

"This is the peer reviewed version of the following article:

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J., & Nimmo, D. G. (2021). Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews*, *96*(6), 2735–2754. <https://doi.org/10.1111/brv.12776>

This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions."

<https://authorservices.wiley.com/author-resources/Journal-Authors/licensing/self-archiving.html>

Artificial refuges to combat habitat loss for an endangered marsupial predator: how do they measure up?

Mitchell A. Cowan¹, Judy Dunlop², James M. Turner¹, Harry Moore¹, Dale G. Nimmo¹

¹ Institute for Land, Water and Society, School of Environmental Sciences, Charles Sturt University, Albury, NSW 2640, Australia

² Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, Perth, WA, Australia.

Email:

Mitchell Cowan: mitchcow96@gmail.com

Judy Dunlop: judy.dunlop@dbca.wa.gov.au

James Turner: jaturner@csu.edu.au

Harry Moore: hmoore@csu.edu.au

Dale Nimmo: dnimmo@csu.edu.au

Abbreviated title: Artificial refuges for northern quolls.

Keywords: activity patterns, artificial refuge, artificial den, *Dasyurus hallucatus*, feral cat, habitat restoration, northern quoll, thermal limits, habitat loss, revegetation

Type of article: Contributed paper.

Target audience: Policy makers including government and councils, companies and organisations including mining and agriculture, and other environmental stakeholders.

Abstract word count: 200

Total manuscript word count: 5661

Number of references: 92

Number of figures and tables: 5

Correspondence: Mitchell Alec Cowan, 0448132198, mcowan@csu.edu.au, Charles Sturt University, PO Box 789, Albury NSW 2640, Australia.

1 **Abstract**

2 One technique used to combat the growing global species extinction crisis has been to create
3 artificial refuges—human-made replacements for natural refuges destroyed during habitat
4 modification. However, there is limited knowledge of how closely artificial refuges replicate
5 the natural refuges they seek to replace. Mining threatens many species worldwide through
6 large-scale habitat modification, and artificial refuges have been proposed as a method to
7 offset the resulting habitat loss. Here, we examined the microclimatic, physical, and biotic
8 characteristics of natural dens occupied by the northern quoll (*Dasyurus hallucatus*)—an
9 endangered marsupial threatened by habitat loss—and compared these to 1) superficially
10 similar unoccupied crevices, and 2) artificial dens created by mining companies for northern
11 quolls. Northern quolls occupied natural dens that were cooler and deeper than unoccupied
12 crevices, likely to avoid lethal air temperatures as well as predators. Artificial dens provided
13 similar thermal properties to occupied dens, but lacked key characteristics in having
14 shallower den cavities, less complex surrounding habitat, increased feral cat visitation, and
15 less small mammal prey compared to occupied dens. This study highlights the need to
16 consider multiple facets when constructing artificial refuges, in order to avoid perverse
17 outcomes, such as inadequate shelter, increased predation and food shortages.

18 **1. Introduction**

19 The scale of global habitat loss has rendered the protection of remaining habitat insufficient
20 for maintaining biodiversity (Françoso et al. 2015), requiring active intervention for the
21 restoration of lost and degraded habitats (Croak et al. 2013). However, the replacement of
22 natural habitat is rarely straightforward (Lawrence et al. 2018). Some refuges such as tree
23 hollows and logs, are renewable (*sensu* O'Connell and Keppel, 2016), often returning
24 following restoration, but they can take decades to develop (Haslem et al. 2012). Non-
25 renewable refuges, such as rock crevices (*sensu* Croak et al. 2010), require intervention to be
26 returned to landscapes following their loss (Croak et al. 2010; Dervo et al. 2018).

27

28 Artificial refuges—such as artificial nests (Goldingay et al. 2018), rock crevices (Croak et al.
29 2012), and hibernacula (Zappalorti, 1994)—are human-made substitutes for natural refuges
30 where wildlife can shelter, hibernate, and rear offspring in areas lacking natural refuges
31 (Sherley et al. 2012). Artificial refuges have been used in many restoration efforts across the
32 globe to provide shelter to animals where natural habitat has been altered or destroyed (e.g.
33 Bolton et al. 2004; Keppers et al. 2008; Dervo et al. 2018). Yet, the science of artificial
34 refuges is still in its infancy and artificial refuges can fall short, sometimes with perverse
35 outcomes (Ebrahimi et al. 2012; Griffiths et al. 2017). Recreating habitable refuges requires
36 not only the provision of a thermal and physical environment that replicates natural refuges
37 (e.g., Griffiths et al. 2018), but also the array of resources that animals require, including a
38 safe haven from predators (Anderson et al. 2016).

