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Climate and behaviour influence thermal suitability of artificial hollows for a critically endangered mammal

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Running head: Thermal suitability of artificial hollows for a critically endangered mammal

Abstract

Artificial hollows are commonly used to mitigate the scarcity of den and nest sites that threatens fauna species globally, but there is a risk that these do not provide suitable microclimates for the populations they are intended to support. We monitored temperature, humidity, and occupancy in artificial dens (nest boxes and chainsaw-carved cavities) provided for the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) in south-eastern Australian forests. Monitoring occurred over both winter and summer in five habitat types spanning a broad elevational gradient (110 – 1580 m asl). We then used a biophysical model to explore the physiological consequences of the den temperatures recorded, and the potential effectiveness of behavioural strategies in reducing thermoregulatory costs. Monitoring revealed that nest box temperatures tracked ambient over both seasons, ranging from -5.5°C to 48.5°C, while chainsaw hollows provided more stable internal conditions. However, we found that inferences regarding the thermal suitability of artificial dens were site-specific, and dependent upon habitat type, season, and assumptions around behavioural strategies. During winter, behaviours such as the construction of large, insulative nests and huddling are likely critical in overcoming high energy costs associated with poorly-insulated artificial dens. In contrast, during summer high thermoregulatory costs were predicted for the warmest (lowland) site and coincided with low nest box occupancy. Our study reinforces the importance of factoring in local climates, and behavioural and physiological strategies employed by target taxa, when implementing artificial den programs to support fauna populations.

Keywords: Arboreal marsupial, physiology, climate extremes, nest boxes, chainsaw hollows, Leadbeater's possum, thermal quality, artificial dens

1. Introduction

The widespread loss of large, old, hollow-bearing trees as a result of clearing for agriculture and urbanisation, timber harvesting and bushfire, is a cause of biodiversity loss globally (Lindenmayer, Laurance, & Franklin, 2012). These trees form critical habitats for numerous hollow-dependent fauna, including birds (Cockle et al., 2015), bats (Thomas H Kunz & Lumsden, 2003) and arboreal mammals (Beyer & Goldingay, 2006). Hollows provide sites for nesting and denning, shelter from predators, and play a central role in survival and reproduction (Wiebe, 2001; Gibbons et al., 2002). In turn, the loss of hollow-bearing trees has been linked to population declines of numerous hollow-dependent species (Lindenmayer et al., 2014). In Australia, where there are no cavity-excavating vertebrates to accelerate hollow development (Cockle, Martin, & Wesołowski, 2011), hollows can take a century or more to form (Gibbons et al., 2000).

Given the concerns around declining hollow availability, artificial hollows, and particularly nest boxes, are widely used to provide alternative den and nesting sites (Goldingay, Rohweder, & Taylor, 2020). However, rates of nest box occupancy can vary substantially among species and habitats (Lindenmayer et al., 2009). Their suitability as replacements for natural hollows has been criticised owing to their limited functional life, potential colonisation by non-target taxa, and unsuitable microclimate (Harper, McCarthy, & van der Ree, 2005; Griffiths et al., 2017; Rowland, Briscoe, & Handasyde, 2017). Thin-walled, plywood nest boxes are frequently used across Australia, but the internal temperatures of these can fluctuate substantially compared to natural hollows (Isaac, Parsons, & Goodman, 2008; Goldingay, 2015; Rowland et al., 2017). For example, Rowland et al. (2017) found that, on average, the maximum temperatures in nest boxes were 8°C warmer than tree hollows with a maximum observed temperature of 52°C. Highly fluctuating temperatures and exposure to temperature extremes are likely to impact the survival and reproductive success of individuals using nest boxes (Catry, Franco, & Sutherland, 2011).

Concerns that nest boxes do not provide adequate protection during temperature extremes has motivated research into alternative types of artificial hollows. This technique involves the creation of excavated cavities by arborists who cut into trees using a chainsaw, known as ‘chainsaw hollows’ (Griffiths et al., 2018). One such approach involves carving an internal cavity and fitting a door plate with a specifically-sized entrance hole for the target species. This technique has been used to create hollows for birds (Hurley & Harris, 2014; Stojanovic et al., 2019), microbats, and arboreal mammals (Carey, 2002; Rueegger, 2017; Terry, Goldingay, & van der Ree, 2021), with mixed occupancy rates and success. Recent data collected from unoccupied chainsaw hollows indicates that their microclimates are comparable to natural hollows, most likely because of structural similarities (Griffiths et al., 2018). While recent research has demonstrated that chainsaw hollows will be used by some arboreal marsupials in preference to nest boxes (Terry et al., 2021), further work is required to determine whether they could provide long-term denning or nesting sites for a broader range of species across different habitats.

Scarcity of natural hollows represents a major threat to the Leadbeater's possum (*Gynmobelidius leadbeateri*), a small (100–160 g), cryptic, arboreal marsupial now confined to the Victorian Central Highlands in south-eastern Australia (Lindenmayer, 2014). The species is listed as Critically Endangered under Australia's EPBC Act (1999) and has experienced significant population declines due to habitat loss from timber harvesting and catastrophic bushfires (TSSC, 2015; Todd et al., 2016). A small, outlying, and genetically distinct population (< 40 individuals) exists outside of the Central Highlands in low elevation swamp forest, and has undergone a rapid population decline (Hansen et al., 2009; Harley, 2016). Leadbeater's possums are dependent on tree hollows for denning, which typically take 190 – 220 years to develop in montane ash forests (Smith & Lindenmayer, 1988). Due to this slow development and past major bushfires in the Central Highlands, there is a current and predicted shortage of suitable hollows for Leadbeater's possum over the next 50 – 100 years (Lindenmayer, Cunningham, & Donnelly, 1997; Lindenmayer et al., 2012). To address this, artificial dens including recycled plastic nest boxes and more recently chainsaw hollows have been provided to sustain local populations (Harley, 2006; Harley, 2016). At some localities the nest boxes have high colonisation rates (Harley & Lill, 2007; Harley, 2016), but their microclimates, and corresponding daily and seasonal occupancy patterns across different environments, have not been investigated.

The microclimate of a den is likely to have significant fitness consequences, particularly for species like Leadbeater's possum that may spend up to 20 hours per day in the den (Smith, 1980). Previous research has assumed that while in the den, Leadbeater's possums are in their thermoneutral zone, where costs for thermoregulation are minimal (Smith et al., 1982).

However, poorly insulated dens could shift individuals out of this zone such that they require either additional heat production (energy) to maintain a constant body temperature, or increased water costs associated with evaporative heat loss (Dawson, 1969). Leadbeater's possums appear to possess behavioural strategies to reduce thermoregulatory requirements during colder months by building large insulative nests of shredded bark and huddling together within the nest to share heat (Smith et al., 1982). However, the extent to which these behaviours can counteract the effects of a poorly insulated den is unclear.

Here, we assess the seasonal thermal suitability of nest boxes provided for Leadbeater's possum in several forest types spanning a broad elevational range and compare the microclimates of nest boxes and excavated chainsaw hollows. We investigate how the presence of a colony influences den microclimates, and assess corresponding patterns of den use, colony size and breeding. We use these data to parameterise a biophysical model of Leadbeater's possum to predict physiological costs (i.e. energy and water costs) of possums under a range of scenarios. This research will not only improve the effectiveness of artificial den provisioning for Leadbeater's possum across its range, but also demonstrates how site- and species-specific factors should be accounted for in targeted programs aiming to supplement habitats for threatened species.

