Journal of Urban Ecology, 2021, 1–8

https://doi.org/10.1093/jue/juab032
Short Notes

Insulated nest boxes provide thermal refuges for wildlife in urban bushland during summer heatwaves

Reannan Honey, Chris McLean, Brad R. Murray and Jonathan K. Webb *

School of Life Sciences, University of Technology Sydney, Broadway, NSW 2007, Australia

*Corresponding author: E-mail: jonathan.webb@uts.edu.au

Submitted: 24 May 2021; **Received (in revised form):** 29 September 2021. **Accepted:** 1 October 2021

Abstract

In urban bushland, the installation of nest boxes is widely used to compensate for the loss of natural tree hollows. However, current nest box designs may not provide thermal refuges for wildlife during summer heatwaves, particularly if internal temperatures exceed the upper critical temperatures of wildlife. We investigated whether the addition of roofing insulation to nest boxes deployed for sugar gliders (*Petaurus breviceps*) and squirrel gliders (*Petaurus norfolcensis*) in urban bushland would reduce internal nest box temperatures during summer heatwaves. We measured temperatures of 44 insulated and 47 uninsulated nest boxes during one of the hottest summers on record (2018–2019) in the Lake Macquarie region of NSW, Australia, a period during which several prolonged heatwaves occurred. Over the 90-day study, maximum temperatures were, on average, 3.1°C lower in insulated boxes than in uninsulated boxes. The addition of insulation significantly lowered nest box temperatures regardless of aspect (north or south facing) or day of measurement. Temperatures exceeded the upper critical temperature (35.1°C) of gliders more frequently in uninsulated nest boxes (28% of days) than in insulated nest boxes (8% days). Although the addition of insulation to nest boxes lowered their internal temperatures, during heatwaves spanning 23 days, nest box temperatures exceeded the upper critical temperatures of gliders on 58% and 23% of days in uninsulated and insulated nest boxes respectively. These findings underscore the importance of retaining natural hollows in urban bushland to provide thermally suitable refuges for wildlife during extreme heat events.

Key words: heatwaves, tree hollow, thermal neutral zone, arboreal gliders, marsupial

Introduction

Tree hollows are considered to be keystone structures, and their loss is recognized as a major threat to biodiversity worldwide (Tews et al. 2004). In urban forest fragments, tree hollows are often a scarce resource due to the historical harvesting of trees for firewood, the felling of large trees for public safety and the loss of natural processes that create hollows such as fire (Harper et al. 2005a; Isaac et al. 2014). In Australia, natural hollows can take decades to centuries to form, as there are no hollow-creating vertebrates (Gibbons and Lindenmayer 2002). In response to this lack of hollows, local councils and community groups have deployed nest boxes in urban bushland remnants in an effort to conserve hollow-dependent species (Harper et al. 2005b; Macak 2020). To date, a wide diversity of birds and mammals have been reported using nest boxes in Australian urban areas (Harper et al. 2005b; Macak 2020).

Despite the utility of nest boxes, current designs may fail to provide suitable thermal conditions for nocturnal hollow-dependent species, particularly during the summer months (Griffiths et al. 2017, 2018; Rowland et al. 2017). Nest boxes often have thinner walls than natural hollows, and consequently, air temperatures are often higher and are more variable, inside nest boxes than in natural hollows (Isaac et al. 2008; Maziarz et al. 2017). Studies in Australia and Spain have reported the mortality of bats roosting inside nest boxes during summer, suggesting that nest boxes might act as death traps for nocturnal wildlife (Flaquer et al. 2014; Griffiths 2021). Recent studies have called for improved nest box designs to buffer animals from thermal extremes during the summer months (Rowland et al. 2017; Rueegger et al. 2020; Goldingay and Thomas 2021). To date, several studies have explored the effects of painting and insulation on nest box temperatures. In one study, white painted boxes tracked ambient temperatures during summer and were several degrees cooler than green painted boxes (Griffiths et al. 2017). In another study, the addition of polystyrene insulation to the roof and west wall of boxes reduced internal temperatures by 0.9–1.7°C relative to controls (Larson et al. 2018). However, as far as we are aware, no studies have explored whether modifying nest box designs (via addition of insulation, painting, or both) can reduce internal temperatures during summer heatwaves. Heatwaves, which are defined as three or more days where temperatures exceed the calendar day 90th percentile (Perkins and Alexander 2013), are of interest because they can have major impacts on human health (Williams et al. 2018) and can contribute to mortality events in wildlife (Gordon et al. 1988; O'Shea et al. 2016). Because heatwaves are predicted to increase in intensity and duration in future (Perkins-Kirkpatrick and Lewis 2020) and may be exacerbated by the urban heat island effect (Rizvi et al. 2019), nest boxes will need to provide wildlife with thermal refuges during extended periods of high ambient temperatures.

In this study, we performed a replicated field experiment to investigate whether the addition of roofing insulation could lower temperatures inside nest boxes that we placed on trees in urban bushland remnants during summer. Specifically, we investigated how nest box orientation and insulation affected nest box temperature regimes. Our study coincided with one of the hottest summers on record in Australia, during which several heatwaves occurred in southeast NSW (Bureau of Meteorology 2019a). At our study sites, these heatwaves spanned 23 days, providing us with a unique opportunity to explore whether insulated boxes provided thermally suitable refuges for wildlife during heatwaves.