39

40 The northern quoll (*Dasyurus hallucatus*) is an Australian marsupial mesopredator (~520 g)
41 that has declined substantially over the past 200 years (Braithwaite and Griffiths, 1994;
42 Moore et al. 2019). Range contractions of up to 75% have been recorded (Moore et al. 2019)

43 due to habitat loss, introduced predators (namely the feral cat, *Felis catus*, and red fox,
44 *Vulpes vulpes*), altered fire regimes, and poisoning by the introduced cane toad (*Rhinella*
45 *marina*; Ibbett et al. 2018; Moore et al. 2019). The species is listed as endangered by the
46 IUCN and has a ‘decreasing’ population trend (Oakwood et al. 2016). The Pilbara region of
47 Western Australia is the last remaining stronghold for the northern quoll, likely due to the
48 absence of cane toads (Woinarski et al. 2014; Moore et al. 2019). Yet, this stronghold is far
49 from secure, with predation by feral cats threatening Pilbara quoll populations (Cramer et al.
50 2016; Hernandez-Santin et al. 2016), and > 91% of the region under mining lease
51 (Environmental Protection Authority, 2014). Conventional drill and blast mining in the
52 Pilbara often destroys non-renewable refuges and habitat (e.g., rocky outcrops) and is a
53 primary driver of habitat loss for northern quolls (Cramer, 2016).

54

55 Rocky outcrops and mesas provide crucial denning sites for northern quolls (Burbidge and
56 McKenzie, 1989; Hernandez-Santin et al. 2016), but are the focus of mining activities owing
57 to their rich deposits of iron-ore and gravel (Ramanaidou and Morris, 2010; Cramer et al.
58 2016). Mining companies are sometimes required to offset environmental damage caused by
59 mining by replacing or compensating for destroyed habitat (McGregor et al. 2014;
60 Shackelford et al. 2018), and artificial refuges have been touted as one tool that could—along
61 with other actions—help to offset the destruction of non-renewable refuges (Trulio, 1995;
62 Cramer et al. 2016). Artificial refuges comprised of rock, concrete and gravel have been
63 created by mining companies with the hope to rehabilitate previously destroyed habitat due to
64 mining activities, as well as to provide off-site refuge for northern quolls during mining
65 operations, particularly by trying to replace lost natal dens (i.e., crevices where female quolls
66 raise their offspring; Cramer et al. 2016; Table S1). However, natural dens and their
67 surroundings often have specific thermal, physical and/or biotic characteristics, making their

68 replacement difficult (Gallant et al. 2014; White et al. 2015; Rowland et al. 2017).

69 Importantly, it is not known how artificial dens compare to natural dens.

70

71 In this study, we:

72 1) Identify thermal, physical, and biotic attributes of northern quoll natal dens in the
73 Pilbara, by comparing occupied dens to nearby unoccupied (but superficially similar)
74 crevices.

75 First, we predict that, like other dasyurids (Matthews et al. 2017), quolls will select cool,
76 deep dens that buffer extreme temperatures, particularly given that summer temperatures in
77 the Pilbara regularly exceed temperatures at which quolls are prone to hyperthermia and
78 dehydration (i.e., $> 36\text{ }^{\circ}\text{C}$; Cooper and Withers, 2010). Second, we predict that quolls will
79 select dens with specific physical dimensions that reduce predation risk, such as an opening
80 that is large enough for quolls to enter, but small enough to exclude predators such as feral
81 cats (Oakwood, 2000; O'Connell and Keppel, 2016). Finally, we predict that quolls will
82 select dens in areas that minimise the likelihood of encountering larger predators (e.g.,
83 choosing areas with low feral cat activity and complex surrounding habitat structure;
84 McGregor et al. 2015; Hernandez-Santin et al. 2016), as well as having ample small
85 vertebrate prey (Dunlop et al. 2017).

86

87 2) Assess whether artificially created dens accurately replicate the thermal, physical, and
88 biotic properties of occupied dens.

89 First, we predict that artificial refuges will experience more extreme thermal fluctuations
90 compared to natural dens, as has been found in previous studies (e.g. Rowland et al. 2017;
91 Griffiths et al. 2018). Second, we predict that artificial refuges will be shallower than natural
92 dens because of their difference in size, owing to the selection of deep dens by quolls. Third,

93 because artificial dens are located in previously disturbed areas, we predict that they will be
94 surrounded by simpler habitat structure, and, partly because of this, will have more evidence
95 of feral cat activity (as suggested by Hernandez-Santin et al. 2016). Finally, because of the
96 simplified habitat surrounding artificial dens, we predict a lower availability of small
97 vertebrate prey.

98

99 **2. Methods**

100 **2.1 Study area**

101 Study dens and crevices were distributed across nine sites within the Chichester subregion of
102 the Pilbara bioregion (Figure 1a; Table S1). These sites were chosen either because they
103 were known from previous monitoring to have relatively high densities of northern quolls, or
104 had existing artificial refuges constructed. The Pilbara bioregion is located in a semi-arid
105 climate covering 179,000 km² of north-west Western Australia (as described in McKenzie et
106 al. 2009). The region has mean minimum/maximum temperatures of 25/40°C in summer and
107 12/27°C in winter, while average annual rainfall is variable (250 – 500 mm), falling mainly
108 during summer (~170 mm; Bureau of Meteorology, 2018). Landscapes are comprised of
109 ranges and plateaus with rugged hills, granitic plains, and mesas, together with sandplains
110 and dune fields (Van Vreeswyk et al. 2004). The flora of the region is diverse, dominated by
111 *Acacia*, *Triodia*, and *Eucalyptus* species (Van Vreeswyk et al. 2004), while mining is the
112 dominant land use (Environmental Protection Authority, 2014).

