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4  
5 **Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-**  
6 **management of arboreal marsupials**

7  
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28

## 29 **Abstract**

30 Hundreds of species rely on tree-hollows for shelter and breeding, however land-clearing has  
31 reduced their availability worldwide. While nest-boxes are deployed extensively in hollow-  
32 deficient habitats, their thermal value for arboreal marsupials compared to tree-hollows is  
33 unclear, particularly in temperate environments. We analysed thermal regimes in nest-box and  
34 tree-hollow pairs during summer and winter environmental conditions. Using a biophysical  
35 model, we quantified the relative suitability of den-sites for several marsupial species, estimating  
36 the impact of microclimates (and ambient conditions) on predicted heat-production and heat-  
37 loss. Nest-box temperatures were strongly influenced by ambient temperatures and solar  
38 radiation, whereas tree-hollows buffered external temperature fluctuations. On average, nest-  
39 boxes reached maximum temperatures 8°C higher than tree-hollows in summer, and 3°C higher  
40 in winter, with maximum temperatures of 52°C recorded in nest-boxes, compared to 38°C in  
41 tree-hollows. During summer, estimated heat-loss required by marsupials was 1.5-2.4 times  
42 higher in nest-boxes than tree-hollows. Conversely, predicted winter heat-production  
43 requirements were slightly lower in nest-boxes (0.95-0.97 of hollow requirements). Our study  
44 emphasises the importance of retaining tree-hollows as thermal refuges for hollow-dependent  
45 marsupials in temperate zones to reduce thermoregulatory costs during heat-events. Current nest-  
46 box designs are likely of limited value during high temperatures and solar radiation loads if they  
47 consistently reach temperatures exceeding species upper critical temperatures, however may  
48 provide suitable microclimates during winter. With increasing and more prolonged heat-events  
49 predicted under climate change, future conservation-management programs should focus on  
50 improving nest-box thermal properties to enhance suitability for wildlife.

51

## 52 **1. Introduction**

53 Tree-hollows form essential habitat for hundreds of species worldwide, particularly birds and  
54 mammals (Scott et al. 1980; Goldingay 2009, 2011). For many vertebrates, tree-hollows are

55 critical for shelter, breeding and predator protection (Gibbons & Lindenmayer 2002;  
56 Wesolowski 2002), however, widespread land-clearing has dramatically reduced their  
57 availability (Eyre et al. 2010). Hollows large enough for arboreal mammals can take at least 100  
58 years to develop (Wormington & Lamb 1999; Gibbons et al. 2000). Ongoing habitat loss  
59 combined with time-lags in hollow-development, will likely maintain the deficit of tree-hollows  
60 (Gibbons et al. 2008; Vesk et al. 2008). This is of major concern for hollow-dependent species,  
61 as den availability and quality can impact survival, growth and reproduction (Dawson et al.  
62 2005; Catry et al. 2011).

63  
64 To compensate for tree-hollow loss, nest-boxes have been deployed by wildlife managers,  
65 individuals and community groups to support a range of hollow-dependent species (Beyer &  
66 Goldingay 2006; Goldingay & Stevens 2009; British Trust for Ornithology). Nest-boxes can be  
67 highly valuable for conservation (Durant et al. 2009; Goldingay et al. 2015). However, low  
68 occupancy (Lindenmayer et al. 2009) and suboptimal cavity temperatures (Catry et al. 2011) can  
69 limit their value. While there has been considerable research into how nest-box design and  
70 placement influence occupancy, surprisingly few data are available on thermal suitability of  
71 nest-boxes, despite thermal properties likely being a key direct driver of their value for wildlife  
72 (Sedgeley 2001).

73  
74 For endotherms, inappropriate den temperatures almost certainly have acute and long-term  
75 impacts, influencing survival during extreme conditions, and increasing costs associated with  
76 thermoregulation. Endotherms have an optimal range of environmental temperatures (thermo-  
77 neutral zone: TNZ), within which thermoregulatory costs are minimal (Lovegrove et al. 1991).  
78 Below their TNZ, metabolic heat-production (thus energy costs) increase, while above the TNZ,  
79 water costs rise because evaporative heat-loss is used to avoid overheating (Dawson 1969).

80 Hollow-dependent species can minimize thermoregulatory costs by selecting dens providing  
81 temperatures closest to their TNZ.  
82

83 Den microclimates influence breeding success and survival. Due to high thermoregulatory costs,  
84 animals experiencing unfavorable microclimates are likely to invest fewer resources in growth  
85 and reproduction (Garcia-Navas et al. 2008). Tree swallow (*Tachycineta bicolor*) chicks in  
86 cooler nests have lower survival, slower growth rates, and smaller body size than those in  
87 warmer nests (Dawson et al. 2005). However, higher temperatures are not always beneficial:  
88 extreme den temperatures during a heat-wave led to 22% juvenile mortality in a lesser kestrel  
89 (*Falco naumanni*) population, with heat-related deaths occurring over two days when ambient  
90 temperatures exceeded 39°C (Catry et al. 2011). Some evidence suggests that arboreal  
91 marsupials may avoid dens experiencing temperature extremes (Isaac et al. 2008a; Goldingay  
92 2015), which is almost certainly related to factors discussed above.  
93

94 Despite the potentially high fitness consequences of denning in thermally sub-optimal  
95 microclimates, the thermal suitability of nest-boxes across seasons has not been comprehensively  
96 studied across the range of environments where they are deployed. The few previous studies  
97 suggest that thermal properties of empty nest-boxes and tree-hollows differ significantly, with  
98 tree-hollows buffering extremes in daily temperature fluctuations more than nest-boxes  
99 (McComb & Noble 1981; Isaac et al. 2008b). However, Isaac et al. (2008b) only compared nest-  
100 box microclimates to tree-hollows during summer in a tropical climate, and McComb and Noble  
101 (1981) only compared microclimates in a few pairs of nest-boxes and tree-hollows across  
102 seasons in a humid subtropical climate. Minimal research has examined the thermal suitability of  
103 nest-boxes in temperate Australia, a region that experiences a wide temperature range, has  
104 undergone extensive habitat loss, and has had many nest-boxes installed (Lindenmayer et al.  
105 2003; Harper et al. 2005).

106  
107 Artificial and natural dens differ in structure, which is likely to drive differences in their thermal  
108 properties. Characteristics that influence nest-box temperatures include their insulative properties  
109 (relating to wall thickness and construction materials), orientation, and level of solar exposure  
110 (García-Navas et al. 2008; Charter et al. 2010; Goldingay 2015). Temperatures in tree-hollows  
111 are also influenced by their structure (including wall thickness, cavity size and entrance area), in  
112 addition to tree health (Paclik & Weidinger 2007; Coombs et al. 2010). Such differences in tree-  
113 hollow and nest-box properties may create disparities in their suitability for wildlife under  
114 different environmental conditions, between seasons or times of day (Vel'ky et al. 2010). To  
115 maximise the success of nest-boxes for conservation it is essential to understand the drivers of  
116 variation in cavity temperatures.

117  
118 While nest-box temperatures are likely to differ from those in tree-hollows, it is important to  
119 determine whether these translate to biologically meaningful differences in fitness for species  
120 using them. Few studies have examined the fitness consequences of denning in nest-boxes, and  
121 these focused predominantly on reproductive success in birds (e.g. Dawson et al. 2005; Charter  
122 et al. 2010), with little information about arboreal hollow-dependent mammals. Overall, studies  
123 of den microclimates rarely relate differences in temperature to eco-physiological consequences  
124 for species (although see Willis & Brigham 2005, 2007), important information for predicting  
125 and testing drivers of fitness.

126  
127 We investigated how daily fluctuations in thermal microclimates differed between nest-boxes  
128 and tree-hollows across seasons in a temperate environment. We also examined factors  
129 influencing daytime den temperatures. We determined the relative thermal suitability of nest-  
130 boxes for four hollow-dependent marsupial species across seasons by estimating the energy and  
131 water costs of denning in nest-boxes, tree-hollows, or outside in a sheltered position, using a

132 biophysical model that predicts how morphology, physiology and behaviour interact with the  
133 environment to determine animals' metabolic rate and rate of evaporative heat-loss (Porter &  
134 Kearney 2009). Our research will inform management decisions regarding nest-box design and  
135 installation, with a particular focus on understanding daily fluctuations in cavity temperature  
136 during extreme conditions.