Methods

Study sites

We carried out our study at five urban bushland remnants near Lake Macquarie, New South Wales, eastern Australia (Fig. 1). These sites host populations of sugar gliders (*Petaurus breviceps*), squirrel gliders (*Petaurus norfolcensis*) and feather-tail gliders (*Acrobates pygmaeus*) (Smith and Murray 2003), all of which are hollow-dependent species that use nest boxes (Goldingay et al. 2007, 2015). Study sites were spaced 1.5–15 km apart and were located in remnant native forests with patch sizes ranging from 35 to 165 ha (Fig. 1). Vegetation at the sites consisted of dry sclerophyll forest dominated by *Angophora costata and Eucalyptus haemastoma* with an understorey of *Banksia*, *Casuarina* and *Lomandra* species. The average annual rainfall for the region is 1030 mm while the mean minimum and maximum temperatures range from 2.6°C in July and 31.2°C in January (Bureau of Meteorology 2019b). Over the period of 20 December 2018–19 March 2019, air temperatures at the nearest weather station (Newcastle University 061390) ranged from 13.2 to 40.6°C and the total rainfall for the 3-month period was 220 mm. We identified days during which heatwaves occurred using temperature data for the closest weather station (Newcastle University), and the 90th percentiles for daily maximum temperatures from the closest weather station with long-term records of temperature data (Newcastle Nobbys Signal Station AWS 061055). As there were missing data for Newcastle University, we calculated mean daily maximum temperatures from Cooranbong and Newcastle University to identify heat wave days for the study region. For Lake Macquarie, we identified three prolonged heatwaves spanning 23 days (durations of 11, 5 and 7 days), which occurred from 26 December 2018 to 5 January 2019, 15–19 January 2019 and 25–31 January 2019. These dates were similar to those published by the Bureau of Meteorology 'Special climate statement 68—widespread heatwaves during December 2018 and January 2019' (Bureau of Meteorology 2019a). Maximum daily temperatures during the heatwaves ranged from 30.0 to 40.6°C.

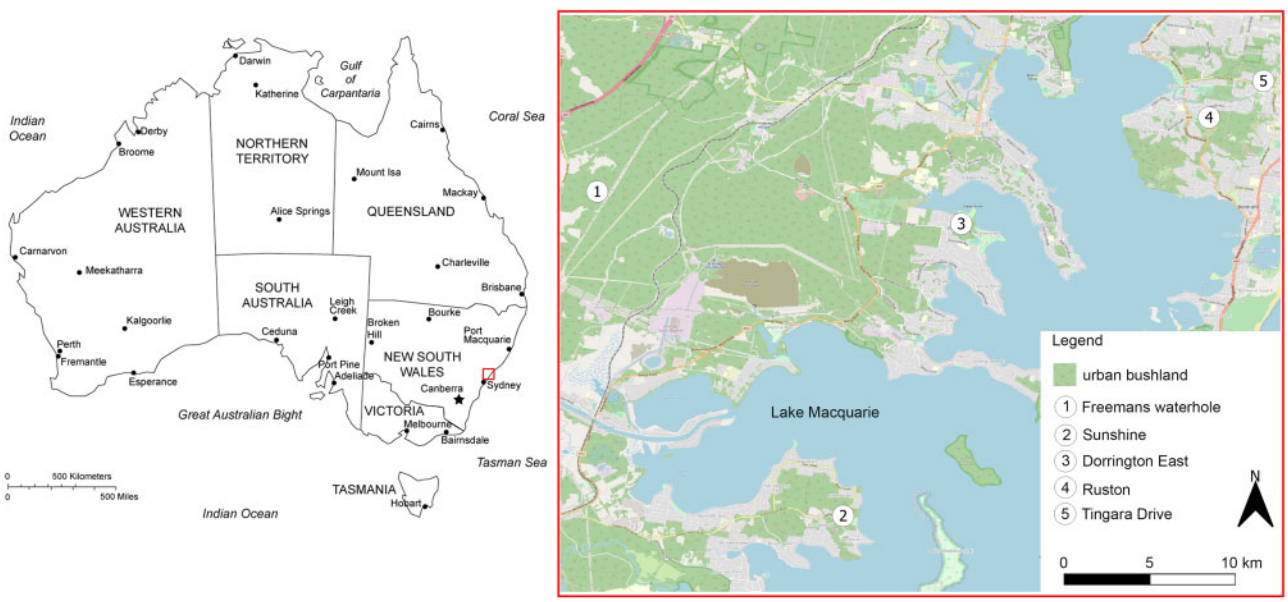

Figure 1: Locations of the five study sites in urban bushland patches near Lake Macquarie, NSW, Australia. Data courtesy of Openstreetmap.org.

Nest box installation

We constructed 100 nest boxes from 19-mm marine plywood to suit squirrel and sugar gliders (internal dimensions 400 mm × 175 mm × 175 mm, 40 mm entry hole, Nest Boxes Australia) and painted them green (Walpamur, pine green). We installed the lid on each box with a metal hinge to facilitate visual inspections. We covered half of the nest boxes ($n = 50$) with 4-mm aluminium insulation (Bradford Polyair Performa, Fig. 2). This insulation has two external reflective layers of aluminium foil coated in anti-glare, with an internal foam structure that reduces heat transfer. We stapled the insulation to the outside of each nest box so that it covered the sides and the roof. We did not affix insulation to the bottom of the boxes so that the 7-mm drainage holes could remain open to allow water egress.

