig. 3*b*). Two days exceeded 40°C during the study (45.0°C and 44.0°C; Fig. 3*a*), which captured the hottest days of the 2019/2020 austral summer within the study area. Correspondingly, these days also had the lowest humidity levels during the study period (7.7% and 10.4% respectively; Fig. 3*b*).

Cavity microclimates differed substantially among the hollow types. Nest box-cavity temperatures tracked ambient temperature very closely (Fig. 3*a*), but were drier than ambient humidity during both day and night (Fig. 3*b*). LHs were more buffered against ambient temperatures, increasing more slowly and retaining heat longer into the night than did nest boxes (Fig. 3*a*). LHs retained greater humidity during the day but had night-time humidity similar to that of nest boxes (Fig. 3*b*). CH microclimates were dramatically different from those of externally attached artificial hollows and were highly buffered against variation in ambient climate. CH-cavity temperatures increased very slowly and retained heat longer into the evening (Fig. 3*a*), and had a very stable (and high) humidity that was much greater than ambient conditions during the day (Fig. 3*b*), compared with LHs and nest boxes.

Cavity microclimates on the hottest day (20 December 2019) highlighted the climate-buffering capacity of CHs, and, to a lesser extent, LHs (Fig. 3*c*, *d*). Both LHs and CHs retained heat over night and remained cooler than ambient temperature throughout the day. LHs warmed rapidly in afternoon peak temperatures, whereas CHs performed much better in terms of keeping cool during afternoon peak temperatures, with mean temperature differences from the ambient maximum of 16°C (range 10.8–18.8°C), compared with 9°C (range 6.7–10.8°C) for LHs (Fig. 3*c*). LHs and CHs also maintained ~30% and ~50% respectively, higher humidity than the ambient humidity throughout the afternoon until nightfall (i.e. from 11 am to 8 pm; Fig. 3*d*). Nest-box temperatures were similar to ambient temperatures throughout the day, whereas humidity was lower overnight and typically only marginally higher than the ambient humidity during daylight hours (Fig. 3*c*, *d*).

Visual inspection of the data showed no clear patterns in CH microclimate extremes (maximum daily temperature and minimum daily humidity) in relation to cavity wall volumes (Appendix 1). CHs in two trees with smaller wall volumes had consistently high humidity regardless of ambient conditions, which appeared to be unrelated to canopy openness because one had the highest canopy openness and the other the lowest. Canopy openness was poorly correlated with microclimates and was excluded from subsequent models. Statistical models examining the effect of CH wall volume during the day had moderate model fit (conditional R^2: temperature = 0.56, humidity = 0.83 [marginal R^2 = 0.14]) and indicated no significant effect of wall volume on temperature (estimate = 0.30 ± 0.20 s.e., d.f. = 6, P = 0.19) or humidity (estimate = −4.67 ± 5.11 s.e., d.f. = 6, P = 0.40). Full model outputs are provided in Appendix 2.

Model simulations were used to predict cavity microclimate conditions from ambient conditions for each cavity type. We made predictions for hotter historical and potential future climate scenarios at the study site, which suggested that hotter future climates with higher peak temperatures may result in CHs and LHs up to 20°C and 10°C below ambient temperatures respectively, whereas nest boxes remain close to ambient (Fig. 4, Table 1). Predictions

