CONTRIBUTED PAPER

Spout hollow nest boxes provide a drier and less stable microclimate than natural hollows

Clare Strain1 | Christopher S. Jones2 | Stephen R. Griffiths3,4 | Rohan H. Clarke1

1School of Biological Sciences, Monash University, Clayton, Victoria, Australia
2Department of Environmental Land Water and Planning, Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria, Australia
3Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, Victoria, Australia
4Research Centre for Future Landscapes, La Trobe University, Bundoora, Victoria, Australia

Abstract

Artificial tree hollows (e.g., nest-boxes) are commonly deployed to mitigate the loss of mature trees within human-disturbed landscapes. Their effectiveness as a habitat resource, and thus conservation management tool, is strongly influenced by the suitability of internal microclimate conditions. In southeastern Australia, spout hollows are a nesting resource used by a diverse community of vertebrate species. We tested the suitability of a novel nest box design (spout boxes) that mimicked the physical characteristics of spout hollows. We monitored the occupancy (n = 193) and internal microclimate (n = 131) of natural hollows and spout boxes within a woodland where natural tree hollows were once abundant. Both natural hollows and spout boxes were occupied and used for breeding by birds and mammals. Natural hollows had consistently higher humidity, and thermal maxima and minima were buffered, when compared with spout boxes. These differences were largely explained by wall thickness. Spout boxes displayed even more extreme temperature variation and lower humidity when not shaded. While more extreme microclimate conditions did not prevent usage, tolerable thresholds for hollow-dependent species may soon be exceeded under current climate change projections. Managers need to carefully consider nest box design and positioning to ensure the suitability of these supplementary resources for conservation purposes.

KEYWORDS

Brown Treecreeper, cavity microclimate, cavity-nesting bird, Climacteris picumnus, habitat restoration, Neophema pulchella, threatened species, tree hollow, turquoise parrot

1 INTRODUCTION

Tree hollows are an important component of woodland and forest habitats worldwide as they provide shelter for a range of vertebrate species, including reptiles, frogs, terrestrial and arboreal mammals, insectivorous bats, and birds (Bryant, Dundas, & Fleming, 2012; Remm & Lõhmus, 2011). Ongoing anthropogenic disturbance has led to declining numbers of hollow-bearing trees in landscapes used for agriculture, timber harvesting, and urban development (Manning, Gibbons, Fischer, Oliver, & Lindenmayer, 2013). This represents a significant threat...
to hollow-dependent fauna, and can lead to localized population declines and ultimately the loss of biodiversity from impacted areas (Heinsohn, Murphy, & Legge, 2003; Lindenmayer et al., 2014; Strubbe & Matthysen, 2009). Management strategies are therefore required to increase localized availability of hollows, and to ensure that, where possible, mature hollow-bearing trees are retained (Le Roux et al., 2014).

Given that formation of tree hollows by natural processes can take decades to centuries (Gibbons, Lindenmayer, Barry, & Tanton, 2000; Mac Nally, Soderquist, & Tzaros, 2000), artificial hollows (e.g., timber or plywood nest boxes) are commonly used to provide temporary habitat resources for hollow-dependent wildlife (Lambrechts et al., 2010; Lindenmayer et al., 2017; Mering & Chambers, 2014). The effectiveness of nest boxes is dependent on their ability to provide microhabitats that approximate natural hollows (Lindenmayer et al., 2009). However, tree hollows and nest boxes can vary significantly in their structural properties (e.g., cavity size and shape). Designing nest boxes that more accurately mimic the structural characteristics of natural hollows used by wildlife has been shown to increase usage rates and breeding success by target species, for example, the Gouldian Finch (*Erythrura gouldiae*; Brazill-Boast, Pryke, & Griffith, 2013). However, conservation-focused nest box programs often use generic nest box designs (Goldingay & Stevens, 2009), despite limited evidence of their effectiveness when targeting threatened species, or species that select hollows with particular physical characteristics (Le Roux et al., 2016).