Between 5 and 19 December 2018, we installed 100 nest boxes onto 100 different trees across five urban bushland sites in Lake Macquarie, NSW (Fig. 2). At each site, we attached 10 insulated and 10 uninsulated green nest boxes on trees with a minimum diameter at breast height of 35 cm (mean = 54.5 cm), and which did not have any visible hollows. Boxes were attached at a mean height of 4.6 m above ground (range 3.9–5.1 m). We attached each box to a 600-mm-long wooden backing piece (18-mm thick) and screwed this into the tree using 120-mm-long metal wood screws. Half of the nest boxes had a northerly aspect, while the other half had a southerly aspect. Boxes were randomly distributed throughout sites (depending on where suitable trees were located) and were spaced >15 m from the closest nest box.

Nest box temperatures

In each nest box, we suspended a temperature logger (Thermochron iButton model DS1922L, Maxim Integrated Products, San Jose, CA, USA; operating range −10 to +65°C, precision ±0.5°C) from a fishing line so that it hung near the centre of the box. Data loggers recorded temperatures every 30 min from 20 December 2018 to 19 March 2019 (90 days of data). Some data loggers failed, so we obtained thermal data from 44 insulated nest boxes (22 north-facing, 22 south-facing) and 47 uninsulated boxes (23 north-facing, 24 south-facing). After the placement of data loggers within boxes, we covered the entry hole of each box with aluminium fly mesh to prevent the ingress of animals into the boxes as the presence of endotherms within the boxes would have altered air temperature measurements (Rowland et al. 2017).

Figure 2: Photographs of nest boxes installed on trees without insulation (**A**) and with 4-mm reflective aluminium insulation (**B**).

Statistical analyses

We fitted a linear model using generalized least squares in R (R Core Team 2019) to determine whether the addition of insulation affected maximum temperatures in nest boxes. The model specified the fixed factors insulation (insulated or uninsulated), aspect (north or south) and day (each of the 90 days of measurement) and included all two-way interactions and the three-way interaction. To account for repeated measurements on the same nest boxes over time, we used the nlme package (Pinheiro et al. 2019) and the function corAR1 to specify a temporal autocorrelation structure of order one in the model (Mangiafico 2016).

To determine whether nest boxes could provide thermal refuges for gliders during summer, we calculated the number of hours per day that nest box temperatures exceeded the upper critical temperature of the thermal neutral zone (TNZ) of gliders. The TNZ is the optimal range of ambient temperatures within which mammals use minimal energy for thermoregulation (Lovegrove et al. 1991). For the glider species that use nest boxes in the study area, the TNZ ranges from 27.0 to 31.0°C for sugar gliders (Fleming 1980) and 34.0 to 35.1°C for feather-tail gliders (Fleming 1985). When ambient temperatures exceed 34.0°C, sugar gliders use evaporative cooling, by licking their forelimbs, to avoid overheating. As temperatures increase further, they extend salivation across their abdomen, tail, scrotal region and hind limbs and may also using panting and vasodilation (Robinson and Morrison 1957; Fleming 1980; Holloway and Geiser 2001a). Given this information, we opted to use 35.1°C as the upper critical temperature. We assumed that animals would experience heat stress and water loss if exposed to temperatures above 35.1°C for long periods (Dawson 1969).

We carried out two analyses, as follows. First, we used a two-factor Analysis of Variance (ANOVA), with insulation treatment and aspect as factors, and number of days where temperatures exceeded 35.1°C as the dependent variable. We analysed the entire data (90 days), and the subset of days during the three heatwaves (Bureau of Meteorology 2019a). Data were log-transformed prior to analysis to meet the assumptions of normality. Log-transformed data met assumptions of homogeneity of variances (Levene's tests, all $P > 0.05$) and data for insulated boxes were normally distributed (Kolmogorov–Smirnov test, $P = 0.20$). Data for uninsulated boxes showed departures from normality (Kolmogorov–Smirnov test, $P = 0.04$), but given that ANOVA is robust to departures from normality we elected to use log-transformed data. Next, we used a repeated-measure ANOVA to determine whether insulation treatment affected the number of hours per day during which nest box temperatures exceeded 35.1°C during the 23 heat wave days. In this analysis, day was the repeated measure (within-subject effect), hours per day >35.1°C was the dependent variable and treatment (insulation, aspect) was the between-subjects effects. Because the assumption of sphericity was violated (epsilon = 0.2), we used the Greenhouse–Geisser correction for determining the significance of *F*-tests.

Results

Throughout the study maximum daily air temperatures ranged from 22.5 to 40.6°C. the maximum temperatures inside insulated nest boxes were significantly lower than in the uninsulated boxes ($\chi^2 = 404.75$, d.f. = 1, $P < 0.001$; Fig. 3A). There were no significant effect of aspect on nest box temperatures ($\chi^2 = 1.58$, d.f. = 1, $P = 0.21$; Fig. 3B) and no significant interaction