137

## 138 **2. Materials and methods**

### 139 2.1 STUDY AREA AND SPECIES

140 We conducted this research in the Strathbogie Ranges, (36°79' S, 145°80' E) Victoria, Australia  
141 (Figure S1). The area has an average altitude of c. 570 m above sea level (a.s.l) and high annual  
142 rainfall (c. 1000 mm). It experiences considerable thermal variation, with temperatures  
143 exceeding 40°C during summer and falling below 0°C during winter. Temperatures range from a  
144 mean monthly maximum of 27.4°C in February to a minimum of 1.7°C in July (Bureau of  
145 Meteorology).

146

147 This region has experienced substantial habitat loss and fragmentation (Martin & Handasyde  
148 2007), but retained some eucalypt-dominated open sclerophyll forest, which provides habitat for  
149 arboreal marsupials that rest in tree-hollows during the day. These include sugar gliders  
150 (*Petaurus breviceps*), common ringtail possums (*Pseudocheirus peregrinus*, henceforth common  
151 ringtail), greater gliders (*Petauroides volans*), common brushtail possums (*Trichosurus*  
152 *vulpecula*, common brushtail), and mountain brushtail possums (*Trichosurus cunninghami*,  
153 mountain brushtail) (Downes et al. 1997). Greater gliders and brushtail possums use a suite of  
154 tree-hollows solitarily (Lindenmayer et al. 2004; Martin 2005; Harper 2006), while common  
155 ringtails typically rest in small groups in dreys or tree-hollows (Pahl 1987). Nest-box use has  
156 been recorded for common ringtails, both brushtail *spp.* (Lindenmayer et al. 2003; Harper et al.  
157 2005) and sugar gliders (Menkhorst 1984; Goldingay et al. 2015).

158

## 159 2.2 COMPARISON OF DEN THERMAL MICROCLIMATES

160 We compared daytime thermal microclimates of nest-boxes, tree-hollows, and ambient  
161 conditions during two summer periods (27/11/2014 to 3/01/2015 and 2-27/02/2015 between  
162 06:00-20:30h) and winter periods (29/06/2014 to 2/08/2014 and 7/06/2015 to 5/07/2015 between  
163 07:30-17:30h). Sampling periods within each season had similar environmental conditions  
164 (Figure S2).

165

166 We selected 41 tree-hollows spread over 150 km<sup>2</sup> (Figure S1), ranging from 481-674 m a.s.l. We  
167 considered tree-hollows suitable if the entrance and cavity were large enough to accommodate  
168 common ringtails (Beyer & Goldingay 2006), less than 5.5 m high (for safety), and in live trees.  
169 Dead trees were excluded as their thermal properties may differ (Wiebe 2001; Paalik &  
170 Weidinger 2007). We used hollows in *Eucalyptus* trees with entrances opening on the trunk  
171 (n=20) or tree-base (n=21) to reflect the natural range used by wildlife (K. Handasyde  
172 unpublished, based on radio-tracking data for brushtail *spp.*). We measured the entrance  
173 orientation (measured as °, converted into cardinal direction: north, n=13; east, n=13; south, n=7;  
174 west, n=8), entrance height above ground (to the nearest 5 mm), and DBH (mean ± sd: 1.3 ± 0.5  
175 m). Hollows varied in structure: entrance area range 38.48-30210 cm<sup>2</sup>; cavity depth range 18-  
176 140 cm; and cavity volume range 0.002-5.655 m<sup>3</sup>.

177

178 We installed 40 plywood nest-boxes (300x370x475 mm, 17 mm thick) between February and  
179 June 2014. One nest-box was relocated after the first two sampling periods (it was too dangerous  
180 to access) and paired with a different base-hollow for the remaining periods. Nest-boxes were  
181 painted dark-green, consistent with common practice. Each nest-box was mounted on a tree  
182 within 17m (mean ± sd, 8.1 ± 2.7 m) of a tree-hollow, with the entrance at the same height and  
183 orientation, and similar canopy cover (mean difference ± sd, 5.8 ± 4.1%;  $t_{39}=1.36$ ,  $P=0.18$ ). We



184 calculated canopy openness above each den by analyzing hemispherical photos, taken with a  
185 fisheye lens (Sigma 8mm 6.3, Japan) attached to a full frame camera (Canon 5D MkII, Japan),  
186 using Gap Light Analyzer (Version 2.0) (Beckschäfer et al. 2013). We initially covered nest-box  
187 entrances with wire-mesh to exclude wildlife (02/2014 to 3/01/2015), then uncovered entrances  
188 to allow access (from 4/01/2015). After nest-box entrances were uncovered, we checked each  
189 den (nest-boxes and tree-hollows) for occupants using a camera (Nikon Coolpix P310, Japan) on  
190 a pole (summer: 15 days; winter: 20 days). Animals were not further disturbed after determining  
191 occupation status.

192  
193 Using thermal data loggers (Thermochron iButton; Alfa-Tek, Bayswater, Australia) mounted in  
194 plastic mesh or holders, we recorded cavity temperatures ( $^{\circ}\text{C}$ ;  $\pm 0.5$ ) simultaneously in each nest-  
195 box and tree-hollow, as well as ambient temperature ( $T_a$ ), at 30-minute intervals during all  
196 sampling periods. iButtons were positioned on the back wall of each nest-box suspended by  
197 string 2 cm below the entrance (25.5 cm above cavity base and 22 cm from lid), with the  
198 temperature recording side facing into the cavity. This central location aimed to minimise the  
199 impact of sun and wind exposure and reduce the chance of animals sitting on the logger, while  
200 sampling the temperature adjacent to the upper half of the body of larger species (brushtail  
201 possums); logger position may have a minor effect on the recorded temperatures due to  
202 temperature gradients in nest-boxes (Goldingay 2015). We secured iButtons in each tree-hollow  
203 away from the entrance and near where a marsupial might rest; the exact position varied with  
204 tree-hollow structure. To record  $T_a$ , iButtons were placed in permanent shade behind each nest-  
205 box, facing away from adjacent surfaces.

206

### 207 2.3 STATISTICAL ANALYSIS

208 Occupied dens (3/70 den checks), and those deemed likely to be occupied during the non-  
209 monitoring period, indicated by atypical jumps in temperature (over  $10^{\circ}\text{C}$ ), were examined

210 separately. We also excluded records when iButtons were ejected from dens or faulty (seven  
211 during 29/06/2104 to 2/08/2014; one during 27/11/2014 to 3/01/2015).

212

213 Daily maximum ( $T_{\text{denMAX}}$ ), mean ( $T_{\text{denMEAN}}$ ) and minimum ( $T_{\text{denMIN}}$ ) cavity temperatures, and  
214 maximum hourly difference between den temperature and  $T_a$  during daylight hours were  
215 calculated for each nest-box ( $T_{\text{boxDIFF}}$ ) and tree-hollow ( $T_{\text{holDIFF}}$ ). To examine the effect of den-  
216 type, weather and den characteristics on cavity temperatures across seasons, we fitted linear  
217 mixed-effects models with the package ‘nlme’ (Pinheiro et al. 2015) using the software ‘R’ (R  
218 Core Team 2014). We included den-type within site as a random effect to account for repeated  
219 measures in each den and spatial correlations, and fit a corARMA correlation structure,  
220 assuming correlation across days for each den. For models with only categorical predictors, we  
221 fit a varIdent variance structure (Zuur et al. 2009). For models with continuous predictors, a  
222 variance structure was fitted based on Akaike’s Information Criteria (AIC), as multiple  
223 structures were appropriate (Zuur et al. 2009). Where residuals plots indicated deviations from  
224 homoscedasticity or normality, variables were log or square-root transformed.