Microclimate is another factor that strongly influences the selection and use of hollows by wildlife (Geiser & Brigham, 2000; Kerth, Weissmann, & Konig, 2001). Internal temperature can vary markedly between tree hollows and nest boxes, with traditional timber or plywood nest boxes often being more strongly influenced by daily fluctuations in solar exposure and ambient temperature (Rowland, Briscoe, & Handasyde, 2017). As a result, nest boxes often experience greater extremes in daily maxima and minima than natural hollows, plus a larger range of temperatures over a 24-hr cycle (Amat-Valero, Calero-Torralbo, Vaclav, & Valera, 2014; Bartonička & Rehak, 2007; Griffiths et al., 2018; Isaac, Parsons, & Goodman, 2008; Maziarz, Broughton, & Wesolowski, 2017; McComb & Noble, 1981a; Rowland et al., 2017). This thermal variation is driven by the wood surrounding hollows within tree trunks and branches typically being much thicker than the walls of nest boxes (Coombs, Bowman, & Garroway, 2010), and water flow within the vascular tissue (cambium) of living trees acting to cool the outer layers of the trunk and branches (Briscoe et al., 2014). As variation in cavity temperature can strongly influence the metabolic costs of thermoregulation for hollow-dependent birds and mammals (Dawson, Lawrie, & O’Brien, 2005; Griffiths et al., 2017; Huey, 1991; Rowland et al., 2017), nest boxes should be designed to mimic, or improve upon, the thermal characteristics of natural tree hollows used by target species, particularly during hot and cold weather extremes (Flaquer et al., 2014; Salaberría, Celis, López-Rull, & Gil, 2014).

Along with cavity temperature, humidity also affects thermoregulation for hollow-dependent endotherms, especially during hot conditions when the water costs of an animal rise as evaporative heat-loss is used to avoid overheating (Dawson, 1969). For hollow-nesting birds, suitable cavity humidity is particularly important during the incubation of eggs, where fluctuations outside of a narrow range can result in large differences in water loss from eggs, and ultimately in embryo death (Ar & Rahn, 2015; Cooper, Hochachka, Butcher, & Dhondt, 2005; Kern & Cowie, 1995; Prokop & Trnka, 2011; Rahn & Ar, 1974). Given that birds cannot move eggs or nestlings to another hollow if microclimate conditions become physiologically stressful (e.g., too dry, hot, or cold), it is critical to ensure that nest boxes provide suitable microclimate conditions for the development of eggs and subsequent rearing of nestlings.

Here, we installed nest boxes in the box ironbark woodlands of the Warby Ranges, Victoria, Australia. We developed a novel nest box design (hereafter, “spout boxes”) based on the structural characteristics of “spout hollows,” which form within various *Eucalyptus* spp. Spout hollows are approximately cylindrical-shaped cavities that form naturally within the center of a branch, or a small trunk, running parallel to the stem length. In central Victoria these spout hollows are commonly used by Turquoise Parrots (*Neophema pulchella*) and Brown Treecreepers (*Climacteris picumnus victoriae*; Quin & Baker-Gabb, 1993); both of which are hollow-dependent, woodland bird species, the former listed as near Threatened within Victoria (FFG Act, 1988; State of Victoria, 1988), and the latter listed as Threatened within Victoria (DSE, 2013) and assessed as Vulnerable nationally (Ford et al., 2021). We then monitored wildlife use and microclimate conditions (temperature and relative humidity) within paired natural spout hollows and spout boxes. Our study aims were to: (a) determine whether our novel nest box design replicated microclimates of natural hollows such that Turquoise Parrots and Brown Treecreepers made use of them, (b) compare internal microclimate conditions within natural and artificial hollows, (c) explore how location and position of natural and artificial hollows influenced internal microclimates, and (d) provide recommendations for future design and installation of artificial hollows targeting hollow-dependent fauna.
2 | MATERIALS AND METHODS

2.1 | Study location

The study was conducted in the Warby-Ovens National Park and surrounding areas west of Wangaratta in northern Victoria, Australia (Figure 1). The area has a temperate climate with annual rainfall of 615 mm (Australian Bureau of Meteorology, 2020). The Park is primarily an open grassy woodland system with a “box-ironbark” eucalypt canopy dominated by Blakely’s Red Gum (*Eucalyptus blakelyi*), Red Stringybark (*E. macrorhyncha*), Mugga Ironbark (*E. sideroxylon*), Red Box (*E. polyanthemos*), Yellow Box (*E. melliodora*), Grey Box (*E. microcarpa*), and Long-leaved Box (*E. goniocalyx*). The Park was logged for timber harvesting until 1979. The Park is an important habitat site for a range of hollow dependant vertebrates, including some threatened and declining species such as the Squirrel Glider (*Petaurus norfolcensis*), Brush-tailed Phascogale (*Phascogale tapoatafa*), Carpet Python (*Morelia spilota*), Lace Monitor (*Varanus varius*), Turquoise Parrot, and the Brown Treecreeper.