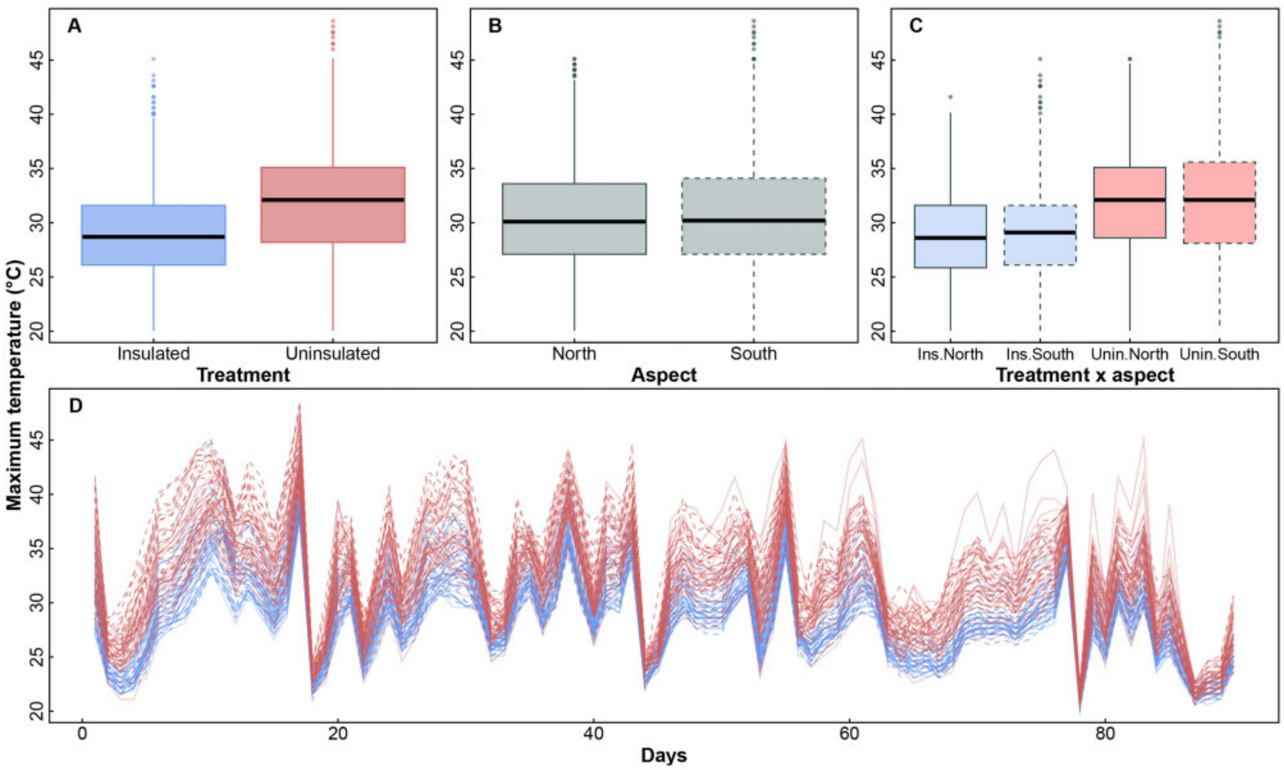

Figure 3: Maximum temperatures inside nest boxes as a function of insulation (**A**), aspect (**B**), insulation and aspect (**C**), and day of study (**D**). Day 1 refers to 20 December 2018. In (D), blue lines show data from insulated nest boxes and red lines show data from uninsulated boxes.

between insulation and aspect ($\chi^2 < 0.001$, d.f. = 1, $P = 0.99$; Fig. 3C). In addition, there was no significant interaction between insulation and day ($\chi^2 = 2.80$, d.f. = 1, $P = 0.09$; Fig. 3D). Thus, the significant effect of insulation in lowering nest box temperatures was consistent regardless of aspect or the day of measurement. Furthermore, the three-way interaction (insulation × aspect × day) was also not significant ($\chi^2 = 2.98$, d.f. = 1, $P = 0.08$), meaning that the effect of insulation on maximum temperatures did not depend on how aspect and day interact.

There were a significant effect of day on nest box temperatures ($\chi^2 = 327.28$, d.f. = 1, $P < 0.001$; Fig. 3D), which reflects daily variation in temperatures, and a significant interaction between aspect and day ($\chi^2 = 11.98$, d.f. = 1, $P < 0.001$; Fig. 3D), reflecting the changing position of the sun over time. On average, maximum temperatures inside nest boxes were positively correlated with maximum daily air temperatures; that is, maximum daily air temperature explained 90.4% and 85.2% of the variation in average maximum temperatures recorded inside insulated and uninsulated nest boxes, respectively (Fig. 4). Over the 90-day study, internal temperatures exceeded 35.1°C on more days in uninsulated (mean = 24.2 days, range 4–55 days) than in insulated nest boxes (mean = 6.8 days, range 1–33 days; $F_{1,88} = 83.0$, $P = 0.0001$). There were no effect of aspect ($F_{1,88} = 0.52$, $P = 0.47$) and no interaction between aspect and treatment ($F_{1,88} = 0.14$, $P = 0.71$). This pattern also occurred during heatwaves, when internal temperatures exceeded 35.1°C on more days in uninsulated boxes (mean = 13.4 days, range 3–22 days) than in uninsulated boxes (mean = 5.2 days, range 1–19 days; insulation $F_{1,88} = 50.328$, $P = 0.0001$; aspect $F_{1,88} = 2.38$, $P = 0.13$; aspect × insulation: $F_{1,88} = 0.89$, $P = 0.35$).

During heatwaves, the number of hours per day where temperatures exceeded 35.1°C inside nest boxes was higher in uninsulated boxes (mean = 2.5 h, range 0–9.5 h per day) than in insulated boxes (mean = 0.7 h, range 0–8 h per day). This difference was significant (repeated-measures ANOVA, between-subject effects, insulation: $F_{1,88} = 43.79$, $P < 0.001$; aspect $F_{1,88} = 0.21$, $P = 0.65$; insulation × aspect $F_{1,88} = 0.10$, $P = 0.76$). The repeated-measures ANOVA also showed a significant within-subject effect of day of study on the number of hours above 35.1°C ($F_{4.2,369}$