225

226 We constructed models for each response variable to determine the effect of den-type on cavity  
227 temperatures across seasons. We tested the effect of  $T_a$  and solar exposure (proportion canopy  
228 openness x total daily solar radiation over 24 hours, kWh m<sup>2</sup>) on den temperatures ( $T_{\text{denMAX}}$  and  
229  $T_{\text{denMEAN}}$ ) in summer and winter. Because minimum temperatures predominantly occurred very  
230 early in the morning, and were thus more likely influenced by exposure to cold sky rather than  
231 solar radiation, we included canopy openness rather than solar exposure as a predictor for  
232  $T_{\text{denMIN}}$ . We also analysed the relationship between den and site characteristics on both  $T_{\text{boxDIFF}}$   
233 and  $T_{\text{holDIFF}}$  during summer and winter. Models included site openness (%), cardinal direction  
234 (aspect), den height, tree DBH, and hollow type (for  $T_{\text{holDIFF}}$  only).

235

236 Continuous predictor variables were standardised (mean subtracted, then divided by the standard  
237 deviation) to allow each model to be fitted without the scale of predictors altering their influence  
238 on the results (Quinn & Keough 2002). We selected model predictors and interactions between  
239 predictors using AIC (Burnham & Anderson 2002), where the best-fitting model for each  
240 analysis had the lowest AICc. Full models only included interactions that were deemed  
241 biologically relevant; for example, interactions between DBH and aspect were excluded, as this  
242 was not considered meaningful.

243

#### 244 2.4 MODELING ECO-PHYSIOLOGICAL CONSEQUENCES OF THERMAL 245 MICROCLIMATES

246 We used the model of Porter & Kearney (2009) to calculate the metabolic rate that would allow  
247 an endotherm to maintain core temperature, given the environmental conditions (denning during  
248 the day in nest-boxes, tree-hollows, and outside under ambient conditions) and its traits for four  
249 marsupial species (see below). We assumed heat-loss was required when the predicted metabolic  
250 rate to maintain homeothermy was below the basal metabolic rate (i.e. we calculated how much  
251 additional heat must be lost to allow the animal to maintain its basal metabolic rate and core  
252 temperature). As panting is a key mechanism of heat-loss for marsupials (Robinson & Morrison  
253 1957), respiratory heat-loss was only included in heat-loss estimates when animals were not  
254 actively offloading heat.

255

256 To parameterize the model, we estimated morphological characteristics of an average adult  
257 female common brushtail, mountain brushtail, greater glider and common ringtail, and the  
258 environmental conditions in each denning location (Table S1). Using museum specimens ( $n=9$ -  
259 21 for each species, Museum Victoria collection), we measured body length (mm) to estimate  
260 values for posture (ratio of body length:width) when denning, and ventral and dorsal fur depth  
261 using vernier calipers (to the nearest mm). We simulated behavioural responses to temperature

262 by gradually altering posture and fur depth to minimize costs; posture changed from curled in a  
263 near-perfect sphere (1.001) with fur as the average of dorsal fur depth for cold conditions, to  
264 fully uncurled with the average of dorsal and ventral fur depth for high temperatures. For  
265 animals resting outside, we assumed a sheltered position, with the modeled wind-speed 50% of  
266 wind-speed recorded in the open. We calculated seasonal daytime heat-production and heat-loss  
267 costs (MJ) for each den and outside under ambient conditions for each species by summing  
268 estimated daily values across summer and winter.

269

### 270 3. Results

#### 271 3.1 COMPARISON OF TEMPERATURES IN NEST-BOXES AND TREE-HOLLOWS

272 For dens unoccupied by an animal,  $T_{\text{denMAX}}$  in nest-boxes was 8.0°C higher on average than tree-  
273 hollows in summer, 3.0°C higher in winter, and showed greater variation (Figure 1; Table S2).

274 The highest nest-box temperature recorded was 52.1°C in summer and 41.1°C in winter, whereas  
275 tree-hollows reached 38.1°C in summer and 20.7°C in winter.  $T_{\text{denMEAN}}$  was also higher in nest-  
276 boxes than tree-hollows: 3.6°C higher in summer and 1.2°C in winter (Figure 1; Table S2).

277 Conversely, across both seasons, daytime  $T_{\text{denMIN}}$  remained higher in tree-hollows (lowest -  
278 3.5°C) than nest-boxes (lowest -5.4°C) (Figure 1; Table S2).

279

280 The limited data we were able to collect suggested that occupied dens were warmer than  
281 unoccupied dens. During summer, one tree-hollow containing cockatoo chicks for  
282 approximately 29 days, was substantially warmer ( $T_{\text{denMEAN}}$  27.2°C) when occupied than when  
283 unoccupied (18.1°C) under similar ambient conditions. A common brushtail occupied one tree-  
284 hollow on two separate days. Under similar ambient conditions,  $T_{\text{denMEAN}}$  on an occupied day  
285 (22.5°C) was considerably warmer than on the previous and following days (18.5°C), when the  
286 den was unoccupied. A sugar glider occupying a different tree-hollow had a negligible effect on  
287 den temperature. No nest-box use was recorded during the study.

288

## 289 3.2 EFFECT OF WEATHER AND HABITAT CHARACTERISTICS ON DEN

### 290 TEMPERATURES

291 The effects of  $T_a$  and solar exposure were dependent on den-type: nest-box temperatures  
292 responded more strongly to changing environmental conditions than tree-hollows (Figure 2;  
293 Table 1). During both seasons,  $T_{denMAX}$ ,  $T_{denMEAN}$  and  $T_{denMIN}$  increased substantially more in  
294 nest-boxes as  $T_a$  increased compared to tree-hollows (Figure 2a, c; Table 1), leading to greater  
295 disparity in temperature between den-types at higher  $T_a$ . For example, based on the fitted  
296 models, during an average summer day ( $T_a$  28°C, daily solar exposure 1.5 kWh m<sup>2</sup>), nest-boxes  
297 were predicted to be 9°C warmer than tree-hollows (31.4°C versus 22.3°C respectively). Under  
298 extreme recorded weather conditions (40°C, 4.1 kWh m<sup>2</sup>), the predicted difference between den-  
299 types rose to 19.6°C (45.7°C versus 26.1°C).  $T_{denMAX}$  and  $T_{denMEAN}$  in nest-boxes also increased  
300 as exposure to solar radiation increased, but decreased slightly in tree-hollows (Figure 2b, d;  
301 Table 1). During summer,  $T_{denMIN}$  increased slightly more with increasing  $T_a$  at sites with higher  
302 canopy openness (Table 1). For  $T_{holDIFF}$  and  $T_{boxDIFF}$ , canopy openness, den aspect, den height,  
303 tree DBH and hollow type (for  $T_{holDIFF}$  only) had little impact on den temperatures as the null  
304 models had the best fit (Table 1).

305

## 306 3.3 PREDICTED ECO-PHYSIOLOGICAL CONSEQUENCES OF DEN TEMPERATURES

307 Estimates of TNZs from the biophysical model for the four arboreal marsupials were similar to  
308 those previously observed (see Table S1). This suggests that the model captures key heat  
309 exchange processes for these species.

310

311 Den-type (nest-box, tree-hollow, none/outside) had a strong effect on estimated heat-loss  
312 required for all species (Table 2; Table S3). During summer, total heat-loss required in nest-  
313 boxes was approximately double that required in tree-hollows (e.g. 2.4 and 1.5 times higher for

314 common brushtails and common ringtails, respectively), and 1.3-2.3 times higher compared to  
315 resting outside for all species (Table 2; Table S3). During summer, the predicted average  
316 daytime heat-loss (calculated as the % basal metabolic heat-production required to be lost via  
317 evaporative cooling) for mountain brushtails was higher in nest-boxes (29.5%) than in tree-  
318 hollows (10.5%), with mean hourly rates of heat-loss required in nest-boxes up to 5.4 times that  
319 required in tree-hollows.

320

321 Heat-loss requirements were higher for larger species, with higher predicted heat-loss required  
322 for mountain brushtails than common ringtails when resting in nest-boxes during summer  
323 (29.5% and 10.3% basal metabolic rate, respectively, Table 2). During winter, predicted heat-  
324 loss required was typically slightly lower in nest-boxes, and similar between tree-hollows or  
325 resting outside (Table 2; Table S3).