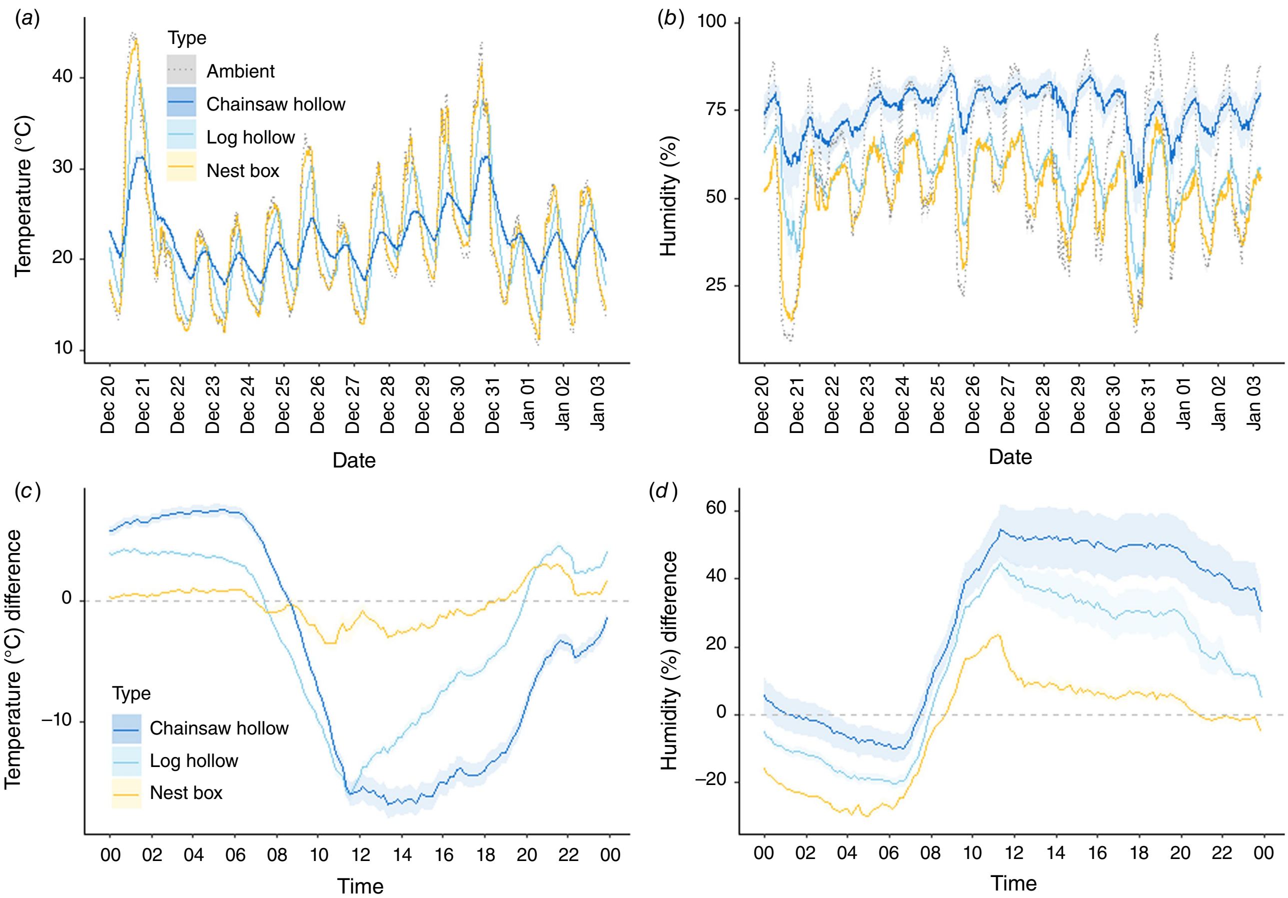

Fig. 3. Cavity and ambient microclimate data from the study including: (*a*) mean cavity and ambient temperatures (°C) throughout the study; (*b*) mean cavity and ambient relative humidity (%) throughout the study; (*c*) the difference between cavity and ambient temperatures on the hottest day (20 December 2019; sunrise 05:53 am, sunset 08:41 pm); and (*d*) the difference between cavity and ambient relative humidity on the hottest day. Lines indicate mean values with shaded areas around each line indicating one standard error around the mean. The horizontal dashed line in (*c*) and (*d*) indicate no difference from ambient conditions.

showed the near 1:1 relationship between ambient temperature and nest box-cavity temperature, compared with much flatter relationships for LHs and CHs, which are buffered against extreme temperatures (Fig. 4*a*). There were large differences in humidity between cavity types at low ambient humidity and much less at high humidity (Fig. 4*b*). Model fits were good for temperature ($R^2 = 0.81$) and humidity ($R^2 = 0.75$) because of the availability of accurate ambient climate data and consistent effects of cavity type, which resulted in model predictions within less than 2°C (temperature) or 8% (humidity) of observed values (Table 1). Full model outputs are provided in Appendix 3.