2. Materials and methods

2.1. Study sites and design

Study sites were located in Victoria, south-eastern Australia, in areas where artificial dens had previously been installed for Leadbeater's possum (Figure S1). The sites encompassed a range of vegetation types across an elevational gradient, including: a) lowland swamp forest dominated by Mountain Swamp Gum (*Eucalyptus camphora*, Yellingbo Nature Conservation Reserve, 110 m elevation); b) montane ash forest at low elevation dominated by Mountain Ash (*E. regnans*, Dowey Spur, 730 m); c) montane ash forest at high elevation dominated by Alpine Ash (*E. delegatensis*, Toorongo Plateau, 1050 m elevation); d) montane riparian thickets (subalpine; Mt Baw Baw and Mt Erica, 1400 m elevation) and e) subalpine woodland (Mt Baw Baw and Mt Erica, 1480 m elevation). In subalpine woodland, nest boxes were monitored in Snow Gum (*E. pauciflora*) woodland lacking any mid-storey vegetation, while montane riparian thickets supported a dense mid-storey of shrubs. Chainsaw hollows were located in high elevation montane ash forest on the Toorongo Plateau (1000 m elevation), the only habitat type where chainsaw hollows have been installed for the species. Monitoring was conducted during two periods: the austral winter (June – September 2017) and summer (December 2017 – March 2018).

2.2. Artificial den types

Nest boxes constructed of recycled plastic have been established for Leadbeater's possum since 2008, with more than 600 currently installed across the species' range (D. Harley and J. Antrobus, unpublished data). The boxes (mean width, depth and height 23 cm, 24 cm and 40 cm respectively) have 25 mm thick walls and a small entrance hole (51 mm diameter, Figure 1), and are attached to trees 3 – 4 m above the ground where there is good mid-storey or canopy connectivity to facilitate possum movements. The nest boxes chosen for this study were predominantly light grey in colour, however a small subset were dark grey. All nest boxes have a south-east orientation to reduce exposure to direct sunlight in the afternoon.

Chainsaw hollows had been installed to trial the suitability of these structures. They were created by arborists who cut out a large cavity (mean width, depth and height 23 cm, 26 cm, and 30 cm respectively) in large-diameter (mean = 83 cm, range = 44 – 170 cm) living Mountain Ash, Mountain Grey Gum (*Eucalyptus cypellocarpa*) and Shining Gum

(*Eucalyptus nitens*) trees. These were fitted with a 5 cm wide wooden door plate, leaving a roughly circular 5 cm diameter entrance above the plate (Figure 1). The hollows were installed at heights between 3 – 16 m above the ground, where there was dense mid-storey connectivity nearby. Seventy-two chainsaw hollows were installed at sites occupied by Leadbeater's possum in 2015, and were subsequently monitored at approximately 4-month intervals.

While ideally we would have also monitored microclimates in natural hollows used by Leadbeater's possum for comparison, this was not possible due to (i) concerns about causing additional disturbance, (ii) lack of known natural hollows at the study sites, (iii) safety risks associated with installing loggers in hollows typically located high up in dead and decaying trees.

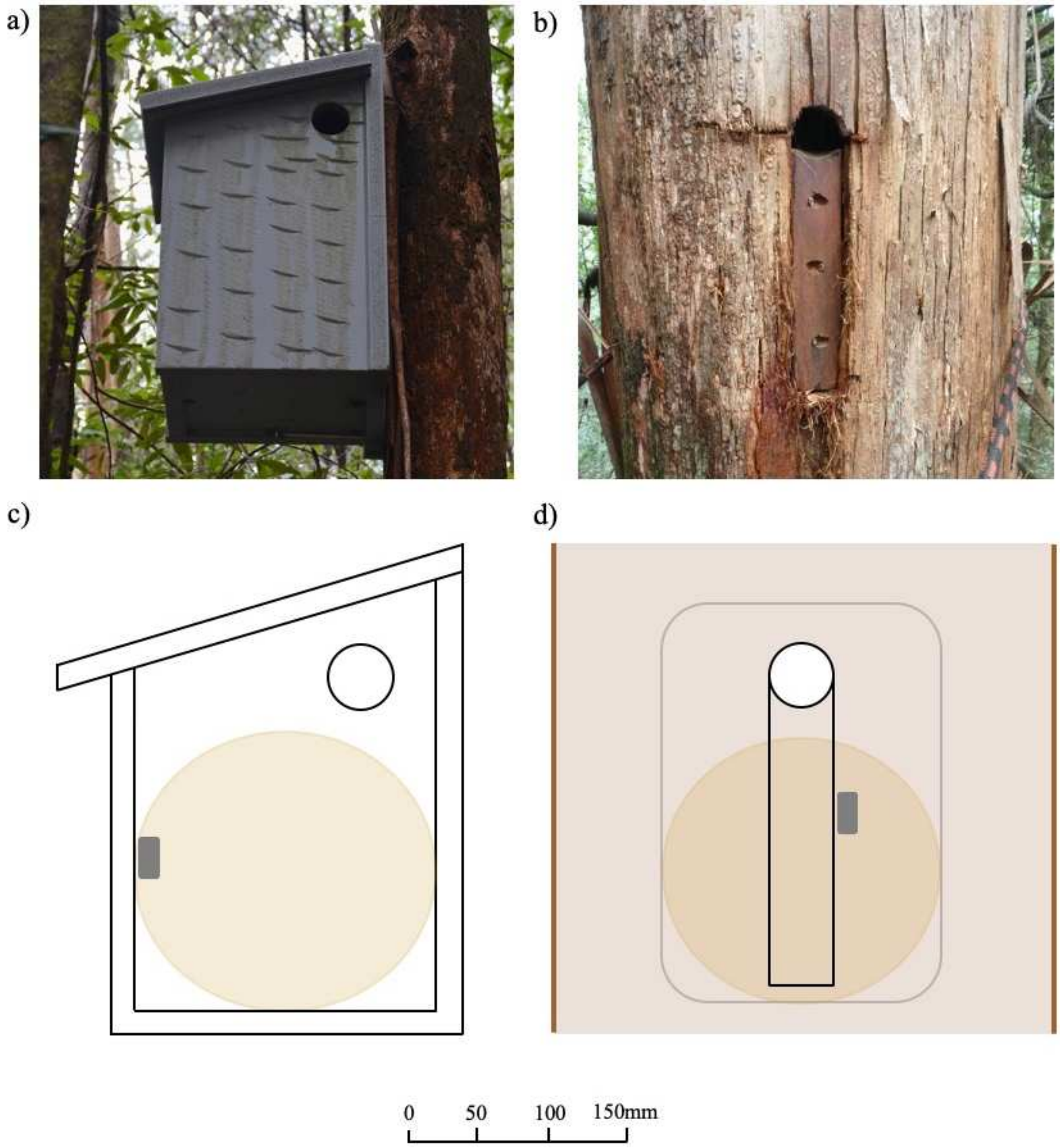

Figure 1. Photos and diagrams of the two artificial den types: (**a**, **c**) recycled plastic nest box (dimensions 40 cm height, 23 cm width, 24 cm depth); (**b**, **d**) excavated chainsaw hollow (av. height 30 cm, av. width 23 cm, av. depth 26 cm). Artificial den diagrams show data logger (dark grey rectangle) position on the wall of the nest box (c) and through the gap along the side of the chainsaw hollow door plate (d). The shaded circle represents the position of the large shredded bark Leadbeater's possum nest. The scale bar is indicative for diagrams (c) and (d).

2.3. Measuring artificial den microclimate

The number of artificial dens sampled per habitat type ranged from 5 – 20 (Table 1). We preferentially sampled occupied nest boxes to examine the microclimatic conditions experienced by denning individuals. However, as Leadbeater's possums are known to shift dens (Lindenmayer & Meggs, 1996; Harley, 2004), we also sampled some unoccupied nest boxes containing nests in the same territory (< 100 m distant). The number of days that dens were occupied varied substantially between habitat types and seasons, ranging from 13 – 937 days (Table 1; see section 2.4. for description of how occupancy was assessed). Where possible the same artificial dens were sampled over both seasons (84% sampled in both seasons), however the numbers sampled varied slightly across habitat types, with fewer boxes sampled in lowland swamp forest, particularly over summer, due to low occupancy (Table 1).