326

327 The total predicted daytime heat-production (MJ) required during winter for animals in tree-  
328 hollows was 1.04-1.05 times that in nest-boxes, but marginally higher in nest-boxes during  
329 summer for most species (Table 2; Table S3). Predicted daytime heat-production (% basal) for  
330 common ringtails in winter was lower in nest-boxes (187.7%) than tree-hollows (197.0%), with  
331 the highest costs predicted for an animal resting outside (203.4%).

332

#### 333 4. Discussion

334 Nest-boxes support a range of hollow-dependent wildlife, particularly birds (Catry et al. 2011)  
335 and mammals (Durant et al. 2009), across a wide range of ecosystems globally (Harper et al.  
336 2005; Isaac et al. 2008b; Charter et al. 2010). Despite the widespread use of nest-boxes, their  
337 thermal value has received little attention. Our study demonstrates that thermal properties of  
338 nest-boxes and tree-hollows differ substantially. We found that nest-boxes can experience highly  
339 fluctuating temperatures that are likely to pose risks for wildlife during very hot weather. Our

340 modeling showed that eco-physiological costs of thermoregulation are likely to be considerably  
341 higher for arboreal marsupials in nest-boxes compared to tree-hollows during summer, but  
342 marginally lower during winter. These findings highlight the importance of retaining tree-  
343 hollows as thermal refugia. Although nest-boxes clearly provide valuable habitat for arboreal  
344 marsupials under many environmental conditions, we found that during hot weather they provide  
345 inadequate protection from extreme daytime temperatures, a critical issue with the predicted  
346 increase in heat-waves with climate change (Coumou & Rahmstorf 2012).

347

#### 348 4.1. NEST-BOX AND TREE-HOLLOW THERMAL PROFILES

349 In our study, nest-boxes reached greater daytime temperature extremes than tree-hollows,  
350 consistent with the few previous studies examining natural versus artificial den temperatures  
351 (McComb & Noble 1981; Isaac et al. 2008b). We found that nest-box microclimates responded  
352 more strongly to changes in ambient temperature and solar radiation than tree-hollows, which  
353 may largely be attributed to differences in physical structure. Tree-hollows large enough for the  
354 possums at our site typically occurred in trees over 1m DBH (Martin 2005). While this can vary  
355 among tree species (Wormington & Lamb 1999; Gibbons et al. 2000), wood surrounding tree-  
356 hollows will generally be much thicker than nest-box walls. Tree-hollows with thicker walls  
357 have greater heat-retaining capacity (Coombs et al. 2010), and slower rates of heat-gain from the  
358 external environment due to low thermal inertia (Derby & Gates 1966). Our results are  
359 consistent with this: nest-box cavities heated and cooled faster than tree-hollows, indicating that  
360 nest-boxes have lower insulative capacity. However, our results are based on empty dens, and  
361 the thermal properties of occupied dens may show some differences. Dens provide wildlife with  
362 protection from daily temperature fluctuations and extremes (Cooper 1999). Our study indicates  
363 that nest-boxes of one commonly used design may have limited capacity to perform this critical  
364 function under extreme conditions, with wildlife being exposed to substantially hotter daytime  
365 temperatures in nest-boxes than in tree-hollows, even in temperate environments. Retaining large

366 trees and reforestation are therefore vital in regions experiencing large daily and seasonal  
367 temperature fluctuations and high average temperatures, because nest-boxes of commonly used  
368 designs are unlikely to provide suitable thermal microclimates throughout the whole year.  
369  
370 Along with ambient temperature, solar radiation influenced daytime den temperatures,  
371 particularly in nest-boxes. Higher solar exposure (calculated from daily solar radiation and  
372 canopy openness) increased daytime temperatures in nest-boxes. Conversely, temperatures in  
373 tree-hollows decreased when solar exposure was high, possibly due to higher transpiration rates  
374 (water-loss) as radiation heated the leaves (Gates 1964; Mehajan et al. 2008), enhancing water  
375 flow through the trunk to heighten cooling (Vines 1968). However, further research is required,  
376 as factors governing tree-trunk temperatures, and thus tree-hollow temperatures, are not well  
377 understood. We also analysed several physical traits typically used when examining den  
378 temperature profiles (e.g. Isaac et al. 2008a), however none showed strong relationships with den  
379 temperatures. A few studies have found that orientation affects nest-box temperatures in fields  
380 (Adria et al. 2006; Butler et al. 2009), however, in our study, orientation had minimal effect,  
381 consistent with Stamp et al. (2002) who also worked in forests. Den height also had no effect on  
382 cavity temperatures, possibly because canopy openness (thus solar exposure) did not differ with  
383 height above the ground across the range measured here. In contrast with Isaac et al. (2008a)  
384 who found that maximum daytime temperatures were lower in hollow-bearing trees with larger  
385 DBH, in our study, which focused on comparing nest-boxes with the natural range of tree-  
386 hollows available, DBH had minimal impact on den temperatures. Collectively, our results  
387 suggest that canopy openness may be more influential than orientation in regulating exposure to  
388 solar radiation in forested environments, particularly for nest-boxes. In regions prone to high  
389 ambient temperatures, nest-boxes should be installed in sites with high canopy cover to reduce  
390 excessive heating from solar exposure.

391



392 4.2 MODELED ECO-PHYSIOLOGICAL CONSEQUENCES FOR ARBOREAL

393 MARSUPIALS

394 Our study revealed seasonal differences in the value of natural and artificial dens for arboreal  
395 marsupials due to variation in thermal microclimates. Nest-box use was predicted to  
396 substantially increase heat-loss requirements in summer, and therefore the potential for heat-  
397 stress and dehydration, but slightly reduce energy requirements in winter. Marsupials  
398 predominantly rely on evaporative heat-loss to maintain homeothermy at temperatures above  
399 their TNZ (Robinson & Morrison 1957). Water-loss rates can increase substantially at high  
400 ambient temperatures (Dawson 1969), and evaporative heat-loss may not be sufficient to  
401 maintain homeothermy. In addition, free-water can be limited during the hot, dry conditions  
402 typical of temperate Australian summers. Under such conditions, dehydration and heat-stress are  
403 more likely for animals in nest-boxes than in tree-hollows, where evaporative heat-loss is  
404 predicted to be 1.5-2.4 times higher. Estimates of heat-loss required in our study were based on  
405 temperatures in empty dens, however the expected added thermal impact of occupation by an  
406 endotherm (Kearney et al. 2011; J. Rowland, unpublished data) would inflate eco-physiological  
407 costs over summer. Under high ambient temperatures, animals may avoid nest-boxes reaching  
408 high temperatures (Goldingay 2015) and trade-off predator protection to avoiding acute heat-  
409 stress if suitable shelter is not available (Havera 1979). Alternatively, wildlife using thermally  
410 unsuitable nest-boxes may experience reduced growth and body condition, and high mortality  
411 rates, particularly juveniles (Catry et al. 2011). Temperature-related mortality and reduced  
412 fitness are important to address in the future because conservation-management programs using  
413 nest-boxes often target endangered species (e.g. Leadbeater's possum: Lindenmayer et al. 2009).  
414 Nest-boxes can contribute to species conservation, but may also contribute further to population  
415 declines during rare, but increasingly frequent, catastrophic heat events, which can cause  
416 substantial mortality (Catry et al. 2011). Investing in improved nest-box designs to buffer  
417 extreme temperatures is of high-priority to ensure nest-boxes are of maximum value for wildlife.