Discussion

Recent studies trialling the use of cavities carved directly into trees have reported promising results, with a range of native hollow-dependent birds and mammals visiting and using these novel supplementary shelters (Hurley and Harris 2014; Bengtsson and Wheater 2021; Terry *et al.* 2021; Best *et al.* 2022). However, little is known about microclimate conditions inside mechanically carved hollows (Griffiths *et al.* 2018; McComb *et al.* 2021), particularly during weather extremes. In this study, we used the opportunity presented by extremely hot weather that occurred during December 2019 (austral summer) in Melbourne, Australia, to compare microclimate conditions in plywood nest boxes, which are commonly used in habitat restoration and wildlife conservation programs (Macak 2020), with two relatively novel and untested types of artificial hollow that are increasingly being used across south-eastern Australia, namely (1) CHs (Griffiths *et al.* 2020; McComb *et al.* 2021; Terry *et al.* 2021) and (2) LHs (Griffiths *et al.* 2018). We found that CHs carved into the trunks of live *Eucalyptus* trees were well insulated, remaining much cooler (16°C) and six times more humid than ambient conditions during the hottest part of the day on extremely hot summer days. In comparison, off-the-shelf plywood nest boxes provided minimal buffering and essentially tracked ambient conditions throughout the

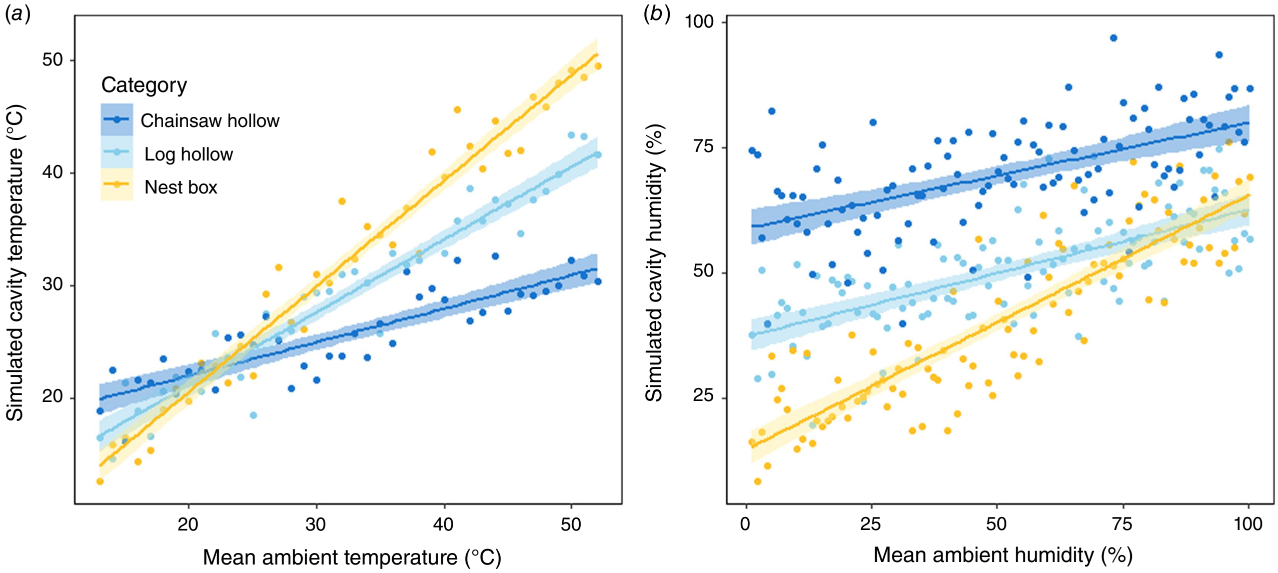

Fig. 4. Simulated predictions of cavity (*a*) temperatures (°C) and (*b*) relative humidity (%) within chainsaw hollows, log hollows and nest boxes on the basis of LMMs of study data. Predictions extend beyond the limits of our study data to evaluate hypothetical extremes (using Coupled Model Intercomparison Project Phase 5 [CMIP5] predictions; Australian Bureau of Meteorology and CSIRO 2020). Lines indicate mean values, with shaded areas indicating 95% confidence intervals around the mean.

Table 1. Observed and predicted cavity microclimates (temperature, °C; relative humidity, %) for chainsaw hollows, log hollows and nest boxes within the study area.