113

114 **2.2 Experimental design**

115 The experimental design included three treatments (n=10 each) based on den type: occupied
116 dens, unoccupied crevices, and artificial dens. Occupied dens were chosen as a natural
117 baseline against which the other two den types could be compared (Figure 1b). Unoccupied

118 crevices were used to determine whether northern quolls selected crevices with specific
119 thermal, physical, and/or biotic characteristics. Artificial dens were created specifically for
120 northern quolls by mining companies as part of rehabilitation works on previously developed
121 land, as well as in areas outside existing mine works to mitigate damaged habitat. Most
122 artificial dens were created between 2012 and 2015, with two dens created between 2015 and
123 2018. All artificial dens were constructed with a similar method—using large earthmoving
124 vehicles to pile up rock/concrete and create crevices and cavities among the material. Two
125 types of artificial dens were created: 1) large piles of variously sized waste rock (Figure 1d),
126 and 2) smaller piles of concrete slabs and gravel (Figure 1e). Two artificial dens were
127 selected from a railway rock armoury where quoll activity had been previously recorded by
128 Roy Hill (H. Davie, personal communication, 12 October, 2018), and these were classed the
129 same as the first den type (for further details on artificial dens see Table S1).

130

131 We used natural positives (occupied dens) and negatives (unoccupied crevices) to determine
132 the specific natural den characteristics that quolls use, allowing us to reveal whether northern
133 quolls actively select specific den characteristics compared to other random crevices. We
134 note that the types of crevices that quolls chose for dens is likely to be affected by the local
135 density of quolls, with quolls potentially choosing less optimal dens when competition for
136 dens—caused by high densities—is high. However, examining the impact of density on quoll
137 den choice was beyond the scope of this study. We compared these characteristics to existing
138 artificial dens, regardless of their occupancy, because we sought to define how artificial dens
139 in their current form replicate refuges that northern quolls use *in situ*. Occupied dens and
140 unoccupied crevices were paired so that each were subject to similar environmental variables
141 including rainfall, temperature, quoll population density, and topography. The den type
142 characteristics were:

- 143 1) Occupied dens—rock crevices with evidence of regular occupancy by female quolls
144 (outlined below; Figure 1b).
- 145 2) Unoccupied crevices—rock crevices within 50 m of, and superficially similar to, a
146 nearby occupied den, but with no evidence of continued quoll occupancy (Figure 1c).
- 147 3) Artificial dens—crevices within existing restoration works comprised of human-made
148 refuges, constructed with either rock (Figure 1d) or concrete and gravel (Figure 1e).

149

150 **2.3 Den selection**

151 To locate occupied dens, we trapped northern quolls using cage traps and tracked them to
152 their dens using VHF radio-tracking, spool-and-line tracking, and fluorescent pigment
153 tracking (for details see Table S2). We confirmed den occupation using camera traps (see
154 section 2.4.3). Within 50 m of each occupied den, we located a paired ‘unoccupied
155 crevice’—crevices that were superficially similar to nearby occupied dens, but showed no
156 evidence of occupation (i.e., tracks, scats or camera trap images). This categorisation was
157 reversed for two den types due to camera traps showing that one ‘occupied den’ at Red Rock
158 was unoccupied, and one ‘unoccupied crevice’ at De Grey Ridge was occupied. Occupied
159 dens and unoccupied crevices were located among five sites, while artificial dens were
160 located among four sites (for further details on dens and sites see Table S1). .

161 **2.4 Data collection**

162 ***2.4.1 Thermal properties***

163 We recorded temperature and relative humidity using DS1923 Hygrochron Temperature and
164 Humidity Data Loggers (iButtons; Maxim Integrated Products, USA). iButtons were placed
165 inside small fibreglass mesh pouches (5 x 10 cm) and programmed to record temperature (\pm
166 0.5°C) and relative humidity (\pm 0.6%) hourly. Each den or crevice had one internal and one

167 external iButton deployed from October 2018 until January 2019. Internal iButtons measured
168 thermal properties of the den cavity. Placement was minimally invasive to quolls and we saw
169 no den abandonment. External iButtons measured ambient conditions outside dens/crevices
170 and were attached to the underside of the forward-facing camera trap to protect them from
171 rain and direct sunlight. In total, 11.7 percent of all iButtons failed, of the 30 dens monitored,
172 internal iButtons failed at two occupied dens and two unoccupied crevices, while external
173 iButtons failed at one occupied den, one unoccupied crevice, and one artificial den.