We measured the temperature and humidity of artificial dens and ambient conditions using iButton Thermochron DS1922L (temperature) and Hygrochron DS1923 (temperature and humidity) (Maxim Integrated, USA), which have an operating range -20°C to 85°C (precision ± 0.5°C) and 0% to 100% relative humidity (precision ± 5%). We had a limited number of Hygrochrons so these were used to measure ambient conditions and placed in a subset of nest boxes (n = 40/57 in winter, n = 34/61 in summer). All other nest boxes had temperature-only loggers. Data loggers mounted on plastic fobs were positioned in nest boxes on the south-east facing wall (the wall away from the tree; Figure 1). Leadbeater's possum nests vary in size and can fill an entire nest box. We installed data loggers on the nest box wall outside of the nest, and adjacent to the midpoint of the nest height (Figure 1). In chainsaw hollows, data loggers were installed between the side of the cavity and the nest by means of a metal bracket positioned approximately 4 – 12 cm below the entrance hole. Data loggers were orientated to ensure the sensor surface was facing towards the nest, which has been shown to be the correct orientation to accurately measure relative humidity (Shin et al., 2017). Ambient temperature and humidity were recorded for a cluster of four chainsaw hollows within a 200 m radius, or for a cluster of two to four nest boxes within a 500 m radius. Ambient data loggers were attached underneath the nest box or to the trunk of the tree at chainsaw hollow sites 1 - 2 m off the ground on the south side, to ensure they were not exposed to any direct sunlight. Temperature and humidity were recorded every 30 minutes for 7 – 12 weeks over winter (June – September 2017), and 10 – 11 weeks over summer (December 2017 – March 2018).

Table 1. Number of nest boxes and chainsaw hollows sampled in winter and summer across different habitat types and sites, including the number of occupied and unoccupied sampling days determined from reviewing camera-trap images.

Winter	**Summer**

	Number of artificial dens	Number of occupied (& unoccupied) sampling days	Number of artificial dens	Number of occupied (& unoccupied) sampling days
Nest boxes				
Lowland swamp forest (Yellingbo)	15	139 (485)	12	13 (749)
Montane ash forest – low elevation (Dowey Spur)	5	215 (53)	6	230 (129)
Montane ash forest – high elevation (Toorongo Plateau)	11	287 (296)	11	281 (514)
Montane riparian thicket (Mt Baw Baw/ Mt Erica)	15	937 (316)	17	894 (313)
Open snow gum (Mt Baw Baw/ Mt Erica)	11	502 (424)	15	277 (635)
Chainsaw hollows				
Montane ash forest – high elevation (Toorongo Plateau)	20	682 (538)	17	596 (567)

2.4. Monitoring den occupancy and measuring environmental variables

To determine artificial den occupancy we used motion-heat-activated camera traps (Recoynx HC600 and PC900 Hyperfire) positioned on an adjacent tree 0.7 – 3 m distant and directed at the den entrance. Camera traps were programmed to take five pictures per trigger at high sensitivity, with no delay between triggers. We reviewed all camera trap photos to assign occupancy status (occupied, unoccupied, uncertain) for each den at 30-minute intervals. As Leadbeater’s possums are nocturnal, a den was designated as ‘occupied’ during the day if photographs showed individuals emerging at dusk and returning at dawn; we found emergence and return times to be highly consistent between nights. The batteries of some cameras did not last the full sampling period (eleven boxes in winter and nine in summer), and nest boxes in lowland swamp forest (n = 15) were not monitored with cameras during the winter period owing to a shortage of cameras. Temperature differences between ambient and nest boxes with known occupancy were used to assign occupancy to boxes for which camera images were not available. Nest boxes were treated as occupied if recorded nest box temperatures were consistently > 2°C higher than ambient during daytime hours (see Table

S1 for details and evaluation). This method was only applied over winter when heat signals from animals in occupied nest boxes were stronger. In summer, nest box occupancy was classed as uncertain when camera data were not available. For all nest boxes monitored with cameras, we also determined colony size and breeding activity (based on the presence of juveniles).

Vegetation cover in the canopy and mid-storey at each nest box location was quantified by analysing hemispherical photos taken directly above the nest box with a fisheye lens (Sigma 8 mm 6.3), using Gap Light Analyzer image processing software (Version 2.0). Photographs were standardised in the field following the methods described by Beckschäfer et al. (2013). An equivalent vegetation cover measure was not recorded for chainsaw hollows due to logistical constraints imposed by installation heights (up to 16 m). Daily solar radiation measurements were obtained for each site based on the closest available weather station (e.g. Healesville, Noojee and Baw Baw, Bureau of Meterology 2018).

2.5. Statistical analysis

Based on recorded daily emergence and return times, we restricted analyses to daytime hours that Leadbeater's possums spend inside their dens (winter = 7:00 h to 17:30 h, summer = 6:30 h to 20:30 h). Temperature and humidity recordings associated with uncertain occupancy status were excluded from analyses (3% of records in winter and 10% of records in summer). Some of our humidity recordings showing substantial fluctuations (sudden increases or decreases > 30 RH% between records, or sudden drops to negative values), followed by the flat lining of readings, which based on comparisons with other nearby loggers appeared to have been caused by equipment faults rather than environmental phenomena. Hence, these were assumed to be erroneous and were excluded from analyses (28% of records in winter and 9% of records in summer). All humidity values were corrected for saturation drift (a known issue when dataloggers are exposed to constant high humidity levels; Maxim Integrated Products 2011, p. 53). We excluded whole-day temperature recordings with rapid jumps (> 5°C between 30-minute intervals), that were likely due to the effect of direct body heat from possums moving inside the cavity and resting on data loggers, and also tested whether excluding these data impacted our results.

Daytime daily minimum (T_{boxMIN}), mean ($T_{boxMEAN}$) and maximum (T_{boxMAX}) nest box temperatures were calculated for each nest box over the winter and summer sampling periods. We fitted linear mixed effects models (LMMs) with the package '*nlme*' using the software 'R-Studio' (R Core Team 2017) to examine the effect of ambient temperature, occupancy status, daily solar exposure (measured as vegetation cover × daily solar radiation), nest box colour, and habitat type on nest box temperatures. An interaction term between occupancy status and ambient temperature was also included, as we expected there to be a greater influence of occupancy at lower ambient temperatures (due to metabolic heat production). To examine the effect of den type (nest box vs chainsaw hollow), we also fitted LMMs for nest box and chainsaw hollow daily temperature recordings in high elevation montane ash forest, where both types of artificial dens were installed. We examined the effect of den type, occupancy status and ambient temperature on den temperature responses (T_{denMIN}, $T_{denMEAN}$, T_{denMAX}), as well as daily temperature range (max – min, $T_{denRANGE}$). Interaction terms between den type and occupancy status, and den type and ambient temperature were also included. Continuous predictors (ambient temperature and solar exposure) were standardised (subtracting the mean, then dividing by the standard deviation) to aid comparison across coefficient estimates. We included a random effect of den ID nested within the study site on the intercept to account for repeated measures and spatial autocorrelation. Models were fitted with a corARMA correlation structure to account for temporal correlation between records across days (Zuur et al., 2009) and a varIDent variance structure to account for heterogeneity in the variance of the model's residuals for different habitat types. All predictors and interactions were included in the model fitting process, as they were all considered ecologically relevant and were not strongly correlated with each other ($r < 0.7$).