Period and cavity type	Humidity (Dec. 2019)	Temperature (Dec. 2019)	Temperature (Feb. 2009)	Temperature (2070)
Ambient	**9.2**	**45.0**	46.5	49.5
Chainsaw hollow	**59.2** (64.8)	**28.8** (29.7)	30.2	31.1
Log hollow	**38.4** (41.9)	**35.9** (37.6)	38.6	40.6
Nest box	**15.6** (23.6)	**42.9** (44.4)	45.9	48.7

Predictions were made for the current study, peak historical temperature (recorded in February 2009; Australian Bureau of Meteorology 2021) for the study site and maximum predicted future temperatures (using Coupled Model Intercomparison Project Phase 5 [CMIP5] predictions; Australian Bureau of Meteorology and CSIRO 2020). Observations made during this study are indicated by bold type, with predictions in parentheses and/or non-bold type.

day. LHs had an intermediate microclimate profile, getting warmer and drier than CHs during the day, but remaining cooler and more humid than nest boxes. Our results suggest that, of the three artificial hollow designs tested, CHs were the most effective microclimate refugia in terms of their capacity to buffer occupants from external ambient conditions during extremely hot weather. This finding confirms that artificial hollows may ultimately be more effective in mimicking the stable microclimates of naturally occurring hollows if placed inside the tree (e.g. carved into the trunk; Zapponi *et al.* 2014; Griffiths *et al.* 2018), rather than attached to the outside (Maziarz *et al.* 2017).

Cavity microclimates

Thermal variation within tree cavities is important for hollow-dependent endotherms because it influences the metabolic costs of thermoregulation and water balance required to maintain core body temperature (Huey 1991; Stawski *et al.* 2014; McComb *et al.* 2021). Previous studies have shown that birds and mammals using artificial hollows on extremely hot days are likely to experience significant thermal stress because their capacity to reduce body heat via evaporative cooling is reduced when cavity temperatures exceed 40°C (Catry *et al.* 2011; Griffiths *et al.* 2017; Rowland *et al.* 2017; Griffiths 2021). Our results showed that birds and mammals occupying cool, humid CHs during extremely hot weather would need to use much less water to avoid overheating via evaporation, than would those in nest boxes, which reached temperatures above the thermo-neutral zone of most endotherms (>40°C; Dawson 1969; Porter and Kearney 2009; Turner 2020).

The differences we recorded in thermal profiles of CHs versus nest boxes could have been amplified with minor modifications to box design and installation characteristics.

For example, a previous study at the same field site found that similar-sized nest boxes, made from 1.2 cm plywood and painted dark green, reached 40–45°C when ambient temperatures were 35–38°C, with boxes facing north and west getting hotter than those facing south and east (Griffiths *et al.* 2017). This also suggests that the extreme temperatures recorded in nest boxes during our study would have been much greater if boxes had faced a north or west orientation and, hence, received direct sunlight during the hottest parts of the day (Griffiths *et al.* 2017; Strain *et al.* 2021), which we avoided by using best-practice methods suggesting an easterly orientation (Roads and Traffic Authority 2011).

The insulative capacity of the CHs carved into live trees that we found was likely to be driven by the surrounding wood tissue impeding convective heat transfer between external ambient air and the air inside the internal cavity (Coombs *et al.* 2010). Moisture (with high specific heat capacity) in the outer layers of wood tissue (cambium and alburnum) in live trees would also reduce conductive heating of the cavity through the walls as they heat up from solar radiation (Briscoe *et al.* 2014). In addition to buffering cavity temperatures as ambient air temperature increases during the day, these processes would also reduce convective heat loss from inside the CH cavity as ambient temperatures cool overnight. This pattern can be observed in our data, where variation in CH temperatures, and to a lesser extent LHs, lagged behind changes in ambient conditions, while less well insulated nest boxes closely tracked temporal variation in ambient temperatures and humidity. This pattern appears to be a consistent feature of microclimates inside natural tree hollows, compared with timber or plywood nest boxes (Maziarz *et al.* 2017; Rowland *et al.* 2017).