174

175 ***2.4.2 Physical properties***

176 We measured the physical properties of dens, crevices, and their immediate surroundings
177 including counting the number of entrances to the internal cavity, and measuring the width
178 and height of the largest entrance with a tape measure. Den or crevice depth was measured
179 using a 1.8 m in length, PVC-coated metal garden stake pushed in from the entrance to where
180 it could go no further. For dens deeper than 1.8 m, garden stakes were cable tied together, end
181 on end. By using a straight pole to measure depth, it is possible that we at times
182 underestimated den depth if dens continued after sharp bends. To quantify habitat
183 immediately surrounding each den or crevice, we measured ground cover at one metre
184 intervals along two perpendicular 25-metre transects, centred on each den or crevice (n=50
185 points per den/crevice). Ground cover was classified as rock, bare ground, *Triodia* spp., or
186 grass/herb. Within a 50 × 50 m grid, we visually assessed the percent cover of rocks within
187 four different size classes (embedded rock or individual rock diameters of <0.5 m, 0.5-2 m
188 and >2 m). Embedded rock was part of a rock formation fixed to the ground (i.e. inselbergs).

189

190 **2.4.3 Quoll interactions with predators and prey**

191 We used forward-facing camera traps to measure the activity of feral cats, northern quolls
192 and their prey. We installed an unbaited, forward facing Reconyx PC900 Hyperfire covert
193 cameras (camera traps) (Reconyx, Wisconsin, USA) on a 0.5-m high wooden stake, 1-3 m
194 from each den or crevice (n = 30 in total), facing the entrance. Cameras were set on high
195 sensitivity to take three shots per trigger at one second intervals, and remained in place from
196 October 2018 to January 2019. To detect potential vertebrate prey species, one baited (rolled
197 oats, peanut butter, and sardines) camera trap was installed within ten metres of each den and
198 crevice, mounted 1.5 m above the ground, facing downwards. Both camera trap types were
199 deployed at each den or crevice from October 2018 to January 2019. When forward-facing
200 cameras also detected prey species, these data were included in estimates of prey availability,
201 however predators were only included in visitation analysis when detected by forward-facing
202 cameras. Potential prey were animals that could be depredated by northern quolls, based on
203 their diet in the Pilbara (Pollock, 1999; Dunlop et al. 2017). To avoid repeatedly counting
204 single individuals over short periods of time, we defined an ‘independent detection’ as any
205 triggers of the same species separated by more than 15 minutes (Rendall et al. 2014; Diets et
206 al. 2016; Hofmeester et al. 2017). Visitation was defined as the number of independent
207 detections of a given species over the duration of sampling (excluding cameras that failed),
208 which was corrected for trap nights. For potential prey species, visitation data was pooled
209 into three groups: “mammal”, “reptile”, and “bird” prey (Table S3).

210

211 **2.5 Data analysis**

212 We used R version 2.15.3 for our analyses (R Core Development Team, 2013), and first
213 examined whether northern quoll visitation differed among den types, using Generalised
214 Linear Models (GLMs) (Zuur et al. 2009). The response variable was northern quoll

215 visitation, and den type was included as a categorical predictor variable with three levels
216 (occupied den, unoccupied crevice, artificial den). Because the response variable was a count,
217 a Poisson distribution was initially specified, but showed evidence of over dispersion.
218 Therefore, the model was refit specifying a negative binomial distribution (Zuur et al. 2009).
219 Occupied dens were specified in this, and all GLMs, as the reference category (Crawley,
220 2012).

221

222 *2.5.2 Thermal properties*

223 To compare thermal properties of dens, we first fitted Generalised Additive Mixed Models
224 (GAMMs) (Zuur et al. 2009), with temperature and humidity as response variables. Predictor
225 variables were time of day (continuous variable), and a six-level categorical variable that
226 concatenated den type (occupied den, unoccupied crevice, artificial den) and iButton location
227 (internal or external). Site was included as a random effect to account for repeated measures
228 (Zuur et al. 2009). We included an interaction between time of day and the concatenated
229 predictor using the ‘by’ function to allow a separate curve of internal and external
230 temperature and humidity with time of day for each den type (Zuur et al. 2009). Separate
231 models were constructed for spring and summer. GAMMs were fitted using the ‘gamm4’
232 package (Wood and Scheipl, 2017).

233

234 Predictions from GAMMs were plotted in relation to the northern quoll’s ‘thermal stress
235 range’, which is the range of temperatures within which quolls are likely to experience
236 thermal stress, defined by two thresholds: 1) 36°C, the ambient temperature where quolls
237 significantly increase physiological cooling via evaporative water loss, resulting in thermal
238 stress (Cooper and Withers, 2010), and 2) 41°C, the lethal body temperature of other

239 marsupials, including green ringtail possums (*Pseudochirops archeri*) and quokkas (*Setonix*
240 *brachyurus*) (Robinson and Morrison, 1957; Krockenberger et al. 2012).