2.6. Modelling eco-physiological consequences of artificial den use across habitat types

We estimated the physiological costs to Leadbeater's possums denning in nest boxes and chainsaw hollows for the temperature extremes recorded in winter and summer, using a simple endotherm model (Porter & Kearney, 2009) that was parameterised with morphological characteristics of an average adult Leadbeater's possum (Table S2). This model has been used previously to predict heat production and heat loss requirements for arboreal marsupials denning in tree hollows and nest boxes (Rowland et al., 2017). The model was run based on temperature extremes recorded in artificial dens on the coldest (lowest daily minimum in winter) and hottest (highest daily maximum in summer) day in each habitat type. To predict Leadbeater's possum heat production requirements during cold temperatures, we simulated an average-sized colony of Leadbeater's possum (n = 4, Figure S2) huddled together to determine equivalent metabolic rates of the colony. We also adapted the model to include an additional nest insulation resistance parameter, using an approximate nest depth (75 mm thickness of nesting material surrounding a central nesting chamber, calculated from measurements of nests and approximating the size of possums huddled inside) and estimates of nest thermal conductivity from bird nests (Skowron & Kern, 1980). We predicted heat loss requirements over summer for an individual possum without the insulation of the nest, as Leadbeater's possums have been observed sleeping on top of the nest during extreme summer temperatures in both nest boxes and chainsaw hollows (D. Harley and L. Lumsden unpublished data).

3. Results

3.1. *Ambient conditions*

Ambient temperatures recorded during the study period ranged from -5.5°C to 20.5°C in winter, and 1°C to 40.5°C in summer, with considerable variation between habitat types. Mean ambient temperatures decreased with increasing elevation, although over summer high elevation montane ash forest, montane riparian thicket (subalpine) and subalpine woodland all experienced similar mean temperatures (Table 2). Ambient humidity recordings were high across all habitat types in both seasons, and particularly over winter.

Table 2. Mean artificial daytime den and ambient temperatures and humidity (± SD) recorded across habitat types at different elevations.

Habitat type	**Average elevation**	**Measure**	**Winter temp** (°C)	**Summer temp** (°C)	**Winter RH (%)**	**Summer RH (%)**
Lowland swamp forest	110 m	Nest box	7.7 ± 2.5	20.0 ± 5.6	89.4 ± 0.6	79.2 ± 2.6
		Ambient	8.0 ± 2.3	19.4 ± 5.0	83.2 ± 5.4	71.3 ± 15.8
Montane ash forest (low elevation)	730 m	Nest box	5.7 ± 1.1	16.7 ± 3.0	98.4 ± 0.2	91.0 ± 1.1
		Ambient	5.7 ± 0.9	16.4 ± 2.7	87.7 ± 1.4	76.0 ± 7.9
Montane ash forest (high elevation)	1050 m	Nest box	3.0 ± 0.8	14.4 ± 3.1	97.0 ± 0.3	87.7 ± 1.9
		Ambient	2.6 ± 0.7	13.5 ± 2.7	93.3 ± 0.7	81.2 ± 7.5
Montane riparian thicket (subalpine)	1400 m	Nest box	3.1 ± 0.9	14.6 ± 2.3	95.1 ± 0.3	87.8 ± 0.6
		Ambient	1.5 ± 0.6	13.6 ± 1.8	87.2 ± 0.4	74.4 ± 2.3
Subalpine woodland	1480 m	Nest box	1.9 ± 1.1	14.2 ± 2.8	91.9 ± 0.3	71.4 ± 1.4
		Ambient	0.7 ± 0.8	13.7 ± 2.3	84.9 ± 0.9	70.2 ± 3.3
Montane ash forest (high elevation)	1000 m	Chainsaw hollow	4.4 ± 0.3	16.2 ± 0.9	97.1 ± 0.2	90.3 ± 0.5
		Ambient	3.1 ± 0.6	14.2 ± 1.9	97.0 ± 0.3	84.6 ± 3.7

3.2. *Artificial den occupancy, den shifting, colony size and breeding activity*

Leadbeater’s possum colonies used both types of artificial dens over winter and summer. In total, 15 colonies were recorded using the same artificial den over the entire winter and summer periods, with 29 other colonies shifting dens at least once across the monitoring periods. In nest boxes, colony size ranged from 2 - 7 individuals, with a mean of 3.9 individuals in winter (n=31) and 4.4 over summer (n=36). Colonies in chainsaw hollows ranged from 2 - 4 individuals, with a mean of 3.5 in winter (n=8) and 3.3 in summer (n=8). In winter, breeding was observed in nest boxes in montane riparian thickets and subalpine woodland, and also in chainsaw hollows (ten colonies contained one juvenile and one contained two juveniles; Figure S2), while in summer breeding was observed in nest boxes across all habitat types and chainsaw hollows (twenty colonies had one juvenile and two had two juveniles; Figure S2).

3.3. Seasonal variation in nest box temperatures across habitat types

Nest box temperatures in all habitat types were strongly influenced by ambient temperatures over both winter and summer, with the greatest differences between nest box and ambient temperatures observed at higher elevation sites (Table 2). Over winter, daytime nest box temperatures ranged from a minimum of -5.5°C (unoccupied) in subalpine woodland to a maximum of 20.5°C (unoccupied) in lowland swamp forest (Figure S3). The lowest occupied nest box temperature recorded was -4°C in subalpine woodland. Temperatures below 0°C were recorded in nest boxes in all habitat types over winter, and 25% of all daytime nest box temperatures recorded in subalpine woodland were < 0°C.

In summer, the temperatures recorded in nest boxes ranged from 0.5°C (unoccupied) in subalpine woodland to a maximum of 48.5°C unoccupied dark grey nest box) in lowland swamp forest. The highest occupied nest box temperature recording across all habitat types was 35°C (in subalpine woodland). There was less variation in minimum, mean and maximum box temperatures between habitat types than recorded in winter, with the exception of lowland swamp forest which had higher mean and maximum temperatures (Table 2; Figure S3). In lowland swamp forest, temperatures above 40°C were recorded in 75% of nest boxes, and 9% of all nest box recordings were > 30°C in summer. Across all other habitat types, 0.001% of occupied nest box recordings were > 30°C in summer (Figure S3).

The linear mixed-effects models of daily nest box temperatures indicated that, across sites, occupied boxes were warmer than unoccupied boxes, irrespective of season and despite the extreme maximum temperatures recorded in some unoccupied boxes in lowland swamp forest (Table S3). However, there was a moderate interaction between ambient conditions and occupancy, such that the temperature difference between occupied and unoccupied boxes was greatest in winter when ambient temperatures were low (Table S3). Higher solar exposure increased maximum nest box temperatures and decreased minimum temperatures (Table S3). Nest box colour only influenced summer maximum temperatures, with darker-coloured boxes experiencing higher maximum temperatures.

3.4. Comparison of nest box and chainsaw hollow thermal profiles in high elevation montane ash

Winter daily minimum temperatures were lower and summer daily maximum temperatures higher in nest boxes relative to chainsaw hollows, with the chainsaw hollows providing a more stable environment (Figure 2). Daily temperature fluctuations (calculated as the daily maximum minus the daily minimum) in occupied nest boxes were up to four times greater than in occupied chainsaw hollows (winter means: 2.74°C vs 1.36°C, summer means: 9.14°C vs 2.22°C; Figure 2c and 2d). Den type strongly influenced all temperature response variables (Table S4), and there was evidence of an interaction between den type and ambient temperatures, which amplified the effect of den type at extreme temperatures (Figure 2). Based on the fitted models, winter minimum den temperatures were on average 3°C warmer in chainsaw hollows than nest boxes for both occupied and unoccupied dens (Figure 2). This pattern was also apparent over summer, but temperature differences were more pronounced: summer maximum den temperatures were 9°C cooler in occupied chainsaw hollows than nest boxes (22.3°C vs 31.4°C, Figure 2). Additionally, a significant interaction between den type and occupancy indicated that occupancy had a greater effect on mean and maximum summer temperatures within chainsaw hollows (Figure 2; Table S4).