Humidity within natural and artificial hollows has received less attention than has temperature (Maziarz *et al.* 2017; Strain *et al.* 2021). Our results showed that CHs had a very stable and high humidity that was much greater than ambient conditions during the day. In comparison, artificial hollows attached to the outside of the tree, particularly nest boxes, were much dryer. All nest boxes and LHs used in this study were stored indoors for >12 months prior to being installed on trees, and so their walls were likely to contain little moisture. The only rainfall that occurred during this study was 2.6 mm on 31 December 2019 (Australian Bureau of Meteorology 2021), which was unlikely to have significantly influenced moisture levels in the walls of the nest boxes and LHs. The consistently higher humidity inside CHs, than in nest boxes and LHs, was therefore likely to be driven by water moving through the sapwood (alburnum) and the outer cambium tissue of the live trees, and moisture stored in the inner heartwood tissue. Despite consistently high humidity, there was no evidence of water pooling inside the CHs during this study, which has been observed in similar CHs carved into various *Eucalyptus* spp. in ironbark woodland in central Victoria (Terry *et al.* 2021) and temperate forest in the Victorian Central Highlands (L. Lumsden, pers. comm.). The level to which water pools within CHs, LHs and nest boxes after rainfall events, or in regions with wetter climates, warrants further investigation, as this could potentially influence their availability and suitability as shelters for wildlife (Wesołowski and Martin 2018).

The extreme temperatures recorded within the study period (45°C) were the hottest in austral summer 2019/2020 and were only 1.5°C lower than the hottest temperature on record for the study area (February 2009) (Australian Bureau of Meteorology 2021). Climate predictions for greater and more frequent extreme conditions throughout Australia (Australian Bureau of Meteorology and CSIRO 2020) suggest that the need to provide climate-buffering supplementary shelters is likely to increase in coming years. With predictions of ambient extremes potentially approaching 50°C in Victoria by 2070 (Australian Bureau of Meteorology and CSIRO 2020), the CH design we tested could reduce cavity temperatures by as much as 19°C, compared with nest boxes, and even more if the boxes were painted dark colours and installed so that they are exposed to direct sunlight during ambient peaks (Griffiths *et al.* 2017). Commonly used timber or plywood nest boxes that closely track ambient conditions, or have limited buffering potential (Goldingay 2020), are therefore likely to become increasingly unsuitable during ephemeral weather extremes in the future. Studies are urgently needed to empirically assess the ecophysiological effects (e.g. thermal stress and dehydration) for hollow-dependent fauna occupying different types of supplementary shelters during hot weather.

In this study, our primary interest was to investigate suitability of cavity microclimates during extremely hot weather. However, well-insulated shelters carved into live trees could also provide benefits to endotherms during cold weather. The insulative capacity of CHs would mean that metabolic heat produced by endothermic animals would be more effectively retained inside the cavity than in supplementary shelters with thinner walls, such as nest boxes (Rowland *et al.* 2017). As a result, endothermic animals occupying CHs would be likely to experience lower metabolic heat-production costs to maintain a constant body temperature during cold weather, than would animals in nest boxes or LHs (Griffiths *et al.* 2017; McComb *et al.* 2021). The CH design we tested could therefore provide microclimate refugia that reduce the risks of hollow-dependent wildlife experiencing either hyperthermia in regions with hot summer climates (e.g. Mediterranean, warm and hot temperate), or hypothermia in areas with cold winters (e.g. cool and cold temperate).

Management implications

Our results have provided evidence that CHs provide stable (cool and humid) microclimate conditions that could more effectively replicate those within natural tree hollows than would nest boxes or LHs (Zapponi *et al.* 2014; Maziarz *et al.* 2017; Griffiths *et al.* 2018). This could be of particular importance for biodiversity offset programs conducted in Australia, where land development projects seeking approval to clear native vegetation are required under State and Federal legislation to replace any natural hollows in trees that are removed with supplementary shelters. Historically, land developers have fulfilled this requirement by installing 'off-the-shelf' rectangular, cuboid-shaped nest boxes, which are typically constructed from 1.2 to 1.5 cm thick plywood; however, the efficacy of this widespread practice has become contentious in recent years (Lindenmayer *et al.* 2017; Goldingay *et al.* 2020). When considering internal microclimate, the available evidence shows that cavities carved directly into live trees provide hollow-dependent wildlife with supplementary shelters that are more similar to natural hollows in large, old trees than are the current industry-standard plywood nest boxes. We therefore encourage policy makers and managers to consider incorporating CHs as a method of compensating for unavoidable removal of mature hollow-bearing trees in large-scale projects, such as major road developments.