418  
419 During winter, the predicted heat-production costs required for thermoregulation were slightly  
420 lower for marsupials in nest-boxes compared to tree-hollows, and highest when resting outside.  
421 This is because nest-boxes were typically warmer than tree-hollows during the day, thus animals  
422 occupying tree-hollows spent more time exposed to temperatures below their TNZ (98.7-100%  
423 versus 90.1-99.8%, respective). Further, animals resting outside are subjected to wind, increasing  
424 convective heat-loss, and thus energy costs required to maintain homeothermy (Dawson &  
425 Brown 1970). Cooler dens are probably most challenging for smaller mammals and juveniles  
426 that are more susceptible to hypothermia due to their increased thermal conductance and/or poor  
427 thermoregulatory capabilities (Aschoff 1981; Holloway & Geiser 2000; Porter & Kearney 2009).  
428 Higher cumulative energy costs from resting in colder microclimates may also cause progressive  
429 decline in body condition when food availability is low (Speakman 1997) or foraging restricted  
430 (e.g. during rain: van den Oord et al. 1995). In our study, heat-production costs were calculated  
431 for unoccupied dens, thus costs in occupied dens are likely lower than predicted here. Energy  
432 costs may be further reduced in occupied well-insulated tree-hollows where more heat is likely  
433 to be retained, or if multiple animals den together (e.g. mountain brushtails: Martin 2005; sugar  
434 gliders: Durant et al. 2009). A systematic study is required to fully understand all factors driving  
435 thermal differences in tree-hollow temperatures.

436  
437 The relative value of nest-boxes and tree-hollows for particular species' depends on their  
438 physiology, morphology and behaviour. In general, larger mammals with thicker fur are more  
439 sensitive to high temperatures than smaller species with thinner fur (Robinson & Morrison 1957;  
440 Phillips & Heath 1995; Blanckenhorn 2000), with the converse true in cold environments. This is  
441 evident in the predicted relative costs (i.e. % basal heat-production or heat-loss required) for  
442 mountain brushtails (large, thick fur) compared to common ringtails (smaller, thinner fur) (see  
443 Table 2). However, larger animals have higher energy and water reserves, increasing their

444 ability to withstand high physiological costs over short periods (McKechnie & Wolf 2010). Den  
445 use patterns also influences the relative value of nest-boxes. While we focused on arboreal  
446 marsupials exhibiting diurnal den use, our finding that nest-boxes had lower minimum  
447 temperatures than tree-hollows (mean nighttime temperature 8.46°C and 10.96°C respectively)  
448 and more closely tracked ambient conditions, suggests that nest-boxes may provide lower  
449 thermal quality habitat than tree-hollows for temperate species denning nocturnally, including  
450 many birds species (Goldingay & Stevens 2009).

451

### 452 4.3 CONSERVATION IMPLICATIONS FOR HOLLOW-DEPENDENT SPECIES

453 Our biophysical modeling provided a useful method for estimating the relative costs of denning  
454 in nest-boxes versus tree-hollows for endotherms. We showed that nest-boxes and tree-hollows  
455 vary in their temperature regimes and thermal value for several arboreal hollow-dependent  
456 marsupials across seasons, with the largest disparities occurring when thermoregulatory costs are  
457 highest. Our study provides new information about fitness consequences of differing thermal  
458 microclimates of natural versus artificial dens. Our results indicate that tree-hollows generally  
459 provide better microclimates for endotherms, however nest-boxes are still valuable during milder  
460 environmental conditions. While we only assessed one nest-box design, our findings are broadly  
461 applicable to nest-boxes used globally for various species. However more research is needed on  
462 the thermal properties of artificial hollows, including nest-boxes with different dimensions that  
463 target different species (Beyer & Goldingay 2006), variation in construction materials (e.g.  
464 timber vs. clay pots, Catry et al. 2011), and those designed to more closely mimic tree-hollow  
465 properties (e.g. chainsaw cavities, Hurley & Harris 2014).

466

467 The persistence of hollow-dependent species worldwide, under both current and future climates,  
468 requires long-term conservation-management that prioritises retaining large, hollow-bearing  
469 trees and habitat regeneration. However the increasing global deficiency of tree-hollows

470 (Gibbons et al. 2008; Vesk et al. 2008) means that nest-boxes will be increasingly important,  
471 thus we must ensure these are of the highest-value for wildlife. Clear guidelines for nest-box  
472 design and deployment based on scientific evidence of their suitability for target species and  
473 prevailing environmental conditions, are critical to inform conservation decisions. We  
474 recommend that in environments prone to high temperatures, nest-boxes should be installed in  
475 shaded sites to limit high cavity temperatures and adverse impacts on inhabitants. Future efforts  
476 should be directed at improving nest-box design and deployment to improve their quality as  
477 habitat, especially to buffer against large temperature fluctuations. Actions should include  
478 altering surface thermal reflectance (S.R. Griffiths, J.A. Rowland, unpublished data) and  
479 increasing the insulative value of nest-boxes, along with installing nest-boxes with differing  
480 thermal properties to enable animals to select thermally suitable dens under different  
481 environmental conditions.

482

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491

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**Table 1.** Parameter estimates for models of effect of den-type and ambient conditions on maximum ( $T_{\text{denMAX}}$ ), mean ( $T_{\text{denMEAN}}$ ) and minimum ( $T_{\text{denMIN}}$ ) daytime den temperature, and den and site characteristics on maximum daytime temperature difference ( $T_{\text{holDIFF}}$  and  $T_{\text{boxDIFF}}$ ). Variables included in models for  $T_{\text{denMAX}}$ ,  $T_{\text{denMEAN}}$  and  $T_{\text{denMIN}}$  were: Den-type (nest-box, tree-hollow), ambient temperature, and solar exposure or canopy openness above each den. Variables included in full models for  $T_{\text{holDIFF}}$  and  $T_{\text{boxDIFF}}$  included: canopy openness, den height, aspect, tree DBH, and hollow type (for  $T_{\text{holDIFF}}$  only). Coefficients (95% CI) for best fitting models and interactions are presented (lowest  $AIC_c$ ). Response variables for  $T_{\text{boxDIFF}}$  and  $T_{\text{denMAX}}$  were log transformed to meet model assumptions.

Response variable	Predictor variables	Summer	Winter
$T_{\text{denMAX}}$	(Intercept)	3.39 (3.36, 3.41)	2.35 (2.31, 2.38)
	Den-type (Hollow)	-0.32 (-0.35, -0.28)	-0.30 (-0.35, -0.26)
	$T_{\text{aMAX}}$	0.14 (0.14, 0.15)	0.27 (0.27, 0.28)
	Solar exposure	0.03 (0.03, 0.04)	0.10 (0.09, 0.11)
	Den-type (Hollow): $T_{\text{aMAX}}$	-0.05 (-0.05, -0.04)	-0.10 (-0.11, -0.09)
	Den-type (Hollow): Solar exposure	-0.05 (-0.05, -0.04)	-0.18 (-0.19, -0.17)
$T_{\text{denMEAN}}$	(Intercept)	23.29 (22.98, 23.6)	8.2 (7.9, 8.4)
	Den-type (Hollow)	-3.82 (-4.26, -3.38)	-1.0 (-1.36, -0.69)
	$T_{\text{aMEAN}}$	3.43 (3.39, 3.46)	1.89 (1.84, 1.94)
	Solar exposure	0.86 (0.81, 0.91)	1.15 (1.10, 1.21)
	Den-type (Hollow): $T_{\text{aMEAN}}$	-1.38 (-1.44, -1.32)	-0.54 (-0.61, -0.48)
	Den-type (Hollow): Solar exposure	-1.28 (-1.37, -1.20)	-1.08 (-1.14, -1.01)
$T_{\text{denMIN}}$	(Intercept)	13.84 (13.54, 14.13)	4.95 (4.73, 5.16)
	Den-type (Hollow)	2.54 (2.12, 2.96)	1.00 (0.71, 1.30)
	$T_{\text{aMIN}}$	3.85 (3.79, 3.90)	2.39 (2.32, 2.46)
	Canopy openness	0.19 (-0.02, 0.40)	-
	Den-type (Hollow): $T_{\text{aMIN}}$	-1.26 (-1.45, -1.28)	-0.79 (-0.88, -0.70)
	$T_{\text{aMIN}}$ : Canopy openness	0.12 (0.08, 0.16)	
$T_{\text{holDIFF}}$	(Intercept)	2.93 (2.53, 3.32) <sup>a</sup>	1.34 (1.13, 1.54) <sup>b</sup>
$T_{\text{boxDIFF}}$	(Intercept)	1.45 (1.33, 1.57) <sup>c</sup>	0.98 (0.91, 1.05)