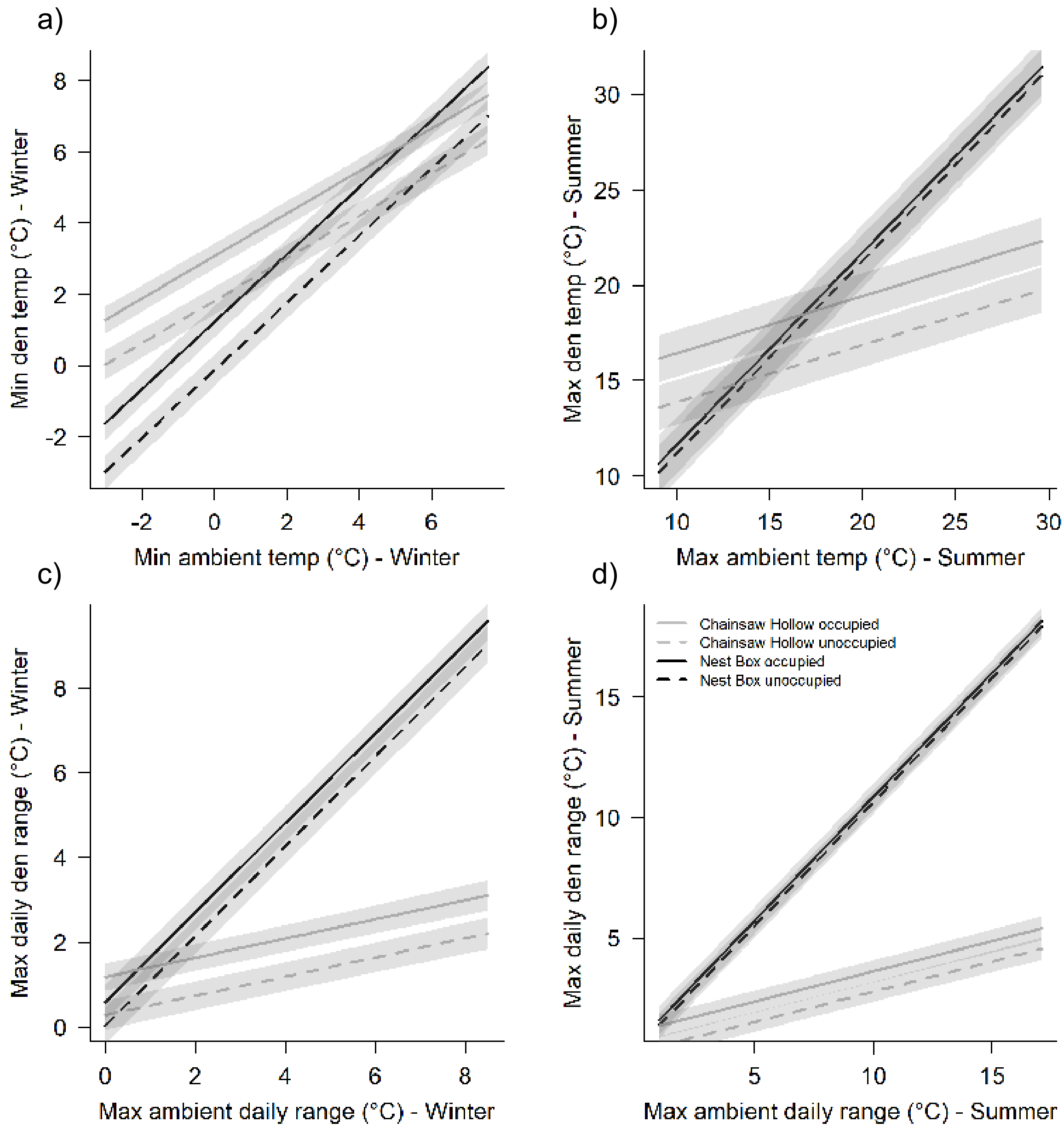

Figure 2. The modelled effect of ambient temperatures on the daily minimum (a), maximum (b) and range (max – min) (c-d) of den temperatures in unoccupied (dashed line) and occupied (solid line) nest boxes (dark) and chainsaw hollows (light) in high elevation montane ash forest over winter (a,c) and summer (b,d). Shaded areas represent 95% confidence intervals. All other variables were held at the mean value to generate predictions.

3.5. Artificial den relative humidity

Daily mean relative humidity (%RH) recorded in nest boxes was consistently higher and less variable than ambient across all habitat types and seasons (Table 2). In chainsaw hollows, mean humidity closely matched ambient in winter, but was higher than ambient in summer (Table 2). Occupied dens typically had higher relative humidity compared to unoccupied dens (88 %RH vs 83 %RH). In artificial dens experiencing high daily maximum temperatures (>30°C), when evaporative cooling may be required, relative humidity ranged from 32-100 %RH (mean: 69 %RH) in nest boxes and 58-98 %RH (mean: 75 %RH) in chainsaw hollows.

3.6. Biophysical model predictions and laboratory experiments of nest insulation

The biophysical model appeared to capture heat exchange processes for an individual Leadbeater's possum, with the predicted increased metabolic rate at cold temperatures and predicted lower critical temperature (26.5°C) closely matching those estimated from empirical laboratory experiments (Figure S5). During extreme winter temperatures, the predicted daytime heat production requirements of an average colony of Leadbeater's possums (four individuals; Figure S2) differed across habitat types, with higher energy production required in subalpine woodland (155% basal, average across daytime hours) than lowland swamp forest (130% basal, average across daytime hours, Figure 3). Predictions from the biophysical model also showed that individual heat production requirements were greatly reduced for larger colonies if they huddled together during cold temperatures. An individual's' predicted heat production costs during minimum winter nest box temperatures (-5°C) recorded in subalpine woodland were significantly lower when huddling as part of a colony of seven (119% basal) compared to an individual huddling in a colony of two (256% basal, Figure S6). During maximum summer temperatures, maximum daytime heat loss (calculated as % basal metabolic heat production required to be lost via evaporative cooling) for an individual possum was relatively consistent for nest boxes across habitat types (<102% basal). Owing to the lower maximum summer temperatures in chainsaw hollows, there was no predicted heat loss for an individual possum (Figure 3). However, based on the maximum temperature recorded for a nest box (48.5°C for an unoccupied nest box in lowland swamp forest), predicted heat loss would reach a maximum of 418% basal (Figure 3b).