2.2 | Spout boxes and natural tree hollows

One hundred and twenty-five spout boxes were established within the study area in 2010 across 13 sites (Figure 1). Spout boxes were hexagonal wooden structures, 800 mm long by 160 mm wide (Figure 2a). The spout boxes had a consistent wall thickness of 25 mm compared to the natural hollow thickness, which varied within and between each hollow from an average minimum thickness of 55 mm (range: 3–220 mm) to an average maximum thickness of 125 mm (range: 19–600 mm). The design of these spout boxes was based on the natural hollow preferences of Turquoise Parrots (Figure 2b) and Brown Treecreepers (Quin & Baker-Gabb, 1993). Spout hollows occur naturally in branches of both live and dead
Eucalyptus trees, and are also abundant in stumps of dead trees that were felled during historical logging within the survey region. Sixty-four spout boxes were attached to trees to mimic branch or trunk hollows and 61 were attached to metal pickets that had been driven into the ground to mimic tree stump hollows (Figure 2c,d) with both attachment methods equally represented at each of the 13 sites. The spout boxes were placed at a range of heights, orientations and ground slope angles. Additionally, 68 natural hollows were identified in the same geographic locations as the artificial hollows and surveyed in the same way as spout boxes for comparison (mean of 5.23 natural hollows per site).

2.3 | Climate data

Climate data (daily maximum and minimum ambient temperatures) for the study period were obtained for the Wangaratta airport logging station, approximately 7 km from the study area (Australian Bureau of Meteorology, 2020).

2.4 | Microclimate data

We used data loggers (Hygrochron iButton model DS1923; Maxim Integrated Products Inc., 2015) to measure temperature and relative humidity inside 67 spout boxes (33 on trees, 34 on pickets) and 64 natural hollows. Each spout box or hollow was surveyed for a six-week period using a logger that recorded data at 30 min intervals for the duration of the survey. Owing to logistical constraints, individual spout boxes or hollows were surveyed in one of three consecutive 6 week blocks in spring and summer of 2011 with allocation of spout box position and hollow type across 6 week blocks to ensure a balanced design. Control loggers were established in two hollows and two spout boxes with mesh covering the entrance to prevent access for the duration of the study.
to identify abnormalities in microclimate data between occupied and unoccupied cavities. These control hollows were used to identify if and when a cavity was occupied. Saturation drift is a known potential problem for humidity data recorded using Hygrochron iButtons, where the measurements becomes 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).

### 2.5 Data analysis

Additional habitat and context variables including height, orientation, aspect, canopy cover, depth, altitude, openness, entrance hole size, and wall thickness were measured for each natural and artificial hollow (Table 1). Diurnal occupancy by fauna was also recorded on a fortnightly basis for all spout boxes and natural hollows during the climate survey period. This fortnightly survey sought to detect hollow-nesting birds (our primary objective) during the austral spring. This approach also detected nocturnal birds in their daytime roost, but did not detect night roosting birds that were otherwise not breeding.

All microclimate data were screened to remove days when hollows were considered to be occupied by one or more endotherms (which increases temperature and humidity cf., controls) or when data loggers were ejected from the hollow. Data were then de-trended (by subtracting the mean daily value over the 6-week period of each variable from the raw data) for use in linear models to account for the seasonal increase through time for comparative analysis of natural and artificial hollows.

Data analysis included general additive models (GAMs), linear models, linear mixed effect models and goodness of fit tests for ratios. Independent models were run for each of the four microclimate variables (maximum and minimum temperature and humidity). GAMs were conducted on the microclimate variables only, each as separate models, to identify differences in trends between the cavity types. The GAM model outputs were plotted as smoothed predictions with 95% confidence intervals using the `geom_smooth` function in the `ggplot2` package (Wickham, 2016) with method specification as “gam.”