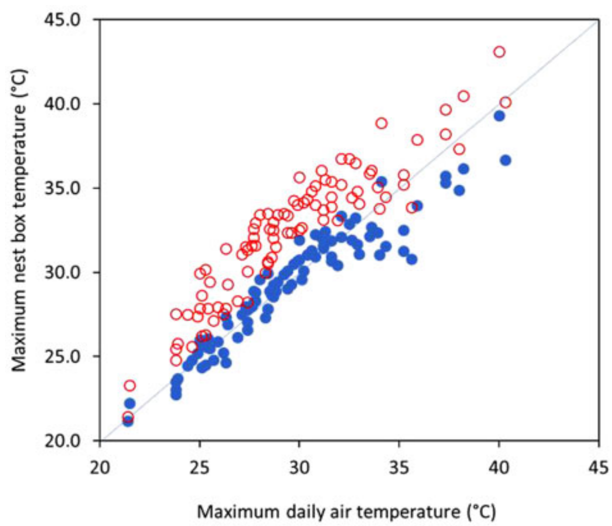

Figure 4: Relationship between maximum daily air temperature and average daily maximum temperatures recorded inside insulated nest boxes (solid blue symbols) and uninsulated nest boxes (open red symbols). Light blue line indicates 1:1 match between air temperature and nest box temperature.

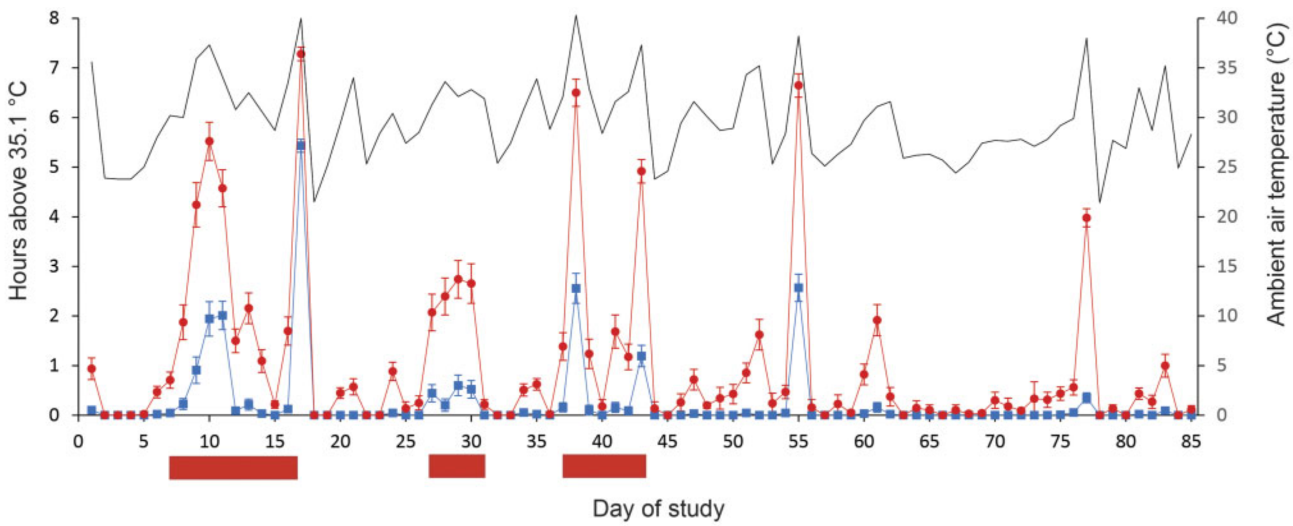

Figure 5: Number of hours during which nest box temperatures exceeded the upper thermal critical temperature (35.1°C) of gliders during the summer of 2018–2019. Day 1 refers to 20 December 2018. Figure shows temperatures within insulated boxes (blue symbols) and uninsulated boxes (red symbols), while the solid black line shows ambient temperatures recorded at Cooranbong weather station. Error bars denote standard errors. Solid red bars below the *x*-axis depict periods when heatwaves occurred. Temperature data courtesy of the Australian Bureau of Meteorology. http://www.bom.gov.au/climate/data/ (15 October 2019, date last accessed).

Table 1: Temperatures recorded inside insulated and uninsulated nest boxes with northerly and southerly aspects

Treatment	Minimum (°C)	Mean (°C)	Maximum (°C)	Average maximum (°C)
Insulated, northerly aspect	10.0	24.1	41.6	28.8
Insulated, southerly aspect	11.1	24.1	43.8	29.0
Standard, northerly aspect	10.1	24.9	45.1	31.9
Standard, southerly aspect	10.1	24.9	48.6	32.1
Air temperature	11.3	not applicable	40.3	29.3

Ambient temperature data are from Cooranbong Weather Station (0614212), courtesy of the Bureau of Meteorology. http://www.bom.gov.au/climate/data/ (15 October 2019, date last accessed)

$= 202.5$, $P < 0.001$). There was also a significant day × insulation effect ($F_{4.2,369} = 23.41$, $P < 0.001$), indicating that the effectiveness of insulation varied across days (Fig. 5). The other within-subjects interaction effects (day × aspect and day × insulation × aspect) were not significant.