241

242 **2.5.3 Physical properties**

243 We used GLMs to compare the physical properties of den types. Den dimensions (number of
244 entrances, depth, entrance height, and entrance width) were specified as having a Gaussian
245 distribution of errors. Ground cover (rock, bare ground, *Triodia* spp., and grass/herb) and
246 rock abundance (embedded, <0.5 m, 0.5-2 m, and >2 m) were proportion data, and were
247 therefore specified as having binomial distributions (Zuur et al. 2009; Crawley, 2012). A
248 quasibinomial distribution was specified when binomial models showed evidence of over
249 dispersion (Bates et al. 2015).

250

251 **2.5.4 Quoll interactions with predators and prey**

252 GLMs were used to examine whether predator visitation and prey availability differed among
253 den types. The response variable was the relative visitation rates of feral cats and prey
254 (pooled into mammals, reptiles, birds) corrected for the number of trap nights. A negative
255 binomial distribution was specified in all models and den type was included as a categorical
256 predictor. In addition to spatial avoidance, smaller predators are known to temporally avoid
257 larger predators (Brook et al. 2012). Therefore, we measured activity overlap of quolls and
258 feral cats at each den type. We fit kernel density curves of activity based on the timing of
259 observations of each species from camera traps using the ‘Overlap’ package (Ridout and
260 Linkie, 2009; Fancourt et al. 2015). A coefficient of overlap between quolls and cats was
261 then calculated for each den type. This coefficient is a quantitative measure of overlap in
262 activity time, ranging from 0 (no overlap) to 1 (complete overlap in activity). We used the Δt
263 estimator (appropriate for datasets with a small number of observations [Ridout and Linkie,

264 2009]) to measure activity overlap for occupied dens and unoccupied crevices, owing to feral
265 cats having fewer than 75 individual detections. The same was used for artificial dens, with
266 northern quolls having less than 75 individual detections (Meredith and Ridout, 2018).

267

268 **3. Results**

269 Camera traps were deployed for a total of 2526 trap nights, during we detected northern
270 quolls at all occupied dens and unoccupied crevices, and at five artificial dens. There was a
271 total of 459 independent detection events—at least 15 minutes apart—of northern quolls
272 across all dens and crevices over the 2526 trap nights, ranging from 2 to 108 at occupied
273 dens, 0 to 28 at unoccupied crevices, and 0 to 40 at artificial dens. There was no significant
274 difference in the number of quoll detections between occupied dens and unoccupied crevices
275 (Figure S1), whereas occupied dens had more detections compared to artificial dens ($p < 0.05$,
276 $CI_{95\%}$: -2.71, -0.12) (Figure S1). There was also no significant difference in the number of
277 quoll detections between unoccupied crevices and artificial dens. Quolls at occupied dens
278 were regularly pictured entering and leaving the den cavity, often with young, whilst quolls at
279 unoccupied crevices and artificial dens were usually moving past or briefly inspecting the
280 crevice. Failed camera traps were removed from analysis with one each at occupied dens and
281 unoccupied crevices, and three at artificial dens. Relative visitation rates of northern quolls
282 were corrected for trap nights.

283

284 **3.2 Thermal properties**

285 Temperatures outside all den types fluctuated more widely than inside (Figure 2a, b). During
286 spring, there were higher peak mean temperatures of $\sim 42^{\circ}\text{C}$ - 45°C externally, compared to
287 $\sim 33^{\circ}\text{C}$ - 36°C internally, and lower mean temperatures of $\sim 22^{\circ}\text{C}$ - 24°C externally, compared to
288 $\sim 29^{\circ}\text{C}$ - 32°C internally (Figure 2a). Occupied dens were on average significantly cooler

289 internally and externally compared to unoccupied crevices, but did not differ significantly
290 from artificial dens (Table S4). Trends during summer showed similar patterns to spring,
291 albeit at higher temperatures (Figure 2b). Unoccupied crevices were significantly warmer
292 than occupied dens, while artificial dens resembled occupied den temperatures internally
293 throughout the day, with no significant differences in average temperature (Table S4; Figure
294 2a; b). Humidity at all den types was also less variable inside the cavity than outside (Figure
295 2c). External humidity was higher during the night (~60%) than internal humidity (~40%)
296 (Figure 2c). Internal and external humidity did not differ significantly among den types
297 (Table S4). Time of day was a significant predictor of temperature and humidity at all den
298 types and in all seasons (Table S5).

299

300 **3.3 Physical properties**

301 Occupied dens were significantly deeper than both unoccupied crevices and artificial dens
302 (Table S6; Figure 3c). There was no significant difference in entrance height, entrance width
303 or number of entrances among den types (Table S6; Figure 3a,b,d). Occupied dens had
304 significantly less bare ground and significantly more cover of *Triodia* spp. and grass/herb
305 compared to artificial dens (Table S6; Figure 3f-h). There was no difference in ground cover
306 between occupied dens and unoccupied crevices (Table S6; Figure 3e-l). Embedded rock
307 cover was significantly higher at occupied dens compared to artificial dens, with artificial
308 dens having no embedded rock at any sites (Table S6; Figure 3i). Artificial dens had no
309 difference in cover of *Triodia* spp. and grass/herb, but concrete artificial dens had less rock
310 and more bare ground compared to rock artificial dens (Table 8). Occupied dens had a
311 significantly lower percentage of rock <0.5 m in diameter compared to artificial dens (Table
312 S6; Figure 3j). Percentage of 0.5–2 m and >2 m rock was not significantly different among
313 den types (Table S6; Figure 3k,l).