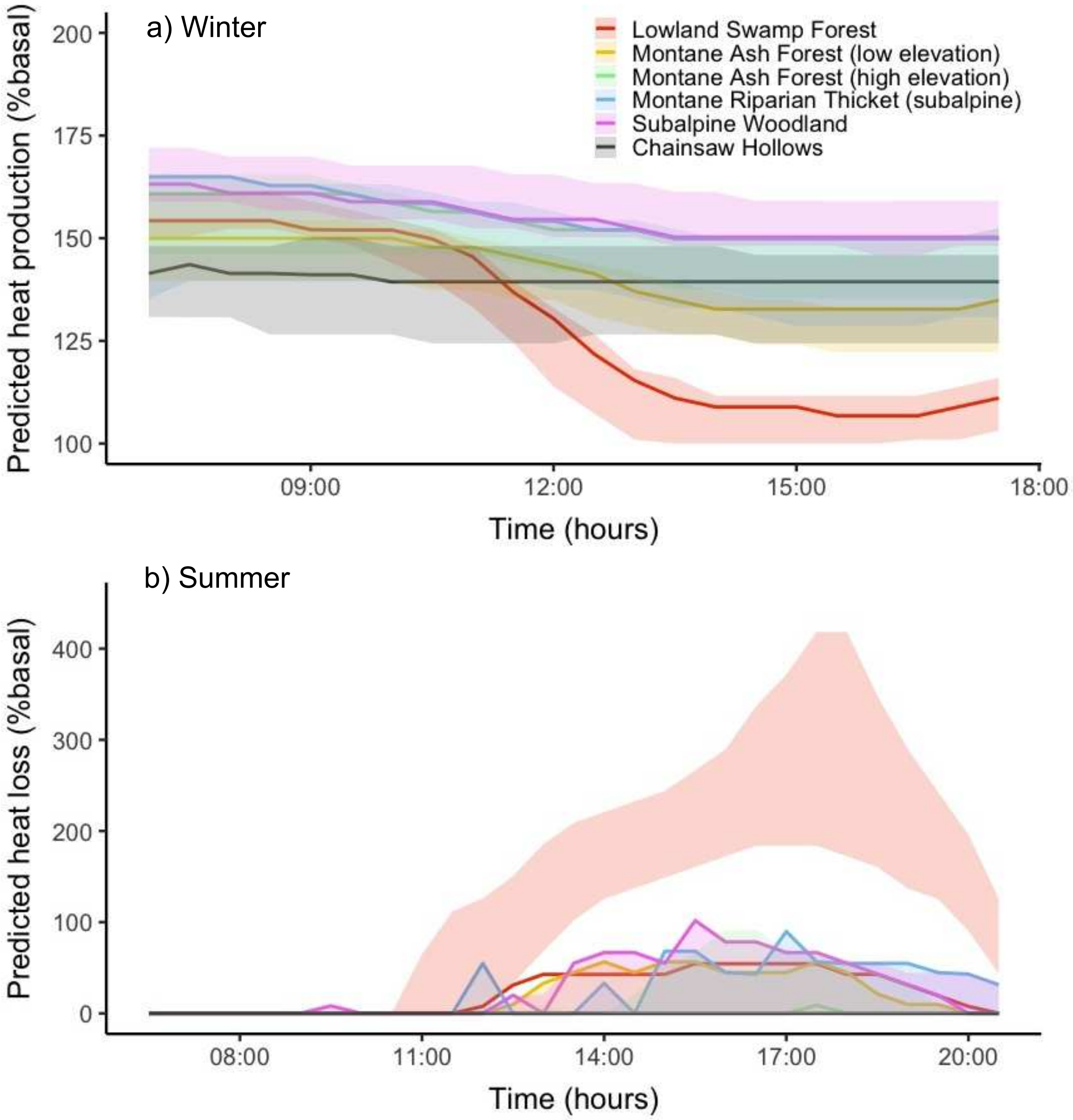

Figure 3. Predicted (a) heat production and (b) heat loss required in each habitat type for (a) an individual Leadbeater's possum huddled in a colony of four denning in a nest box over the coldest day in winter during the monitoring period (-5.5°C ambient temperature recorded in subalpine woodland), and (b) for an individual possum over the hottest day in summer during the monitoring period (40.5°C ambient temperature recorded in lowland swamp forest). Shaded areas represent the range of predicted heat production or heat loss requirements within nest boxes across each habitat type. Solid lines represent predicted costs for the coldest/hottest occupied nest box for each habitat type. For comparison, over summer in lowland swamp forest, on the hottest day recorded (19/01/18) no nest boxes were occupied,

therefore the solid line represents a different day (27/12/17), which had the hottest occupied nest box temperatures.

4. Discussion

Nest boxes are used globally to increase the availability of den and nest sites for hollow-dependent species (Newton, 1994). However, questions have been raised about the suitability of the microclimatic conditions they provide (Isaac et al., 2008; Rowland et al., 2017), and studies from different systems have yielded mixed conclusions regarding their thermal suitability (Goldingay, 2020; Schwartz, Genouville, & Besnard, 2020). Previous studies have focussed largely on the microclimate of unoccupied artificial dens (Goldingay, 2015; Rowland et al., 2017; Griffiths et al., 2018, although see Goldingay & Thomas, 2021), but this fails to account for the potentially confounding effect of individual heat production (Kearney et al., 2011; Maziarz, 2019). Our study provides new insights into seasonal occupancy patterns of artificial dens, in relation to the temperatures that animals could experience.

The temperatures we recorded in nest boxes during this study closely tracked ambient conditions. Large daily fluctuations were evident, particularly over summer, and the seasonal range of temperatures in nest boxes also tracked those recorded across the broad elevational range of the species. In contrast, temperatures in the chainsaw hollows were more stable, being warmer in winter and cooler in summer than nest boxes, so the associated thermoregulatory costs and evaporative heat loss requirements for Leadbeater’s possum colonies would in turn be lower (Figure 2). Our biophysical modelling suggests that Leadbeater’s possums can partially mitigate the energetic impacts arising from the cool nest box temperatures recorded in winter via behavioural strategies such as building large, insulative nests, and huddling. In contrast, Leadbeater’s possum have limited behavioural scope to mitigate high summer nest box temperatures (recorded primarily in lowland swamp forest), other than denning elsewhere. High temperatures were predicted to require substantial heat loss for Leadbeater’s possums, such that during the day, while in their den, they would be outside their thermoneutral zone 9% of the time. During extreme heat events, this could lead to heat stress and dehydration, particularly given the high humidity levels also recorded in nest boxes (Table 2). The low summer occupancy of nest boxes recorded in lowland swamp forest indicates that possums may shift dens to natural hollows to avoid extremely high temperatures - an issue exacerbated by the loss of dense vegetation structure at this site and associated higher solar exposure (Greet et al., 2020).

The low winter temperatures recorded in all habitat types, particularly at high elevations, have the potential to present physiological challenges for denning arboreal mammals. Over winter, all artificial den temperatures fell well below the lower critical temperature for an individual Leadbeater’s possum (26.5°C), as estimated from empirical laboratory experiments (Smith et al.,

1982) and by our biophysical model (Figure S5). This critical temperature, measured within a metabolic chamber, does not factor in behavioural strategies such as communal denning, huddling and building thick tightly-woven nests, which are known to minimise heat loss (Gilbert et al., 2010) and likely mitigate the effect of cold den temperatures (Smith et al., 1982). A study which simulated the huddling of four sugar gliders (*Petaurus breviceps*, a closely related species of similar size) showed that this behaviour allowed them to reduce their lower critical temperature from 27°C to 16°C (Fleming, 1980). Smith et al. (1982) also conducted field energetic studies and assumed that, given the strategies used by Leadbeater's possum, individuals in the nest within their den tree would always be within their thermoneutral zone with a metabolic rate close to basal. However, the extremely low den temperatures that we recorded in this study indicate that this assumption may not be valid for nest boxes. When our biophysical model of a Leadbeater's possum colony was parameterised to mimic the huddling of four individuals in an insulated nest, the minimum box temperature required for individuals to remain within their TNZ decreased from 26.5°C to 11.4°C (Table S2). Nonetheless, this lower limit is still well above the coldest temperatures recorded in occupied nest boxes over winter (-4°C, see also Table 2).

Our biophysical model predictions were sensitive to assumptions about the thermal conductivity of the nest, which we based on previous studies of bird nests due to the lack of equivalent studies for mammal nests (Skowron & Kern, 1980; Heenan & Seymour, 2011). Hence, predicted heat production costs over winter should be taken as preliminary and indicative only. These simulations also do not account for the potential use of heterothermy to help individuals cope with the cold, which has on rare occasion been observed in captivity, but never in the wild despite extensive research on the species (Smith, 1980). Observations of colonies regularly using nest boxes and breeding during winter at the coldest sites suggest that either behavioural and/or physiological strategies employed by Leadbeater's possums are more effective at minimising energy costs than modelled here, or that additional energy costs do not pose a serious constraint on fitness due to other adaptations. To improve our understanding and modelling predictions, future work should specifically examine the thermal and structural properties of Leadbeater's possums' large, tightly-woven nests and the potential use of torpor during extreme temperatures.