Discussion

Heatwaves are increasing in intensity and duration across the globe (Perkins-Kirkpatrick and Lewis 2020) and pose a threat to human populations (Nitschke et al. 2011) and wildlife (Ratnayake et al. 2019). In Australia, loss of tree hollows has led to the widespread use of nest boxes as a conservation tool (Lindenmayer et al. 2016, 2017; Macak 2020). However, high temperatures within nest boxes during summer heatwaves could render them unsuitable for use by target wildlife (Griffiths et al. 2017; Rowland et al. 2017). To address this problem, we affixed roofing insulation to glider nest boxes and recorded their internal temperatures during the 2018–2019 summer that was characterized by prolonged heatwaves (Bureau of Meteorology 2019a). Over the 90-day study, maximum temperatures were on average 3.1°C lower inside insulated nesting boxes than in uninsulated nest boxes (Table 1, Fig. 3). In both insulated and uninsulated nest boxes, maximum temperatures were positively correlated with maximum air temperatures (Fig. 4). However, when maximum daily air temperatures exceeded 34°C, the average maximum temperatures recorded inside insulated boxes were lower than maximum daily air temperatures (Fig. 4). That is, the buffering effects of insulation were greatest during hotter conditions. Interestingly, we found that aspect did not influence temperatures inside nest boxes (Fig. 3), though we only compared north-facing and south-facing boxes. Other studies have reported that orientation can affect nest box temperatures (Ardia et al. 2006; Butler et al. 2009). In two North American studies, orientation affected temperatures during spring, when boxes with south or easterly orientations were warmer than those with north or west facing orientations. In summer, orientation did not affect temperatures. This latter result accords with the results of this study and previous studies that have found no effect of aspect on nest box temperatures during summer (Goldingay 2015; Rowland et al. 2017). During summer, the sun's path is directly overhead, so canopy cover above nest boxes can have a stronger effect on temperature than box orientation (Griffiths et al. 2017).

Although the addition of insulation reduced nest box internal temperatures, the thermal suitability of boxes will depend on internal box temperatures relative to the animal's TNZ (Isaac et al. 2008). During the heatwaves recorded in this study, temperatures inside uninsulated boxes exceeded the TNZ of gliders for an average of 2.5 h per day versus 0.7 h per day in insulated boxes. Thus, gliders could probably use some insulated nest boxes but not uninsulated nest boxes, during heatwaves. When ambient temperatures exceed upper critical temperatures, gliders use behaviours such as licking their paws and waving them in the air to increase evaporative cooling (Holloway and Geiser 2001b). While laboratory studies have shown that gliders can function in ambient temperatures of up to 39°C (Holloway and Geiser 2001a), prolonged exposure to temperatures above the TNZ would likely lead to physiological impairment from water loss, particularly as free standing water is often absent during heatwaves (Turner 2020). For example, a study on the physiological responses of the common ringtail possum *Pseudocheirus peregrinus* to a simulated heatwave suggested that exposure to 39°C for 17 h would lead to physiological impairment from water loss (Turner 2020). Given that one of the heatwaves reported here stretched over 11 days (Fig. 5), we think that it is highly unlikely that gliders could use uninsulated nest boxes given that the risks of hyperthermia would be high (Turner 2020).

How do the results of our study compare to previous studies that have used reflective paints or insulation to reduce nest box temperatures? In one study, researchers compared temperatures of nest boxes that were unpainted, painted white, or were insulated with aluminium foil batts or 3-cm-thick white polystyrene. In that study, temperatures inside polystyrene insulated boxes were 0.9–1.7°C lower than those of uninsulated boxes (Larson et al. 2018). By contrast, the roofing insulation that we used in our study reduced maximum temperatures by 3.1°C, much lower than was achieved with polystyrene. This could reflect methodological differences between the two studies, differences in the effectiveness of the insulation materials used or the nest box design or differences in canopy cover or solar radiation loads, which can affect internal temperatures (Griffiths et al. 2017). In another study, internal temperatures of boxes painted with white reflective paints were 4.3°C lower than those inside green painted boxes. At the first sight, white reflective paint appears to be better for cooling nest boxes than roofing insulation. However, closer inspection of the data showed that maximum temperatures inside white painted boxes were virtually identical to maximum air temperatures (Griffiths et al. 2017). By contrast, in our study, when maximum air temperatures exceeded 34°C, maximum temperatures inside roofing insulated boxes were lower than air temperatures (Fig. 4). That is, our results suggest that reflective foil batts may provide better cooling during heatwaves than reflective paints. Future studies, measuring temperatures of nest boxes with different modifications, and mounted side by side in the field, would help to clarify the best way of achieving an insulated and thermally suitable nest box for wildlife.

Our study showed that stapling foil batt insulation to the exterior of nest boxes can result in lower internal temperatures. However, this is not a long-term practical solution, for two reasons. First, the insulation may not last long in the field, as animals might chew it off. Second, applying foil insulation to the exterior of nest boxes will make them more conspicuous (Griffiths et al. 2017) and, thus, potentially more prone to predation or vandalism (Henze 1977; Stebbings and Walsh 1991). White reflective surfaces are much more visible in the landscape and could make it easier for predators to find nest boxes, potentially increasing predation rates. In Australia, little is known about predation on fauna using nest boxes, but a recent camera trap study found that feral cats (*Felis catus*) were ambushing Leadbeater's possums (*Gymnobelideus leadbeateri*) from atop of the nest boxes (McComb et al. 2019). To minimize the risk of predation, predator deterrents or exclusion devices could be placed on nest boxes (e.g. metal spikes to prevent cats sitting on boxes) or trees (Bailey and Bonter 2017). To counter the above problems, it would be worth exploring whether placing insulation inside nest boxes (e.g. sandwiched between two layers of wood) can buffer internal temperatures from thermal extremes. If so, then one could paint insulated boxes to match backgrounds, substantially reducing the problems associated with high visibility. Alternatively, 3-D printing could be used to produce more thermally suitable boxes. Recently, researchers from Charles Sturt University produced 3-D-printed plastic boxes with double walls that incorporated an air space between the walls, with timber inserts fitted inside the box. In a laboratory trial, internal temperatures within a box of this design were 7.3°C lower than ambient when air temperatures were 31°C in a test room (Callan 2020). Clearly, this sort of design warrants further field testing.