314

315 **3.4 Quoll interactions with predators and prey**

316 Over 2526 total trap nights, there were 150 independent feral cat detections on 87 trap nights
317 at five occupied dens, three unoccupied crevices, and four artificial dens. Of the dens and
318 crevices visited by feral cats, occupied dens and unoccupied crevices had a range of 1 to 2
319 and an average of 1 individual cat per den, while artificial dens had a range of 1 to 3 and an
320 average of 2 individual cats per den. Feral cats were recorded exploring the entrances of two
321 occupied dens and one artificial den at similar times to which northern quolls were using it
322 (Figure S2). Relative feral cat visitation (corrected for trap nights) did not differ between
323 occupied dens and unoccupied crevices, however feral cat visitation was significantly lower
324 at occupied dens than at artificial dens (Table S7; Figure 4a). This difference however, was
325 driven by an outlier: an artificial den with >100 independent detections. Images showed a
326 feral cat entering and existing the den with kittens, suggesting that the den may have been
327 used for rearing young (Figure S2). Northern quolls were most active at night and feral cats
328 were most active in the early morning. At occupied dens, feral cats were active for longer,
329 with activity only decreasing between approximately 9:00 am and 12:00 pm (Figure 5b).
330 Northern quolls and feral cats were more likely to be active at similar times at occupied dens,
331 compared to unoccupied crevices (Figure 5c) and artificial dens (Figure 5d): activity overlap
332 was highest at occupied dens (0.69, CI_{95%}:0.46, 0.82), followed by unoccupied crevices (0.53,
333 CI_{95%}:0.19, 0.69), and artificial dens (0.20, CI_{95%}:0.17, 0.36) (Figure 5a).

334

335 Mammal prey detections did not differ significantly between occupied dens and unoccupied
336 crevices, but there were significantly more mammal prey detections at occupied dens
337 compared to artificial dens (Table S7; Figure 4b). Over 5631 total trap nights, the common
338 rock rat (*Zygomys argurus*) was the most common mammal prey detected (93 detections;

339 Table S3). Reptile prey detections were significantly lower at occupied dens compared to
340 unoccupied crevices, with no difference at artificial dens (Table S7; Figure 4c). Rock style
341 artificial dens had one site that detected northern quolls and three sites that detected feral
342 cats, while concrete style artificial dens had three sites that detected feral cats and one site
343 that detected northern quolls. There were 614 detections of birds across all den types (Table
344 S3), with significantly more bird prey detections at occupied dens, compared to unoccupied
345 crevices, and no difference compared to artificial dens (Table S7; Figure 4d).

346

347 **4. Discussion**

348 Artificial refuges are used across the world to restore animal populations and offset habitat
349 loss, yet few studies have measured how closely they replicate natural refuges (Ebrahimi et
350 al. 2012; Griffiths et al. 2018). Here, we found that dens occupied by northern quolls were
351 cooler and deeper than unoccupied crevices. Artificial dens constructed for northern quolls
352 closely replicated the thermal environments of occupied dens, but differed in other important
353 aspects, including being shallower in depth, having less complex surrounding habitat
354 structure, having a greater visitation of feral cats, and having fewer available potential
355 mammal prey than occupied dens. This study shows the importance of considering the many
356 factors that comprise natural habitat when constructing artificial refuges, the value of
357 naturally occurring habitat, and the complexity of recreating it to a standard that is
358 ecologically functional.

359

360 **4.1 Thermal properties**

361 A key challenge in the construction of artificial refuges is to closely replicate the thermal
362 environments of natural refuges (Rowland et al. 2017; Griffiths et al. 2018), because natural
363 refuges often have specific thermal properties that are critical for their inhabitants, such as

364 internal temperatures that are more stable than the external climate (O'Connell and Keppel,
365 2016). Artificial refuges that fail to replicate natural conditions can expose animals to thermal
366 stress (Griffiths et al. 2018). For instance, evaporative heat loss of arboreal mammals needs
367 to be 1.5 to 2.4 times higher in nest boxes than natural hollows during summer to avoid
368 overheating, which could lead to dehydration (Rowland et al. 2017). In arid and semi-arid
369 regions, it is particularly important for refuges to buffer high external temperatures and
370 maintain humidity to avoid mortality of the animals inside (Gardner et al. 2015). Ambient
371 temperatures near dens and crevices far exceeded the temperatures at which quolls must
372 increase physiological cooling through evaporative heat loss ($\sim 36^{\circ}\text{C}$), and regularly reached
373 lethal temperatures (i.e., $>41^{\circ}\text{C}$) (Cooper and Withers, 2010). In our study, temperatures
374 inside crevices of all types were cooler and all den types had more stable internal temperature
375 and humidity profiles compared to the outside air. However, occupied northern quoll dens
376 were cooler-still compared to nearby, unoccupied crevices, suggesting that they—like many
377 animals (Scheffers et al. 2014; Isaac et al. 2008; Reside et al. 2019)—select dens that offer
378 additional thermal buffering, presumably to reduce the time spent at stressful temperatures
379 within the refuge (O'Connell and Keppel, 2016). In contrast to unoccupied crevices, artificial
380 dens closely matched the thermal properties of occupied dens. Like occupied dens, artificial
381 dens remained below the thermal stress range for longer and during a greater range of
382 ambient temperatures. This finding is important and implies that—contrary to our
383 predictions, and despite quite specific den selection by northern quolls—artificial dens can
384 provide a suitable thermal environment, potentially allowing quolls to survive and rear young
385 in areas they otherwise could not.