Aside from the use of artificial hollows in biodiversity offset programs, nest boxes are often deployed by researchers, land managers and conservation-focused community groups; many of these projects report ongoing use by wildlife (Brazill-Boast *et al.* 2013; Godinho *et al.* 2020; Macak 2020; Stojanovic *et al.* 2021). For such programs, we recommend that, where possible, stakeholders consider 'value-adding' to their existing projects by installing CHs in trees with existing nest boxes. This approach could provide animals already habituated to using artificial hollows with the choice to select a shelter with a more stable and buffered microclimate during extremely hot or cold weather events. For example, if there had been nocturnal mammals occupying nest boxes during this study, which reached 43°C when daytime ambient temperature was 45°C, they would have needed to move <1 m along the tree trunk to enter a CH that was 16°C cooler and 51% more humid than ambient. Along with the ecophysiological benefits this could provide, it would reduce the risk of predation for nocturnal animals that vacate a box during the day to avoid overheating (Michaelsen *et al.* 2014). Further, adding several supplementary shelters per tree could replicate hollow-availability in large, old trees, which often have multiple hollows of various shapes and sizes that are located in different places throughout the trunk and branches (Westerhuis *et al.* 2019), but are an increasingly rare keystone habitat feature in human-disturbed landscapes (Lindenmayer *et al.* 2014; Treby and Castley 2015).

Although there is clearly potential for CHs, and to a lesser extent LHs, to provide cavity microclimates that more effectively replicate natural tree hollows than supplementary shelters attached to the outside of trees, managers will need to weigh up the ecological value with the costs of making, installing and maintaining different artificial hollows. This presents a trade-off for managers between investing in different types of supplementary hollows with varying costs and functional performance to meet their management objectives. In this study, the CHs cost A$250 each, compared with A$120 each for nest boxes and A$400 for LHs. For these price comparisons, we intentionally chose high-quality, and therefore relatively expensive, premade nest boxes, because we advocate for the use of boxes designed to last for a minimum of 20 years (Griffiths *et al.* 2018). We installed the external hollows for this study, so that did not incur installation costs; however, an arborist or experienced climbing ecologist would typically need to be contracted to safely lift nest boxes and LHs into trees and then permanently attachment them. This additional expense would have brought the overall price per nest box closer to that of the CHs. The ongoing maintenance requirements for nest boxes have been discussed previously (e.g. Lindenmayer *et al.* 2009; Goldingay *et al.* 2018). Less is known about ongoing maintenance requirements and longevity of CHs and LHs. The artificial hollows we monitored are part of a larger, ongoing study, which has shown that ~12% of CHs (using the same design as in this study) require a small amount of maintenance 5 years after installation to cut back wound wood that begins to occlude entrance holes (Best *et al.* 2022). Carving CHs into dead trees would eliminate the problem of wound wood growth closing over entrances (Hurley and Harris 2014, 2015), but introduces other uncertainties about longevity (i.e. standing life of dead trees); additionally, the reduced water content of dead trees may diminish the climate-buffering potential of CHs. Given the lack of published data on rates of weathering and decay in LHs, further systematic investigation is required to determine the medium- to long-term efficacy of this type of supplementary shelter.

Conclusions

Here, we used extremely hot summer weather that occurred in Melbourne, Australia, as an opportunity to compare cavity microclimates in CHs carved into the trunks of live *Eucalyptus* trees, with nest boxes and LHs. We found that CH cavities were much better insulated than were artificial hollows attached to the outside of trees, remaining much cooler and more humid during the hottest part of the day. Our results provided evidence that CHs have the potential to provide supplementary shelters with microclimates that could effectively buffer hollow-dependent wildlife from physiologically stressful conditions during extreme heat, potentially to a similar level as natural hollows in large, old trees (Griffiths *et al.* 2018). We recommend that managers consider incorporating CHs into habitat restoration and conservation programs targeting hollow-dependent wildlife in regions that experience extremely hot weather events. One approach that we believe warrants investigation is pairing existing nest boxes, particularly those that are used on an ongoing basis by target wildlife, with CHs carved into live trees. It will be critical to test the effectiveness of this approach using long-term studies quantifying temporal patterns of use of different types of artificial and natural hollows by free-ranging wildlife. Ideally, these longer-term occupancy studies would be paired with short-term field experiments that combine cavity microclimate data with empirical measures of thermal biology and ecophysiology of target endothermic animals occupying different types of artificial and natural hollows, particularly during hot and cold weather extremes.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare no conflicts of interest.