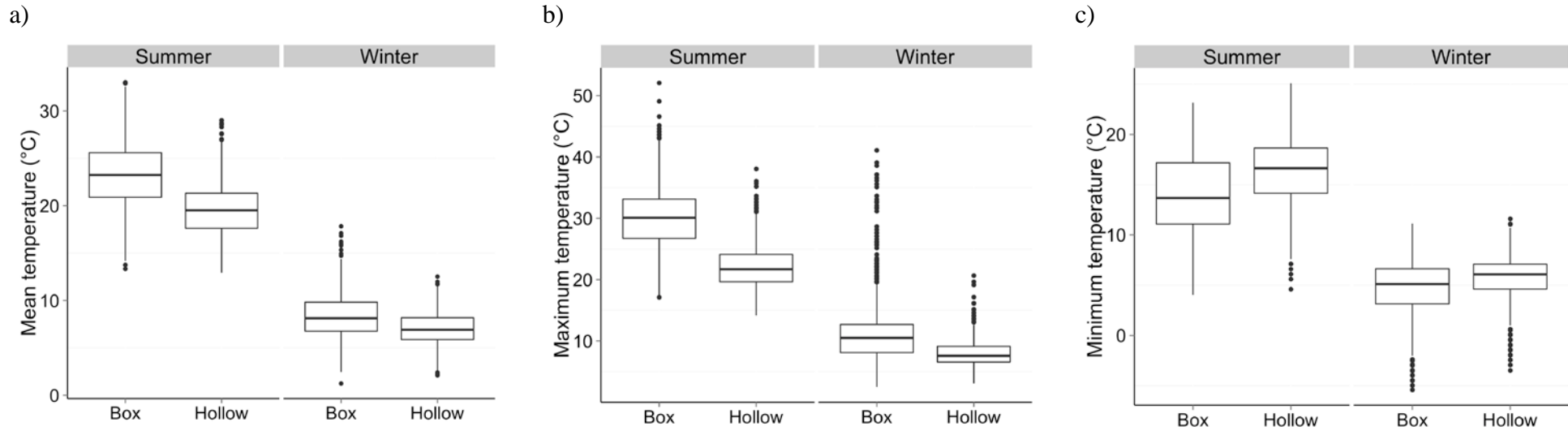
<sup>a</sup> Model  $AIC_c < 2$  lower than competing models with either DBH or hollow type

<sup>b</sup> Model  $AIC_c < 2$  lower than competing models with either den height or hollow type

<sup>c</sup> Model  $AIC_c < 2$  lower than competing models with openness

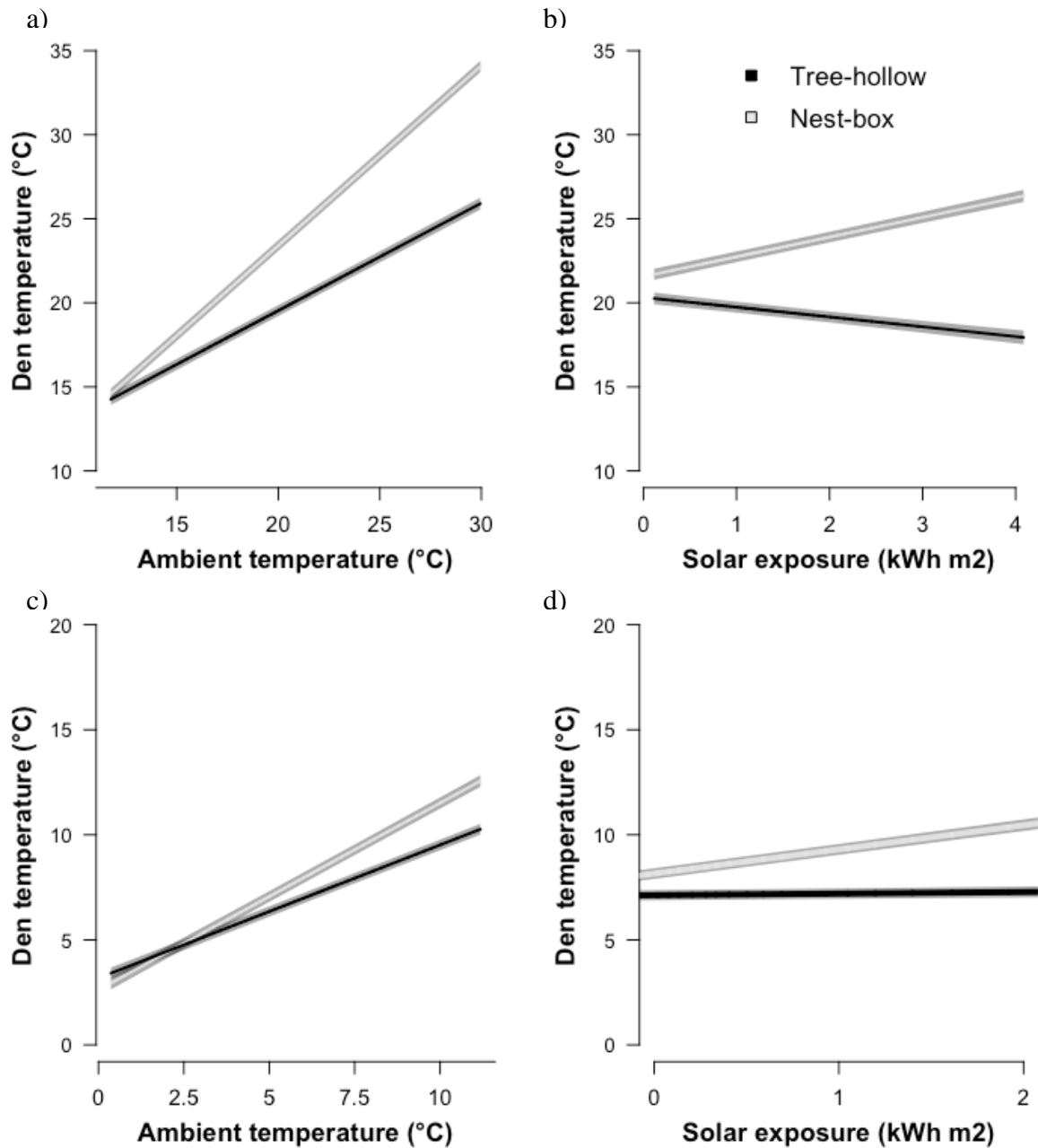
**Table 2.** Total predicted daytime heat-loss and heat-production (mean + 95% confidence intervals, MJ) for arboreal marsupials denning in nest-boxes, tree-hollows, or outside under shaded ambient conditions in the Strathbogie Ranges, Victoria, during summer (n = 37 sites; 53 days) and winter (n = 32; 49 days. See Table S3 for statistical analyses.

Species	Summer			Winter		
	<b>Heat-loss (MJ)</b>					
	Nest-box	Tree-hollow	Ambient	Nest-box	Tree-hollow	Ambient
Common brushtail	3.53 (3.33, 3.74)	1.50 (1.43, 1.57)	2.58 (2.46, 2.69)	0.98 (0.97, 0.99)	1.04 (1.03, 1.05)	1.04 (1.04, 1.05)
Mountain brushtail	5.54 (5.30, 5.79)	2.65 (2.50, 2.81)	4.27 (4.12, 4.43)	1.24 (1.23, 1.26)	1.30 (1.29, 1.31)	1.30 (1.29, 1.31)
Greater glider	1.94 (1.82, 2.07)	0.85 (0.82, 0.88)	1.40 (1.34, 1.47)	0.62 (0.61, 0.62)	0.66 (0.65, 0.66)	0.65 (0.65, 0.66)
Common ringtail	1.25 (1.17, 1.34)	0.85 (0.83, 0.86)	1.00 (0.97, 1.03)	0.84 (0.83, 0.85)	0.90 (0.89, 0.914)	0.92 (0.908, 0.93)
	<b>Heat-production (MJ)</b>					
	Nest-box	Tree-hollow	Ambient	Nest-box	Tree-hollow	Ambient
Common brushtail	25.04 (25.02, 25.07)	24.93 (24.90, 24.95)	25.27 (25.24, 25.31)	19.17 (19.03, 19.31)	20.08 (19.94, 20.22)	20.37 (20.26, 20.48)
Mountain brushtail	34.18 (34.16, 34.19)	34.16 (34.15, 34.18)	34.28 (34.26, 34.29)	22.69 (22.57, 22.81)	23.51 (23.35, 23.66)	23.75 (23.64, 23.87)
Greater glider	16.52 (16.50, 16.53)	16.37 (16.35, 16.40)	16.62 (16.60, 16.64)	12.69 (12.59, 12.79)	13.32 (13.23, 13.42)	13.40 (13.32, 13.48)
Common ringtail	15.24 (15.16, 15.31)	15.94 (15.72, 16.17)	16.22 (16.11, 16.32)	15.40 (15.27, 15.54)	16.16 (16.05, 16.27)	16.69 (16.60, 16.78)