386

387 **4.2 Physical properties**

388 Despite offering similar thermal environments, artificial dens differed from occupied dens in
389 important ways. First, as predicted, occupied dens were deeper than both unoccupied crevices
390 and artificial dens, suggesting that quolls seek crevices with long, internal tunnels. Deep dens
391 are important for the survival of other species in the family *Dasyuridae*, such as the yellow-
392 footed antechinus (*Antechinus flavipes*), which uses deep dens to avoid fire and extreme
393 temperatures (Matthews et al. 2017). Failing to account for internal den dimensions when
394 constructing artificial refuges can lead to negative outcomes, such as enhanced predation risk
395 (Ebrahimi et al. 2012). Shallow artificial dens could expose quolls to a higher predation risk
396 from feral cats, or limit opportunities for behavioural thermoregulation during extreme heat
397 (Briscoe et al. 2014).

398

399 It is reassuring that artificial dens are similar to occupied dens in all other den dimensions
400 (entrance height and width, number of entrances), given den entrances that exclude larger
401 predators can be crucial for the protection of animals and their young (Cockle et al. 2015; Le
402 Roux et al. 2016). Similarly, more den entrances can increase the number of escape routes
403 from predators and create a range of microhabitats within a den (Gaylard and Kerley, 2001;
404 Frafjord, 2003). Artificial refuges that mimic the dimensions of natural refuges can provide
405 suitable shelter for animals (Bolton et al. 2004; Ebrahimi et al. 2012; Sherley et al. 2012), and
406 we found that the artificial dens currently used for northern quolls at least partially fulfill these
407 requirements.

408

409 The environmental context surrounding potential refuges can also influence whether they will
410 be used or not (McElhinny et al. 2006; Bhattacharyya et al. 2015; Reside et al. 2019). Many
411 animals often select natural refuges close to important resources that provide protection,
412 temperature regulation, or food (Croak et al. 2012; Bretscher et al. 2018). Northern quolls in

413 the Pilbara often inhabit complex rocky habitat, likely because it provides protection from
414 predation (Cook, 2010; Hernandez-Santin et al. 2016) and fire (Burrows et al. 2009), and
415 often contains temporary ponds and sheltered crevices (Radford et al. 2015; Henneron et al.
416 2019). Artificial dens in our study area were usually placed in open, flat landscapes, with a
417 history of disturbance—characteristics that have been shown to negatively affect refuge use
418 in other species (Lalas et al. 1999; McGregor et al. 2014). As predicted, we found areas
419 surrounding artificial dens lacked important habitat complexity; they were characterised by
420 less embedded rock, *Triodia* cover, and herbaceous vegetation, and had more small rocks and
421 bare ground. To improve environmental context surrounding artificial dens, further long-term
422 research should focus on the capacity of artificial landscapes to recover over time through
423 both active restoration and on their own, to avoid placing dens in habitat that may never be
424 suitable.

425

426 Restoring habitat complexity is often a focus of ecological restoration at disturbed sites,
427 particularly following mining activities (Nichols and Nichols, 2003; Shackelford et al. 2018).
428 Active restoration (e.g. revegetation, placement of logs, debris, and rock piles) following
429 habitat loss can improve population connectivity and movement patterns for other species,
430 including the closely related chuditch (*Dasyurus geoffroii*; McGregor et al. 2014). Female
431 northern quolls have a relatively small home range (~35 ha; Oakwood, 2002), and for this
432 reason—depending on the aim of the artificial refuges (i.e. habitat connectivity *cf.*
433 relocation)—the distance that artificial dens are placed from natural habitat is important.
434 Currently, it is unknown how the distance from natural habitat affects the use of artificial
435 dens by northern quolls.

436

437 **4.3 Quoll interactions with predators and prey**

438 Many studies have shown that the use of artificial refuges are linked to their attractiveness to
439 predators (e.g. Anderson et al. 2016; Patterson et al. 2016). One of Australia's most
440 successful introduced predators, the feral cat, often prefers open habitats (McGregor et al.
441 2015; Hernandez-Santin et al. 2016; Hohnen et al. 2016; McDonald et al. 2016; Pavey et al.
442 2017). Therefore, we expected them to show a preference for artificial dens. Consistent with
443 this, we found feral cats visited artificial dens more often than occupied dens, and we
444 observed direct evidence of cats searching an artificial den that contained young quolls
445 (Figure S2). Furthermore, camera trap images showed evidence of feral cats using at least
446 one artificial den to raise their young. Regular visitation of artificial dens by feral cats,
447 combined with their increased hunting efficiency in open, simple environments (McGregor et
448 al. 2015), means that artificial dens may have a heightened predation risk for northern quolls.