Conclusion

Nest boxes are widely used to conserve hollow-dependent fauna in urban bushland, but current designs may not provide thermal refuges for wildlife during summer heatwaves. We showed that the addition of insulation to nest boxes partially solved this problem, as maximum temperatures were 3.1°C lower in insulated boxes than in uninsulated boxes. Future studies should aim to develop nest boxes that are more thermally suitable for a diversity of hollow-dependent wildlife, while community-led revegetation programmes could help to ensure that there is sufficient recruitment of natural hollows in urban bushland in the future.

Acknowledgements

We thank Lake Macquarie City Council for granting access to public bushland and Robbie Economos for providing logistical support and reviewing a draft of the manuscript. We thank all of the volunteers who assisted us with fieldwork, especially Jess McGregor. We thank two anonymous reviewers for providing critical comments and suggestions that helped to improve the manuscript and Angelica Varhammar for assistance in producing Fig. 1. This research was carried out under a NSW National Parks and Wildlife Service scientific licence (SL101905) and the approval of the UTS Animal Care and Ethics Committee (ETH17-1361).

Data availability

The dataset used for all analyses in this manuscript is available online from the data repository Figshare, doi:10.6084/m9.figshare.15071121.v1

Funding

The research was funded by a Lake Macquarie City Council Environmental Research Grant (2016-2017/02).

Conflict of interest statement. None declared.

References

Ardia, D. R., Pérez, J. H., and Clotfelter, E. D. (2006) 'Nest Box Orientation Affects Internal Temperature and Nest Site Selection by Tree Swallows', *Journal of Field Ornithology*, **77**: 339–44.

Bailey, R. L., and Bonter, D. N. (2017) 'Predator Guards on Nest Boxes Improve Nesting Success of Birds', *Wildlife Society Bulletin*, **41**: 434–41.

Bureau of Meteorology (2019a) *Special Climate Statement 68—Widespread Heatwaves during December 2018 and January 2019*. Melbourne, Australia: Bureau of Meteorology.

—— (2019b) *Station 061214 Cooranbong. Climate Data*. http://www.bom.gov.au/climate/data/ (15 October 2019, date last accessed).

Butler, M. W., Whitman, B. A., and Dufty, A. M. (2009) 'Nest Box Temperature and Hatching Success of American Kestrels Varies with Nest Box Orientation', *The Wilson Journal of Ornithology*, **121**: 778–82.

Callan, M. N. (2020). 'Thinking Outside of the Box: Investigating Novel Alternatives to Timber Habitat Boxes for Arboreal Vertebrate Fauna', Honours thesis, Charles Sturt University.

Dawson, T. (1969) 'Temperature Regulation and Evaporative Water Loss in the Brush-Tailed Possum *Trichosurus vulpecula*', *Comparative Biochemistry and Physiology*, **28**: 401–7.

Flaquer, C. et al. (2014) 'Could Overheating Turn Bat Boxes into Death Traps?', *Barbastella*, **7**: 46–53.

Fleming, M. R. (1980) 'Thermoregulation and Torpor in the Sugar Glider, *Petaurus breviceps* (Marsupialia, Petauridae)', *Australian Journal of Zoology*, **28**: 521–34.

—— (1985) 'The Thermal Physiology of the Feathertail Glider, *Acrobates pygmaeus* (Marsupilia, Burramyidae)', *Australian Journal of Zoology*, **33**: 667–81.

Gibbons, P., and Lindenmayer, D. (2002) *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing.

Goldingay, R. L. (2015) 'Temperature Variation in Nest Boxes in Eastern Australia', *Australian Mammalogy*, **37**: 225–33.

——, Grimson, M. J., and Smith, G. C. (2007) 'Do Feathertail Gliders Show a Preference for Nest Box Design?', *Wildlife Research*, **34**: 484–90.

—— et al. (2015) 'Specific Nest Box Designs Can Improve Habitat Restoration for Cavity-Dependent Arboreal Mammals', *Restoration Ecology*, **23**: 482–90.

——, and Thomas, K. J. (2021) 'Tolerance to High Temperature by Arboreal Mammals Using Nest Boxes in Southern Australia', *Journal of Thermal Biology*, **98**: 102899.

Gordon, G., Brown, A. S., and Pulsford, T. (1988) 'A Koala (*Phascolarctos cinereus* Goldfuss) Population Crash during Drought and Heatwave Conditions in South-Western Queensland', *Austral Ecology*, **13**: 451–61.

Griffiths, S. R. (2021) 'Overheating Turns a Bat Box into a Death Trap', *Pacific Conservation Biology*,

—— et al. (2017) 'Surface Reflectance Drives Nest Box Temperature Profiles and Thermal Suitability for Target Wildlife', *PLoS One*, **12**: e0176951.

—— et al. (2018) 'Chainsaw-Carved Cavities Better Mimic the Thermal Properties of Natural Tree Hollows than Nest Boxes and Log Hollows', *Forests*, **9**: 235.

Harper, M. J., McCarthy, M. A., and van der Ree, R. (2005a) 'The Abundance of Hollow-Bearing Trees in Urban Dry Sclerophyll Forest and the Effect of Wind on Hollow Development', *Biological Conservation*, **122**: 181–92.

——, ——, and —— (2005b) 'The Use of Nest Boxes in Urban Natural Vegetation Remnants by Vertebrate Fauna', *Wildlife Research*, **32**: 509–16.