Microclimate means across the 6 week period for each nest box and natural hollow were generated and general linear models were used to explore the relationship between these and habitat variables. A correlation matrix was generated for all habitat variables and in situations where a pair of variables was considered highly correlated one variable was excluded. Single factor ANOVAs were used to analyze relationships with categorical variables. Any variables deemed significant were then

| Variable | Description | Units |
|----------|-------------|-------|
| Height   | From ground to the lowest point of the entrance | m |
| Entrance Orientation | Direction cavity entrance faces (N, NE, E etc.) | (categorical) |
| Tree Aspect<sup>a</sup> | Side of the tree the cavity is positioned (N, NE, E etc.) | (categorical) |
| Slope Aspect | Main slope aspect, including F for flat (N, NE, E, etc.) | (categorical) |
| Canopy Cover | Percentage of canopy cover, measured through hemispherical photography and WINPHOTO photograph analyzing software | % |
| Openness | A measure of canopy openness over an area of approximately 1 ha visually estimated from 5 points within 60 m of hollow. | % |
| Location | The different locations containing surveyed cavities | (categorical) |
| Altitude | Elevation from sea level, read from handheld GPS | m asl |
| Depth<sup>b</sup> | From the lowest point of entrance to lowest point of the base of the hollow | cm |
| Maximum and Minimum Entrance Size<sup>b,c</sup> | The largest and smallest diameter across the entrance hole | cm |
| Maximum and Minimum wall thickness<sup>b</sup> | The width of the wall and the widest and thinnest point around the entrance to the hole | mm |

<sup>a</sup>Excluding nest boxes on pickets.

<sup>b</sup>Measured for tree hollows only.

<sup>c</sup>Minimum entrance size was considered highly correlated with maximum entrance size and was not included in statistical analysis.
analyzed jointly in an additional linear model. Each model was compared using the corrected Akaike’s information criteria (AIC), with the lowest value indicating the best fit (Anderson & Burnham, 2002). These models identified the key habitat variables influencing the different microclimate variables.

Linear mixed effect models were then used to evaluate the relative effects of each habitat variable on microclimates. These models were implemented using the lmer function in R package lme4 (Bates, Mächler, Bolker, & Walker, 2015). All nonbinary or factor variables were scaled and centered (mean subtracted, then divided by the standard deviation) prior to analyses so that the relative effect sizes could be compared for each variable. Separate models were run for each of the four microclimate variables and included cavity type, date (as days from the start of the experiment) and two additional variables selected from the linear model results. Cavity ID and location were included as random effect in all models. A 95% confidence interval (95CI) that did not include zero was used as the significance criterion (calculated by CI = mean ± [1.96 × SE]). All analyses were conducted in R 3.6.0 (R Development Core Team, 2019).

3 | RESULTS

Vertebrate species (birds and mammals) were observed in natural and artificial hollows during the study, and successful breeding was observed in spout boxes attached to trees and pickets and in natural hollows. Ten Turquoise Parrot breeding events were detected in spout boxes (8 on pickets and 2 on trees), and four were detected in tree hollows. Ten Brown Treecreeper nests were also found in spout boxes (7 on pickets and 3 on trees), whereas none were detected in tree hollows. This represents an 8% occupancy rate within spout boxes for both focal species in this study. Nests belonging to three other hollow-nesting bird species were also detected (White-throated Treecreeper Cormobates leucophaea,
Red-rumped Parrot *Psephotus haematonotus* \(n = 1\), and Australian Owlet-nightjar *Aegotheles cristatus*, \(n = 1\). A small marsupial, the Yellow-footed Antechinus *Antechinus flavipes*, was also detected sheltering in a single spout box.

Spout boxes were less thermally buffered (i.e., displayed both higher maximum and lower minimum daily temps), than natural hollows. Spout boxes on pickets had cooler minimum temperatures on average and had higher maximum temperatures in summer than boxes on trees (Figure 3a,b). In this study, nesting in both species was largely confined to October and November, which avoided the extreme lows and highs in ambient temperature that occurred in August (lowest minimum temperature = \(-1.0^\circ C\)) and January (highest maximum temperature = \(39.6^\circ C\)), respectively at the nearby Wangaratta airport weather station (Australian Bureau of Meteorology, 2020).