Summer temperature extremes are likely to be more challenging for this species, as Leadbeater's possum colonies have limited capacity to avoid high temperatures in nest boxes other than by choosing to den elsewhere. Summer nest box temperatures recorded in this study add to the growing body of evidence that there may be eco-physiological costs for species reliant on nest boxes year round (Goldingay, 2015; Rowland et al., 2017). However, this is not universal as Goldingay (2017) recorded no fitness costs to squirrel gliders (*Petaurus norfolcensis*) reliant on nest boxes over a 10 year period, and no observations of mortality of sugar gliders following 11 days of temperatures recorded at or above 40°C (Goldingay & Thomas, 2021). In the case of Leadbeater's possum, eco-physiological costs may be more pronounced in more open vegetation types where maximum temperatures are exacerbated by high solar exposure. Nests are likely to provide some insulation from hot ambient temperatures, however they may also trap heat produced by occupants. With reduced air flow inside dens, nest microclimates are likely to lead to elevated physiological stress during the hotter afternoons.

The summer biophysical model predictions indicated that Leadbeater's possum heat loss requirements increase when den temperatures exceed 30°C (Table S2). The nest boxes in montane ash forests and subalpine woodlands (which account for most of the possum's range) exceeded 30°C regularly, but only one nest box recorded a temperature above 35°C on one day over summer. In lowland swamp forest, nest boxes exceeded 40°C on two days over summer (recorded for six of 11 nest boxes being monitored in this habitat type). These temperatures corresponded with periods of low occupancy in this study, and no nest boxes were occupied on the days that reached 40°C. Past monitoring data show some seasonal patterns of nest box use by Leadbeater's possums in lowland swamp forest, with lower occupancy of nest boxes over summer as colonies move to den trees (Harley, 2004; D. Harley unpublished data). This pattern was not observed in a recent study of eastern pygmy possums (*Cercartetus nanus*) with no changes in occupancy in periods following extreme heat days (Goldingay, 2020). Leadbeater's possums are likely to require substantial evaporative heat loss during high summer temperatures in nest boxes, and particularly lactating females with pouch young. High nest box temperatures, combined with the high humidity recorded in nest boxes (> 70 %RH) that can reduce the efficiency of evaporative cooling mechanisms (Dawson, 1969), may result in hyperthermia during extreme heat events. Therefore, during extreme summer temperatures some nest boxes at low elevations (particularly at sites with open vegetation structure and high solar exposure) will not provide thermally suitable dens.

The documented and projected decline of hollow-bearing trees across Leadbeater's possum's range (Lindenmayer & Wood, 2010) suggests that artificial dens will be required to supplement natural dens in order to mitigate predicted population declines (Harley, 2006). Significant financial resources and hours have been dedicated to this, and more than 600 nest boxes and 132 chainsaw hollows have been installed to date (Harley, 2016). Monitoring has revealed high occupancy and evidence of successful breeding in both types of artificial dens, yet little was known about their thermal suitability. This study provides evidence of the microclimatic benefits of chainsaw hollows and suggests that further provisioning should be explored in other habitat types, particularly those that experience seasonal climate extremes. Decisions about deployment of artificial dens, including numbers, design, and location, will be influenced by practical considerations beyond thermal suitability, such as the availability of suitable trees for chainsaw hollows, installation costs, maintenance requirements, and accessibility for installation, monitoring and research purposes. Nonetheless, our findings demonstrate the importance of accounting for site and species–specific factors when assessing the potential suitability of artificial habitats for target populations. In this range-wide assessment of Leadbeater's possum, encompassing all of the major forest types inhabited by the species, we found that although some nest boxes may not provide thermally suitable conditions, the species could substantially reduce thermoregulatory costs through various adaptations and behavioural strategies. These results highlight the importance of considering these factors when interpreting recorded temperatures in (often empty) artificial dens. Many other bird and mammal species construct nests within artificial dens (Gibbons & Lindenmayer, 2002), and thus may have some ability to manipulate temperatures experienced within provided structures. Den-sharing and huddling is also common in several other species of arboreal marsupials and among groups such as bats, and rodents (Gilbert et al., 2010). While these behaviours may help species contend with cold temperatures, behavioural responses may be less effective for species reliant on artificial dens in hot tropical environments, that also face additional challenges due to high humidity, which reduces the effectiveness of evaporative heat-loss. Physical traits, such as fur depth and body size, as well as physiological requirements, such as those associated with breeding, can also influence how sensitive individuals are to temperature extremes and sub-optimal den temperatures (Scholander et al., 1950). Ultimately, decisions about the deployment of artificial dens are also influenced by practical considerations beyond thermal suitability, such as relative costs, maintenance requirements, and accessibility. However, our results suggest the thermal suitability of artificial dens should be a key factor guiding deployment decisions, and include consideration of site (i.e. seasonality, aspect, slope, shade profile) and species–specific physiological, behavioural, and morphological adaptations.

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Data Availability

Data collected in this study and the associated code will be made publicly available on the Dryad Digital Repository upon acceptance of the manuscript.

Conflicts of interest

The authors have no conflict of interest.

References

Beckschäfer, P., Seidel, D., Kleinn, C., & Xu, J. (2013). On the exposure of hemispherical photographs in forests. *iForest* **6**, 228–237.

Beyer, G. L., & Goldingay, R. L. (2006). The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. *Wildl. Res.* **33**, 161–174.

Bureau of Meterology. (2018). Climate Data Online.

Carey, A. B. (2002). Response of northern flying squirrels to supplementary dens. *Wildl. Soc. Bull.* **30**, 547–556.

Catry, I., Franco, A. M. A., & Sutherland, W. J. (2011). Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels. *Biol. Conserv.* **144**, 1111–1119.

Cockle, K L, Martin, K., & Wesołowski, T. (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Front. Ecol. Environ.* **9**, 377–382.

Cockle, Kristina L., Bodrati, A., Lammertink, M., & Martin, K. (2015). Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biol. Conserv.* **184**, 193–200.

Dawson, T. J. (1969). Temperature regulation and evaporative water loss in the brush-tailed possum *Trichosurus vulpecula*. *Comp. Biochem. Physiol.* **28**, 401–407.

Fleming, M. R. (1980). Thermoregulation and torpor in the sugar glider, *Petaurus breviceps* (Marsupialia: Petauridae). *Aust. J. Zool.* **28**, 499–509.

Gibbons, P., & Lindenmayer, D. (2002). Tree hollows and wildlife conservation in Australia. CSIRO PUBLISHING.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., & Tanton, M. T. (2000). Hollow formation in eucalypts from temperate forests in southeastern Australia. *Pacific Conserv. Biol.* **6**, 218–228.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., & Tanton, M. T. (2002). Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biol. Conserv.* **103**, 1–12.

Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J. M., Giroud, S., Blanc, S., & Ancel, A. (2010). One for all and all for one: The energetic benefits of huddling in endotherms. *Biol. Rev.* **85**, 545–569.

Goldingay, R. L. (2015). Temperature variation in nest boxes in eastern Australia. *Aust. Mammal.* **37**, 225–233.

Goldingay, R. L. (2017). Does nest box use reduce the fitness of a tree-cavity dependent mammal? *Ecol. Res.* **32**, 495–502.

Goldingay, R. L. (2020). Does temperature variation influence nest box use by the eastern pygmy-possum? *Aust. Mammal.* **42**, 77–84.

Goldingay, R. L., Rohweder, D., & Taylor, B. D. (2020). Nest box contentions: Are nest boxes used by the species they target? *Ecol. Manag. Restor.* **21**, 115–122.

Goldingay, R., & Thomas, K. (2021). Tolerance to high temperature by arboreal mammals using nest boxes in southern Australia. *J. Therm. Biol.* **98**.

Greet, J., Ashman, K. R., Watchorn, D. J., Harley, D. K. P., & Duncun, D. (2020). The vegetation structure and condition of contracting lowland habitat for Leadbeater's possum (Gymnobelideus leadbeateri). *Aust. Mammal.*

Griffiths, S. R., Bender, R., Godinho, L. N., Lentini, P. E., Lumsden, L. F., & Robert, K. A.