**Figure 1.** Daily daytime a) mean, b) maximum, and c) minimum temperature within nest-boxes and tree-hollows during summer (n = 65 days) and winter (n = 60 days) sampling periods in the Strathbogie Ranges, Victoria. Nest-boxes had significantly higher  $T_{denMAX}$  and  $T_{denMEAN}$ , and significantly lower  $T_{denMIN}$  than tree-hollows during both summer and winter. See Table S2 for statistical analyses.

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**Figure 2.** The modeled fixed-effects of ambient temperature (a,c) and solar exposure (b,d) on mean daytime temperatures of tree-hollows and nest-boxes during summer (689) and winter (c, d) in the Strathbogie Ranges, Victoria, (holding other variables at the 691 mean value). Grey bars represent 95% confidence intervals. See Table 1 for statistical 692 analyses. 693

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705 **Supplementary material**

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**Table S1** Species trait values and climate data used to model eco-physiological costs of den microclimates on Australian arboreal marsupials, and estimated thermoneutral zones (TNZ) for each species. Measurements of fur depth and body dimensions were taken from female specimens of common brushtail possum (*Trichosurus vulpecula*; n = 21), mountain brushtail possum (*Trichosurus cunninghami*; n = 9), common ringtail possum (*Pseudocheirus peregrinus*; n = 17), and greater glider (*Petauroides volans*; n = 17) held at Museum Victoria.

Variables	Species parameter estimates			
	Common brushtail possum	Mountain brushtail possum	Common ringtail possum	Greater glider
<i>Body mass (kg)</i>	Summer: 2.2 Winter: 2.3 <sup>a</sup>	3.4 <sup>b</sup>	Summer: 0.9 Winter: 1.0 <sup>c</sup>	1.25 <sup>d</sup>
<i>Posture (length:width)<sup>e</sup></i>	1.001 – 4	1.001 – 3.5	1.001 – 4	1.001 – 5.5
<i>Fur thermal conductivity, W/m °C<sup>f</sup></i>	0.04	0.04	0.04	0.04
<i>Fur depth (mm)</i>	17-23	21-28	11-15	18-30
<i>Core temperature (°C)</i>	36.2 <sup>g</sup>	37.3 <sup>h</sup>	37.4 <sup>c</sup>	35.4-39.1 <sup>i</sup>
<b>Climate variables</b>				
<i>Wind-speed (m/s)</i>	0.01 in nest-box and hollow; otherwise assumed 50% of wind-speed measured in the open at 9 am <sup>j</sup>			
<i>Humidity (%)</i>	Relative humidity at 9 am <sup>j</sup>			
<b>Thermoneutral zones</b>				
<i>Model-estimated average</i>	16.8°C – 24.5°C	14.6°C – 23.7°C	17.2°C – 24.5°C	22.8°C – 28.6°C
<i>Previously observed</i>	15°C – 25°C <sup>k,l</sup>		20°C <sup>i</sup>	20°C – 30°C <sup>m</sup>

<sup>a</sup> Clinchy *et al.* 2004, <sup>b</sup> Martin 2005, <sup>c</sup> Munks & Green 1995, <sup>d</sup> Tyndale-Biscoe & Smith 1969, <sup>e</sup>

Posture changed to simulate behavioural responses to changes in temperature, from curled to uncurled posture, <sup>f</sup> Default mammal value, see Porter & Kearney 2009, <sup>g</sup> Dawson & Hulbert 1970, <sup>h</sup> Gemmell & Cepen 1993, <sup>i</sup> Rubsamen *et al.* 1984, <sup>j</sup> Bureau of Meteorology Strathbogie North Station 082043, <sup>k</sup> Dawson 1969, <sup>l</sup> van den Oord *et al.* 1995, <sup>m</sup> Munks 1990.

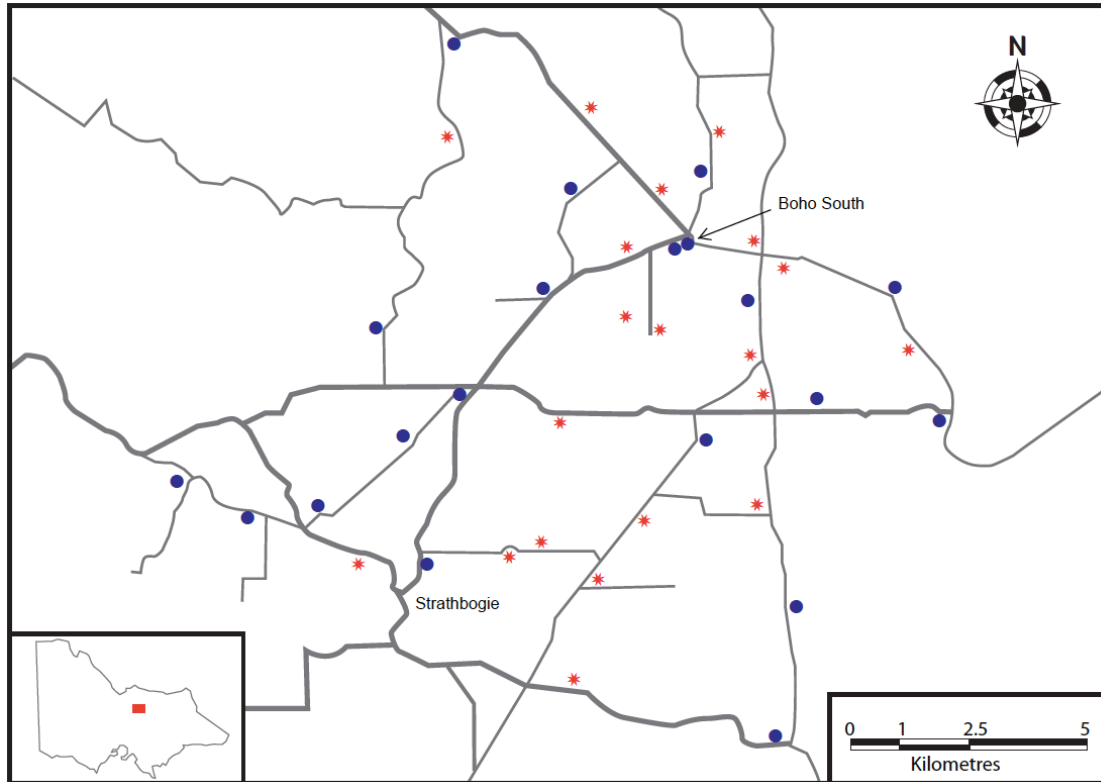
**Table S2.** Parameter estimates for linear mixed models of effect of Den-type (nest-box, tree-hollow) and Season (summer, winter) on 708 maximum, mean and minimum daytime den temperature. Best fitting model presented (lowest AIC<sub>c</sub> value). In all cases, competing models had ΔAIC values greater than 2.