Maximum and minimum ambient humidity declined through time (into summer) and humidity in spout boxes declined more rapidly than in natural hollows (Figure 3c,d). Boxes on pickets had lower maximum humidity than boxes positioned on trees and experienced a greater reduction in humidity into summer.

Daily variation in temperature and humidity (difference between minimum and maximum) was greater in spout boxes than natural hollows (Figure 4). The boxes affixed to pickets also had greater variation than those affixed to trees. Daily variation also increased throughout the surveyed season from late winter to summer, particularly for temperature. Greater variation corresponds with a greater rate of change within each day.

Linear models determined the key predictor variables influencing each of the climate variables other than cavity type (see Tables S1 and S2 for model outputs). The best candidate variables included minimum wall thickness of the cavity (variable in natural hollows, but constant and therefore excluded in spout boxes), canopy cover, openness, altitude, slope aspect, and location. These models indicated that for natural hollows, maximum daily temperatures were lower as wall thickness and canopy cover increased. Minimum temperatures were higher on NW facing slopes, and humidity increased with wall thickness. For spout boxes,
maximum temperatures were lower with greater canopy cover, minimum temperatures were associated with site location, and minimum humidity was higher with greater canopy cover.

Mixed effects models were used to verify the relative effect size of the cavity type while controlling for these important covariates. Ambient temperature was excluded from the models to allow fitting of cavity attributes only. The models indicated that maximum temperature, maximum humidity, and minimum humidity differed considerably to natural hollows but there was no statistical difference between spout boxes on pickets and on trees (Figure 5). For maximum temperature, the difference between boxes on pickets and trees was driven by canopy cover. Wall thickness remained an important driver of the minimum and maximum humidity, with boxes on pickets and trees both having much lower humidity than natural hollows. Minimum temperature was the only microclimate variable that did not differ significantly between natural hollows and spout boxes.

### 4 | DISCUSSION

The ongoing removal of mature hollow-bearing trees from human-disturbed landscapes presents a major threat to cavity-dependent wildlife worldwide (Fischer & Lindenmayer, 2007). Management strategies are urgently required to increase hollow availability in degraded areas (Lindenmayer et al., 2014). In this study, we trialed a novel nest box designed to mimic the physical characteristics of natural spout hollows used by two woodland birds of conservation concern. We also examined whether a range of habitat variables influence internal microclimate conditions in natural hollows and spout boxes attached to trees and pickets. We found that hollow-dependent mammals and birds, including the two target species, used natural and artificial hollows. Spout boxes attached to both trees and pickets were used for successful breeding by Turquoise Parrots and Brown Treecreepers and were more often used for breeding than natural hollows. Microclimatic conditions within spout boxes during this study were therefore tolerable for the target species, despite large differences in temperature and humidity between artificial and natural hollows. Our results suggest spout boxes may provide effective supplementary nesting sites for target woodland birds. However, the large difference in internal microclimate conditions in spout boxes compared to natural hollows, as well as the recent hotter and drier climate (Gibbs, Chambers, & Bennett, 2011; Coumou & Rahmstorf, 2012; Findell et al., 2017, also see Supporting Information SM3) raises concerns regarding their future suitability.

In this study, we achieved our primary objective of providing supplementary nesting sites for Turquoise Parrots and Brown Treecreepers, with an 8% occupancy rate of spout boxes by both focal species combined. This is a promising result when compared to the low nest box occupancy rates reported elsewhere in southern Australia for cavity-dependent woodland bird species, particularly those of conservation concern. For example, in a large-scale biodiversity offsetting program in southern New

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**FIGURE 5** Effect size of predictor variables on the maximum and minimum temperature and humidity within all cavity types: natural hollows, spout boxes on trees, and on pickets. Effect sizes show effect of box attachment category (tree, picket) compared to natural hollows, accounting for the effects of key covariates. Error bars indicate the 95% confidence intervals around each estimate.
South Wales, Lindenmayer et al. (2017) reported Brown Treecreepers using only 0–0.6% of the marine plywood nest boxes that were specifically constructed for this species. Two other studies that used generic rectangular cuboid-shaped plywood boxes constructed for Superb Parrots reported no use by this species (Le Roux et al., 2016; Lindenmayer, Crane, Blanchard, Okada, & Montague-Drake, 2015). In comparison, boxes with physical characteristics designed to mimic natural tree hollows used by target bird species have reported much higher occupancy rates (Brazill-Boast et al., 2013). Our results further support the need for conservation-focused nest box programs to incorporate empirical data on the physical characteristics of natural hollows used by target species into the design, construction, and installation of artificial hollows. This approach may also result in the development of artificial hollows that provide target species with microclimate conditions that resemble natural hollows.