Henze, O. (1977) 'Vogelnistkästen in Augenhöhe?', *Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz*, **50**: 106.

Holloway, J. C., and Geiser, F. (2001a) 'Effects of Helium/Oxygen and Temperature on Aerobic Metabolism in the Marsupial Sugar Glider, *Petaurus breviceps*', *Physiological and Biochemical Zoology*, **74**: 219–225.

——, and —— (2001b) 'Seasonal Changes in the Thermoenergetics of the Marsupial Sugar Glider, *Petaurus breviceps*', *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, **171**: 643–650.

Isaac, B. et al. (2014) 'Urban to Forest Gradients: Suitability for Hollow Bearing Trees and Implications for Obligate Hollow Nesters', *Austral Ecology*, **39**: 963–972.

Isaac, J. L., Parsons, M., and Goodman, B. A. (2008) 'How Hot Do Nest Boxes Get in the Tropics? A Study of Nest Boxes for the Endangered Mahogany Glider', *Wildlife Research*, **35**: 441–445.

Larson, E. R. et al. (2018) 'Nest Box Design for a Changing Climate: The Value of Improved Insulation', *Ecological Management & Restoration*, **19**: 39–48.

Lindenmayer, D. et al. (2016) 'Do Nest Boxes in Restored Woodlands Promote the Conservation of Hollow-Dependent Fauna?', *Restoration Ecology*, **24**: 244–251.

Lindenmayer, D. B. et al. (2017) 'The Anatomy of a Failed Offset', *Biological Conservation*, **210**: 286–292.

Lovegrove, B., Heldmaier, G., and Ruf, T. (1991) 'Perspectives of Endothermy Revisited: The Endothermic Temperature Range', *Journal of Thermal Biology*, **16**: 185–197.

Macak, P. V. (2020) 'Nest Boxes for Wildlife in Victoria: An Overview of Nest Box Distribution and Use', *The Victorian Naturalist*, **137**: 4–14.

Maziarz, M., Broughton, R. K., and Wesołowski, T. (2017) 'Microclimate in Tree Cavities and Nest-Boxes: Implications for Hole-Nesting Birds', *Forest Ecology and Management*, **389**: 306–313.

Mangiafico, S.S. (2016) *Summary and Analysis of Extension Program Evaluation in R, version 1.18.8*. rcompanion.org/handbook/.

McComb, L. B. et al. (2019) 'Feral Cat Predation on Leadbeater's Possum (*Gymnobelideus leadbeateri*) and Observations of Arboreal Hunting at Nest Boxes', *Australian Mammalogy*, **41**: 262–265.

Nitschke, M. et al. (2011) 'Impact of Two Recent Extreme Heat Episodes on Morbidity and Mortality in Adelaide, South Australia: A Case-Series Analysis', *Environmental Health*, **10**: 42. 10.1186/1476-069X-10-42.

O'Shea, T. J. et al. (2016) 'Multiple Mortality Events in Bats: A Global Review', *Mammal Review*, **46**: 175–190.

Perkins-Kirkpatrick, S. E., and Lewis, S. C. (2020) 'Increasing Trends in Regional Heatwaves', *Nature Communications*, **11**: 3357.

Perkins, S. E., and Alexander, L. V. (2013) 'On the Measurement of Heat Waves', *Journal of Climate*, **26**: 4500–4517.

Pinheiro, J., Bates D., and R-core (2019) *Nlme: Linear and Nonlinear Mixed Effects Models*. https://CRAN.R-project.org/package=nlme

Ratnayake, H. U. et al. (2019) 'Forecasting Wildlife Die-Offs from Extreme Heat Events', *Animal Conservation*, **22**: 386–395.

Rizvi, S. H., Alam, K., and Iqbal, M. J. (2019) 'Spatio-Temporal Variations in Urban Heat Island and Its Interaction with Heat Wave', *Journal of Atmospheric and Solar-Terrestrial Physics*, **185**: 50–57.

Robinson, K. W., and Morrison, P. R. (1957) 'The Reaction to Hot Atmospheres of Various Species of Australian Marsupial and Placental Mammals', *Journal of Cellular and Comparative Physiology*, **49**: 455–478.

Rowland, J. A., Briscoe, N. J., and Handasyde, K. A. (2017) 'Comparing the Thermal Suitability of Nest-Boxes and Tree-Hollows for the Conservation-Management of Arboreal Marsupials', *Biological Conservation*, **209**: 341–348.

Rueegger, N. et al. (2020) 'Testing Multichambered Bat Box Designs in a Habitat-Offset Area in Eastern Australia: Influence of Material, Colour, Size and Box Host', *Pacific Conservation Biology*, **26**: 13–21.

Smith, A. P., and Murray, M. (2003) 'Habitat Requirements of the Squirrel Glider (*Petaurus norfolcensis*) and Associated Possums and Gliders on the New South Wales Central Coast', *Wildlife Research*, **30**: 291–301.

Stebbings, R., and Walsh, S. (1991) *Bat-Boxes: A Guide to the History, Function, Construction and Use in the Conservation of Bats*. London: Bat Conservation Trust.

Tews, J. et al. (2004) 'Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of Keystone Structures', *Journal of Biogeography*, **31**: 79–92.

Turner, J. M. (2020) 'Facultative Hyperthermia during a Heatwave Delays Injurious Dehydration of an Arboreal Marsupial', *Journal of Experimental Biology*, **223**: jeb219378.

Williams, S. et al. (2018) 'Regional Morbidity and Mortality during Heatwaves in South Australia', *International Journal of Biometeorology*, **62**: 1911–1926.