Response variables	Predictor variables	Coefficients (95% CI)
T <sub>denMAX</sub>	Intercept	30.2 (29.6, 30.8)
	Den-type (Hollow)	-8.0 (-8.7, -7.4)
	Season (Winter)	-19.3 (-19.8, -18.8)
	Den-type (Hollow): Season (Winter)	5.1 (4.5, 5.6)
T <sub>denMEAN</sub>	Intercept	23.2 (22.9, 23.4)
	Den-type (Hollow)	-3.6 (-3.9, -3.3)
	Season (Winter)	-15.0 (-15.3, -14.7)
	Den-type (Hollow): Season (Winter)	2.4 (2.0, 2.8)
T <sub>denMIN</sub>	Intercept	14.0 (13.6, 14.3)
	Den-type (Hollow)	2.3 (2.0, 2.7)
	Season (Winter)	-9.0 (-9.3, -8.7)
	Den-type (Hollow): Season (Winter)	-1.4 (-1.8, -1.0)



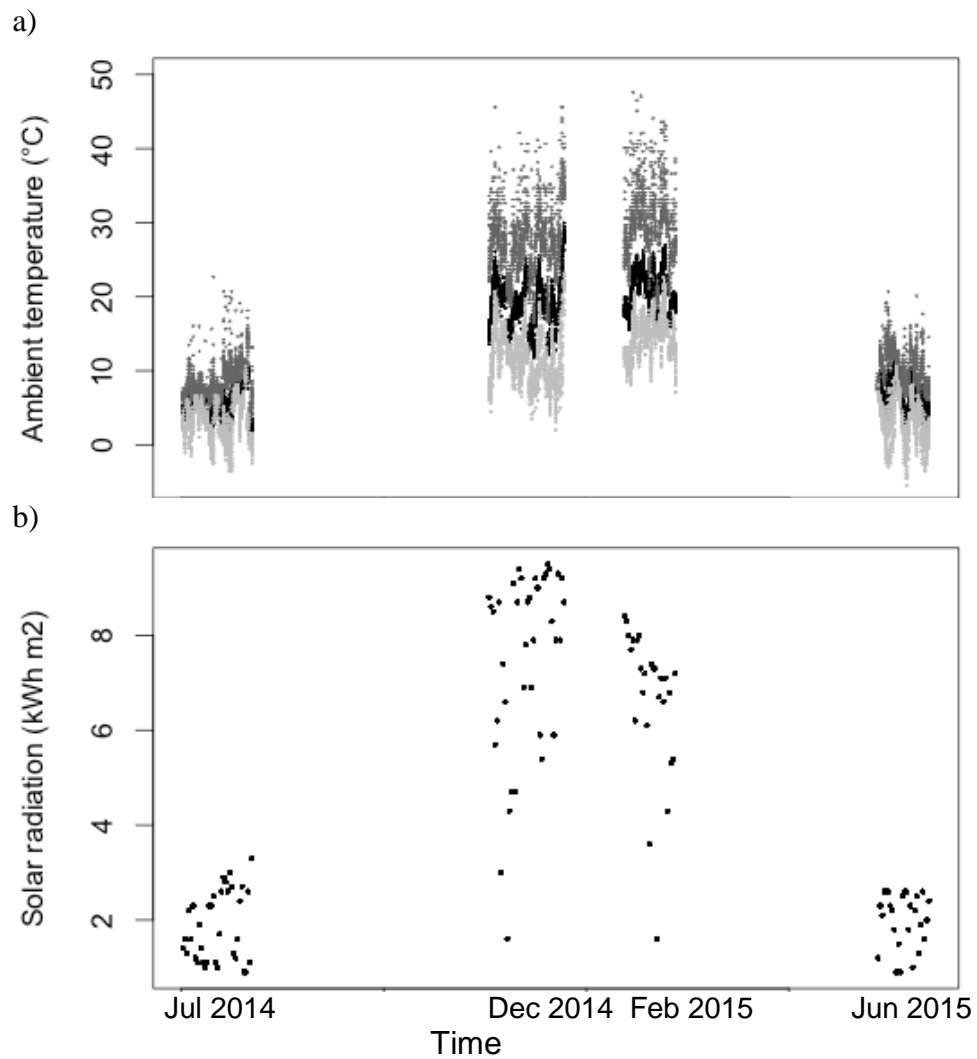
**Table S3.** Effect of den-type on total predicted daytime heat-loss and heat-production (MJ) for arboreal marsupials denning in nest-boxes, tree-hollows or under ambient conditions (outside) in the Strathbogie Ranges, Victoria, during summer (n = 37 sites; 53 days) and winter (n = 32; 49 days). Data for summer heat-loss were square-root transformed to improve normality. Values are coefficient (95% CI), with bold-type indicating where 95% CI do not overlap zero.

Species	Comparison	Heat-loss (MJ)		Heat-production (MJ)	
		Summer	Winter	Summer	Winter
Common brushtail possum ( <i>Trichosurus vulpecula</i> )	Intercept	<b>0.05</b> (0.049, 0.051)	<b>1.04</b> (1.03, 1.05)	<b>25.27</b> (25.24, 25.30)	<b>20.37</b> (20.24, 20.51)
	Den-type (Nest-box)	<b>0.008</b> (0.007, 0.01)	<b>-0.06</b> (-0.08, -0.05)	<b>-0.23</b> (-0.27, -0.19)	<b>-1.20</b> (-1.39, -1.01)
	Den-type (Hollow)	<b>-0.012</b> (-0.014, -0.01)	-0.005 (-0.02, 0.01)	<b>-0.35</b> (-0.39, -0.31)	<b>-0.29</b> (-0.48, -0.10)
Mountain brushtail possum ( <i>Trichosurus cunninghami</i> )	Intercept	<b>0.065</b> (0.063, 0.067)	<b>1.30</b> (1.29, 1.32)	<b>34.28</b> (34.26, 34.29)	<b>23.75</b> (23.62, 23.88)
	Den-type (Nest-box)	<b>0.009</b> (0.007, 0.01)	<b>-0.06</b> (-0.08, -0.04)	<b>-0.10</b> (-0.12, -0.08)	<b>-1.06</b> (-1.25, -0.88)
	Den-type (Hollow)	<b>-0.014</b> (-0.016, -0.012)	-0.002 (-0.02, 0.02)	<b>-0.11</b> (-0.13, -0.09)	<b>-0.25</b> (-0.43, -0.06)
Greater glider ( <i>Petauroides volans</i> )	Intercept	<b>0.037</b> (0.036, 0.038)	<b>0.65</b> (0.65, 0.66)	<b>16.62</b> (16.60, 16.64)	<b>13.40</b> (13.31, 13.49)
	Den-type (Nest-box)	<b>0.007</b> (0.005, 0.008)	<b>-0.04</b> (-0.05, -0.03)	<b>-0.10</b> (-0.14, -0.07)	<b>-0.71</b> (-0.84, -0.58)
	Den-type (Hollow)	<b>-0.008</b> (-0.001, -0.007)	0.003 (-0.01, 0.01)	<b>-0.25</b> (-0.28, -0.21)	-0.08 (-0.21, 0.05)
Common ringtail possum ( <i>Pseudocheirus peregrinus</i> )	Intercept	<b>0.032</b> (0.03, 0.032)	0.92 (0.91, 0.93)	<b>16.22</b> (16.06, 16.37)	<b>16.69</b> (16.58, 16.80)
	Den-type (Nest-box)	<b>0.004</b> (0.003, 0.005)	<b>-0.08</b> (-0.09, -0.07)	<b>-0.98</b> (-1.19, -0.76)	<b>-1.29</b> (-1.45, -1.13)
	Den-type (Hollow)	<b>-0.003</b> (-0.004, -0.001)	<b>-0.02</b> (-0.03, -0.01)	<b>-0.27</b> (-0.49, -0.06)	<b>-0.53</b> (-0.69, -0.37)



**Figure S1.** Location of study sites in the Strathbogie Ranges, Victoria, Australia, symbols indicate location of paired nest-boxes and tree-hollows. Tree-hollows either had the entrance located in the trunk (\*) or base (•) of the tree. Insert shows Victoria with location of the study site shaded in red.

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**Figure S2.** a) Daily maximum (medium-grey), mean (black), and minimum (light-grey) ambient temperature (°C), and b) total daily solar radiation (kWh/m<sup>2</sup>) over 24 hours in the Strathbogie Ranges, Victoria, during the sampling periods.

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