The thermal properties of hollows exert a strong influence on the metabolic costs of thermoregulation and water balance for hollow-nesting birds (Ardia, Pérez, Chad, Voss, & Clotfelter, 2009; Ardia, Pérez, & Clotfelter, 2006). Artificial hollows should therefore be designed to provide similar (or better) protection against environmental extremes as natural hollows (Isaac, Parsons, & Goodman, 2008). Our data suggest that thicker walls of natural hollows provide a greater buffer to ambient temperatures, compared to thinner-walled natural hollows and our spout boxes made with 25 mm thick timber walls. The effect of tree size (trunk diameter), which is directly correlated with the thickness of walls surrounding hollows, has previously been associated with reduced internal temperature variation in tree hollows (Coombs et al., 2010; Isaac, De Gabriel, & Goodman, 2008; McComb & Noble, 1981b; Sedgeley, 2001). In comparison, standard nest boxes constructed with 12–15 mm plywood or timber have been shown to experience greater extremes in daily temperatures, plus a larger daily temperature range than natural hollows (Amat-Valero et al., 2014; Bartonicka & Rehak, 2007; Griffiths et al., 2017; Griffiths et al., 2018; Isaac, Parsons, & Goodman, 2008; Maziarz et al., 2017; McComb & Noble, 1981b; Rowland et al., 2017). Practitioners thinking of adopting our spout box design should therefore consider using thicker timber (>25 mm) for box construction, which will increase their capacity to buffer occupants from external ambient conditions during extremely hot and cold weather events. Further modifications, such as the addition of insulation or the use of reflective surfaces to buffer nest boxes from weather extremes may also warrant consideration (Griffiths et al., 2017; Larson, Eastwood, Buchanan, Bennett, & Berg, 2018). Potential modifications, do however, require careful assessment. For example, thicker timber will result in heavier nest boxes that impose limitations on handling and deployment under field conditions, while surfaces other than natural timbers may prove unattractive to the focal species or alternatively more readily attract the attention of potential nest predators.

In addition to wall thickness, our results indicate that aspect and shade (provided by canopy cover) were also drivers of cavity temperatures in spout boxes. These findings are consistent with previous research showing that the interplay between aspect and shade influences temporal variation in solar exposure (the total amount of solar radiation that the walls of a nest box are exposed to), which in turn drives daily rates of heating and cooling beyond the effect of box aspect alone (Ardia et al., 2006; Griffiths et al., 2017; Rowland et al., 2017). The resultant effect on temperature is likely to be even greater in standard “off the shelf” nest boxes, as our novel spout box design used thicker hardwood walls (25 mm timber) than most generic nest boxes (Lambrechts et al., 2010; Wesolowski, 2011). Further, we found temperature variation was more extreme when the spout boxes were attached to pickets compared to trees, which was likely due to a combination of the lack of canopy cover (Charter et al., 2010), and cooler temperatures in the boundary layer close to tree trunks created by water flow within the vascular (cambium) tissue acting to cool the outer layers of the trunk (Briscoe et al., 2014). This suggests that, when installing nest boxes, canopy cover at installation sites should be considered in combination with box aspect and attachment host (tree vs. pole or picket), to ensure that boxes provide suitable thermal environments for target fauna, especially during critical times such as during the breeding season (Griffiths et al., 2017; Rowland et al., 2017).