(2017). Bat boxes are not a silver bullet conservation tool. *Mamm. Rev.* **47**, 261–265.

Griffiths, S. R., Lentini, P. E., Semmens, K., Watson, S. J., Lumsden, L. F., & Robert, K. A. (2018). Chainsaw-carved cavities better mimic the thermal properties of natural tree hollows than nest boxes and log hollows. *Forests* **9**, 1–27.

Hansen, B. D., Harley, D. K. P., Lindenmayer, D. B., & Taylor, A. C. (2009). Population genetic analysis reveals a long-term decline of a threatened endemic Australian marsupial. *Mol. Ecol.* **18**, 3346–3362.

Harley, D. (2016). An overview of actions to conserve Leadbeater's Possum. *Vic. Nat.* **133**, 429–431.

Harley, D. K.P., & Lill, A. (2007). Reproduction in a population of the endangered Leadbeater's possum inhabiting lowland swamp forest. *J. Zool.* **272**, 451–457.

Harley, Dan K P. (2004). Patterns of nest box use by Leadbeater's possum (*Gymnobelideus leadbeateri*): applications to research and conservation. In R. G. and S. Jackson (Ed.), *Biol. Aust. Possums Glid. Possums*. pp. 318–329. Surrey Beatty: Sydney.

Harley, Dan K P. (2006). A role for nest boxes in the conservation of Leadbeater's possum (*Gymnobelideus leadbeateri*). *Wildl. Res.* **33**, 385–395.

Harley, Dan K P, Worley, M. A. W., & Harley, T. K. (2005). The distribution and abundance of Leadbeater's possum *Gymnobelideus leadbeateri* in lowland swamp forest at Yellingbo Nature Conservation Reserve. *Aust. Mammal.* **27**, 7–15.

Harper, M. J., McCarthy, M. A., & van der Ree, R. (2005). The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. *Wildl. Res.* **32**, 509–516.

Heenan, C. B., & Seymour, R. S. (2011). Structural support, not insulation, is the primary driver for avian cup-shaped nest design. *Proc. R. Soc. B Biol. Sci.* **278**, 2924–2929.

Hurley, V. G., & Harris, G. (2014). Simulating natural cavities in Slender Cypress Pine (*Callitris gracilis murrayensis*) for use by Major Mitchell's Cockatoo (*Lophochroa leadbeateri leadbeateri*): A report to the Department of Environment and Primary Industries.

Isaac, J. L., Parsons, M., & Goodman, B. A. (2008). How hot do nest boxes get in the tropics? A study of nest boxes for the endangered mahogany glider. *Wildl. Res.* **35**, 441–445.

Kearney, M., Ferguson, E., Fumei, S., Gallacher, A., Mitchell, P., Woodford, R., & Handasyde, K. (2011). A cost-effective method of assessing thermal habitat quality for endotherms. *Austral Ecol.* **36**, 297–302.

Kunz, Thomas H, & Lumsden, L. F. (2003). Ecology of cavity and foliage roosting bats. In T.H Kunz & M. . Fenton (Eds.), *Bat Ecol.* pp. 3–89. The University of Chicago Press:

Chicago.

Lindenmayer, D. (2014). Preventing the Extinction of an Iconic Globally Endangered Species – Leadbeater's Possum (Gymnobelideus leadbeateri). *J. Biodivers. Endanger. Species* **2**, 1–7.

Lindenmayer, D B, & Meggs, R. A. (1996). Use of den trees by Leadbeater's possum (*Gymnobelideus leadbeateri*). *Aust. J. Zool.* **44**, 625–638.

Lindenmayer, David B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G. E., Franklin, J. F., Laurance, W. F., Stein, J. A. R., & Gibbons, P. (2012). Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PLoS One* **7**.

Lindenmayer, David B., Cunningham, R. B., & Donnelly, C. F. (1997). Decay and collapse of trees with hollows in eastern Australian forests: Impacts on arboreal marsupials. *Ecol. Appl.* **7**, 625–641.

Lindenmayer, David B., Laurance, W. F., & Franklin, J. F. (2012). Global decline of large old trees. *Science (80-.).* **338**, 1305–1306.

Lindenmayer, David B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A. D., & Stein, J. A. R. (2014). New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conserv. Lett.* **7**, 61–69.

Lindenmayer, David B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R., & Gibbons, P. (2009). Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biol. Conserv.* **142**, 33–42.

Lindenmayer, David B., & Wood, J. T. (2010). Long-term patterns in the decay, collapse, and abundance of trees with hollows in the mountain ash (*Eucalyptus regnans*) forests of Victoria, southeastern Australia. *Can. J. For. Res.* **40**, 48–54.

Maziarz, M. (2019). Breeding birds actively modify the initial microclimate of occupied tree cavities. *Int. J. Biometeorol.* **63**, 247–257.

Newton, I. (1994). The role of nest sites in limiting the number of hole nesting birds: a review. *Biol. Conserv.* **70**, 265–276.

Porter, W. P., & Kearney, M. (2009). Size, shape, and the thermal niche of endotherms. *Proc. Natl. Acad. Sci.* **106**, 19666–19672.

Rowland, J. A., Briscoe, N. J., & Handasyde, K. A. (2017). Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-management of arboreal marsupials. *Biol. Conserv.* **209**, 341–348.

Rueegger, N. (2017). Artificial tree hollow creation for cavity-using wildlife – Trialling an alternative method to that of nest boxes. *For. Ecol. Manage.* **405**, 404–412.

Scholander, P. ., Walters, V., Hock, R., & Irving, L. (1950). Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 225–236.

Schwartz, T., Genouville, A., & Besnard, A. (2020). Increased microclimatic variation in artificial nests does not create ecological traps for a secondary cavity breeder. *Ecol. Evol.* **10**, 13649–13663.

Shin, M., Patton, R., Mahar, T., Ireland, A., Swan, P., & Moi Chow, C. (2017). Calibration and validation processes for relative humidity measurement by a Hygrochron iButton. *Physiol. Behav.* **179**, 208–212.

Skowron, C., & Kern, M. (1980). The insulation in nests of selected North American songbirds. *Springs* **97**, 816–824.

Smith, A. (1980). The diet and ecology of Leadbeater's possum and the sugar glider. PhD Thesis. Monash University, Melbourne.

Smith, A. P., Nagy, K. A., Fleming, M. R., & Green, B. (1982). Energy requirements and water turnover in free-living Leadbeater's possums, *Gymnobelideus leadbeateri* (Marsupialia: Petauridae). *Aust. J. Zool.* **30**, 737–749.

Smith, Andrew P., & Lindenmayer, D. (1988). Tree hollow requirements of Leadbeater's possum and other possums and gliders in timber production ash forests of the Victorian Central Highlands. *Wildl. Res.* **15**, 347–362.

Stojanovic, D., Cook, H. C. L., Sato, C., Alves, F., Harris, G., McKernan, A., Rayner, L., Webb, M. H., & Sutherland, W.J. Heinsohn, R. (2019). Pre-emptive action as a measure for conserving nomadic species. *J. Wildl. Manage.* 1–8.

Terry, W., Goldingay, R. L., & van der Ree, R. (2021). Can chainsaw carved hollows provide an effective solution to the loss of natural tree cavities for arboreal mammals? *For. Ecol. Manage.* **490**, 119122.

Todd, C. R., Lindenmayer, D. B., Stamation, K., Acevedo-Cattaneo, S., Smith, S., & Lumsden, L. F. (2016). Assessing reserve effectiveness: Application to a threatened species in a dynamic fire prone forest landscape. *Ecol. Modell.* **338**, 90–100.

TSSC. (2015). Conservation Advice - *Gymnobelideus leadbeateri* Leadbeater's possum.

Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in northern flickers? *Auk* **118**, 412–421.