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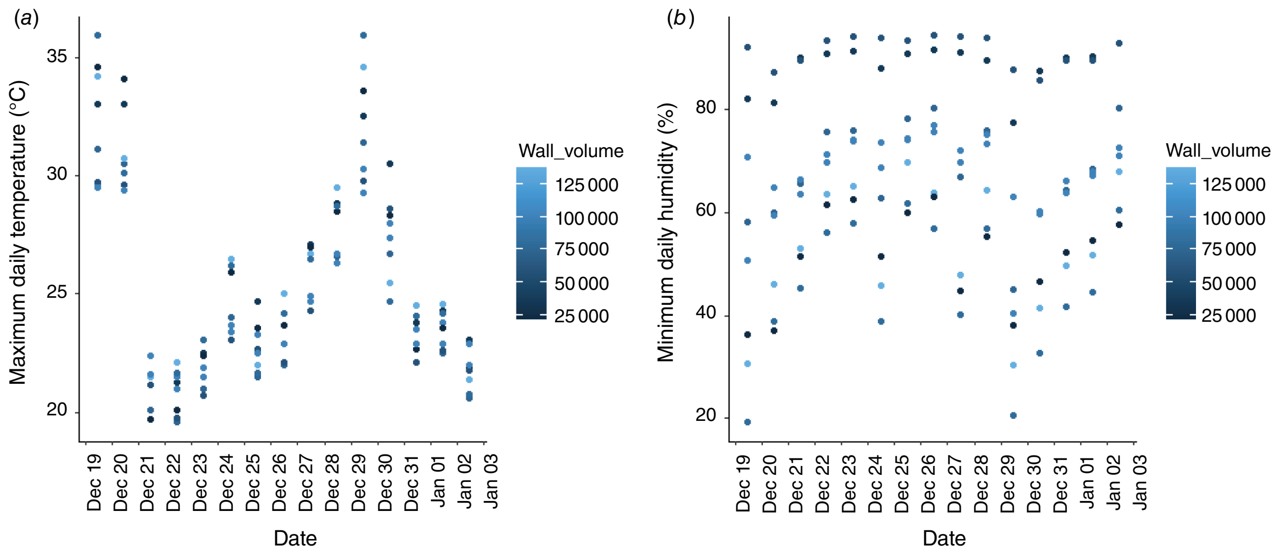

Appendix 1. Plots of (*a*) maximum daily temperature (°C) and (*b*) minimum daily relative humidity (%) within chainsaw hollows throughout the study period. Point colours indicate the relative cavity wall volume (cm^3) of each tree.

Appendix 2. LMM fixed-effect parameter estimates for the chainsaw hollow microclimates during the day.

Explanatory variable	Estimate	s.e.	d.f.	t-value	*Pr*(>|*t*|)
Temperature					
(Intercept)	22.48	0.20	6	113.33	<0.0001
Mean ambient temperature	2.53	0.023	10 360	112.21	<0.0001
Wall volume	0.30	0.20	6	1.49	0.19
Relative humidity					
(Intercept)	73.95	5.11	6	14.48	<0.0001
Mean ambient humidity	4.40	0.069	10 359	63.43	<0.0001
Wall volume	−4.67	5.11	6	−0.92	0.40

Appendix 3. LMM fixed-effect parameter estimates for the cavity microclimates throughout the study period.

Explanatory variable	Estimate	s.e.	d.f.	*t*-value	*Pr*(>|*t*|)
Temperature					
(Intercept)	22.36	0.14	7.65	160.98	<0.0001
Mean ambient temperature	2.33	0.019	49 140	120.92	<0.0001
Log hollow	−0.10	0.037	48 300	−2.77	<0.0001
Nest box	−0.25	0.055	46 750	−4.60	<0.0001
Wall volume	−0.00092	0.024	45 000	−0.038	0.97
Mean ambient temperature: log hollow	2.55	0.027	49 140	93.57	<0.0001
Mean ambient temperature: nest box	4.76	0.027	49 140	174.48	<0.0001
Relative humidity					
(Intercept)	80.35	2.13	7.033	37.75	<0.0001
Mean ambient humidity	4.18	0.069	42 990	60.80	<0.0001
Log hollow	−25.10	0.14	43 000	−176.75	<0.0001
Nest box	−36.48	0.22	42 990	−167.78	<0.0001
Wall volume	−5.44	0.091	42 990	−59.99	<0.0001
Mean ambient humidity: log hollow	1.43	0.11	42 990	13.62	<0.0001
Mean ambient humidity: nest box	6.44	0.10	42 990	64	<0.0001