In this study, nesting by Turquoise Parrots and Brown Treecreepers was largely confined to October and November 2011, thereby avoiding the most extreme daily minimum (−1.0°C) and maximum (39.6°C) temperatures, which occurred in August 2011 and January 2012, respectively. However, in Central Victoria, these species are known to breed from August–January (Doerr & Doerr, 2007; Quin & Baker-Gabb, 1993). Since the completion of this study (i.e., 2013–2019), there has been an increased frequency and intensity of hot weather events in the study region during August–January, with ambient daytime maxima ≥40°C recorded on 58 days, the most extreme being 45.4°C in January 2019 (Australian Bureau of Meteorology, 2020). On the hottest day during this study (39.6°C), cavity temperatures in natural hollows (29.0–45.9°C) were in some cases well below the ambient temperature, while spout boxes on trees (39.0–43.2°C) were always around or above ambient conditions, and boxes on pickets (40.8–47.8°C) were up to 8.2°C hotter.
than ambient. This suggests that when heat wave conditions occur during the nesting period, temperatures inside spout boxes on pickets are likely to be well above 40°C or even 50°C. Exposure to such temperature extremes in nests can result in hyperthermia, dehydration and potentially mortality for nonvolant juvenile birds (Catry, Franco, & Sutherland, 2011; Salaberria et al., 2014), and are likely to be lethal to eggs, as even short exposure to temperatures >40.5°C during incubation can be fatal for developing embryos (Webb, 1987). Behavioral adaptations in response to increasingly extreme conditions are untested for nesting Brown Treecreepers and Turquoise Parrots. However, elsewhere, bird species have been shown to have some capacity to actively modify internal temperature of nest hollows (e.g., Maziarz, 2019) or to change the timing for onset of breeding in response to a changing climate (Both et al., 2004). Consequently, the suitability of spout boxes across the two target species’ entire breeding season remains uncertain.

Humidity within natural and artificial hollows used for nesting has received far less attention than temperature, but the few studies to date (Maziarz et al., 2017) concur with our findings of lower humidity levels in spout boxes when compared to natural hollows. Humidity is known to be an important factor during egg incubation and the subsequent hatching success and survival rates for hollow-nesting birds (Ar & Rahn, 2015; Ardia et al., 2009; Cooper et al., 2005; Prokop & Trnka, 2011). Further field-based research is required to determine how variation in humidity within artificial hollows driven by altering the characteristics of box design (e.g., wall thickness) and installation (e.g., canopy cover, attachment host) influences the fitness of hollow-nesting birds.

Warmer and drier conditions are already occurring across Australia and are likely to intensify in the future (Gibbs et al., 2011). Under these conditions, differences in microclimate identified here between spout boxes and natural hollows are likely to be further amplified. As such, artificial hollow microclimates that buffer against climate variation by providing occupants with higher relative humidity and a more stable thermal profile are likely to influence the ongoing viability of populations of hollow-dependent fauna. This will be critical for the diverse communities of hollow-using fauna endemic to the extensively cleared and degraded woodland ecosystems across south-eastern Australia (Bennett & Ford, 1997; Gibbons & Lindenmayer, 2002), where nest boxes are commonly installed to provide supplementary habitats (Lindenmayer et al., 2017; Macak, 2020); particularly because much of this region is characterized by a Mediterranean climate with large variation in weather conditions from day to day and across seasons (Rowland et al., 2017). Protection of large old trees with existing hollows must remain a priority, but where artificial hollows are required (Griffiths et al., 2018; Griffiths, Semmens, Watson, & Jones, 2020), they should be designed to maximize wall thickness and be installed so that canopy cover and aspect combine to reduce solar exposure during summer, thereby ensuring target fauna have access to well-insulated supplementary habitats.

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CONFLICT OF INTEREST
The authors declare no conflict of interest relating to this manuscript.

AUTHOR CONTRIBUTIONS
Rohan Clarke and Clare Strain: conceived the study, Clare Strain and Rohan Clarke: collected the data, Christopher Jones and Clare Strain: led the analyses, and all authors discussed and interpreted the results. Stephen Griffiths and Christopher Jones: drafted the manuscript, with contributions from the other authors.

DATA AVAILABILITY STATEMENT
A summary of competing general linear model outputs (SM1 and SM2), and temperature profiles at Wangaratta airport (SM3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

ETHICS STATEMENT
Research protocols followed approved standards of Monash University. Research was conducted under animal ethics approval BSC/2009/18 and wildlife permits issued by the Victorian Department of Sustainability and Environment and Parks Victoria.

ORCID
Christopher S. Jones © https://orcid.org/0000-0003-2833-0194
Stephen R. Griffiths © https://orcid.org/0000-0003-3882-3654
Rohan H. Clarke © https://orcid.org/0000-0002-6179-8402
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