449

450 It is possible that, in some instances, artificial dens could act as ecological traps for northern
451 quolls: habitats that are selected by animals because they appear high quality (e.g. having
452 thermally suitable crevices) but are in fact maladaptive as they decrease fitness or increase
453 mortality risk (Battin, 2004). This reinforces the importance of creating (or maintaining)
454 structurally complex habitats around artificial dens, to create less preferable habitat for cats.
455 These findings, including observations of feral cat breeding within an artificial den, also
456 highlight the importance of tailoring den dimensions (e.g., depth, entrance width) such that
457 they exclude predators both from predated upon quolls within dens and using dens for their
458 own recruitment (e.g. Bailey and Bonter, 2017). One possible reprieve for quolls is that cat
459 and quoll activity overlap was lowest at artificial dens, suggesting a reduced probability of
460 animals encountering one another outside of the den. However, high overlap at occupied dens
461 may indicate cats are tracking quolls to their dens and synchronising their activity to increase

462 the probability of an encounter: dasyurids are most abundant in feral cat diet throughout the
463 Pilbara region and adjacent deserts (Murphy et al. 2019). We cannot discount that—should
464 artificial dens become regularly occupied by quolls—it is possible that such temporal
465 tracking of quolls by cats could occur at artificial dens as well.

466

467 The lack of potential mammal prey at artificial dens is important, as small marsupials and
468 rodents can make up a large portion of northern quoll diet (Dunlop et al. 2017), and predators
469 often use habitat based on the availability of prey (Gallant et al. 2014; Khalatbari et al. 2018;
470 Rabelo et al. 2019). The most commonly recorded mammal prey in this study was the
471 common rock-rat (*Zygomys argurus*), which is a favoured food item for northern quolls
472 (Dunlop et al. 2016). Rock-rats feed mainly on seeds, stems, leaves, and fruit of *Ficus* spp.
473 (Begg and Dunlop, 1985; Nano et al. 2003), and are often associated with rock complexity,
474 grasses, and plants that produce seeds (e.g. *Triodia* spp.) (Begg, 1981; Trainor et al. 2000;
475 Radford, 2012). A lack of appropriate habitat in the form of rocky cover, *Triodia* cover, and
476 other herbaceous plants may therefore explain rock-rat absences at artificial dens. Restoring
477 habitat complexity and vegetation around artificial dens may help to attract small mammals
478 like common rock-rats and increase the availability of mammal prey for northern quolls.
479 There is scope for future research to focus on the best practice of restoring habitat complexity
480 for the benefit of northern quolls and their prey, particularly revegetation and the availability
481 of multiple crevices in the artificial landscape.

482

483 **5. Implications and conclusion**

484 The role of artificial refuges in conservation has expanded with the need to ‘offset’
485 environmental damage caused by industry (Maron et al. 2012). Offsets seek to compensate
486 for the environmental costs of human actions, such as mining or urban development, by

487 creating equivalent environmental gains elsewhere (Miller et al. 2015). If artificial refuges do
488 not closely replicate natural refuges, and are therefore not used by target species, they are
489 likely to fail to offset ecological damage (Lindenmayer et al. 2017).

490

491 Providing refuge alone is unlikely to ensure that a species will occupy and breed within it;
492 animals require other resources to survive and reproduce (Croak et al. 2012; Reside et al.
493 2019). At present, artificial dens built for northern quolls provide climatic and structural
494 properties similar to those at occupied dens, but lack other vital habitat characteristics. While
495 currently used materials seem suitable for artificial den construction, deeper dens would
496 provide further protection from extreme temperature, predation, and fire. By improving
497 active restoration efforts surrounding artificial dens, practitioners may decrease the visitation
498 of feral cats, and increase the availability of mammal prey, but this remains to be
499 demonstrated. Placing artificial dens inside existing or minimally disturbed habitat may be an
500 efficient solution to address such issues, but this depends on the overall aim of the artificial
501 refuges (e.g., to increase population size *cf.* the extent of occurrence) and will be location-
502 dependent. If the installation of artificial denning habitat seeks to offset habitat lost during
503 mining, then it must be understood that mining results not only in the loss of dens, but also
504 the modification of the broader environment, including food resources, habitat structure, and
505 predator-prey relationships. We therefore emphasise the value and complexity of quality
506 habitat for native species, and the difficulty of completely replicating ecosystem function.

507 **Acknowledgements**

508 We thank Colin and Betty Brierly, Roy Hill, De Grey Mining, Fortescue Metals Group, Atlas
509 Iron, Stephen van Leeuwen, Harriet Davie, Bruce Turner, and Debra Noy for their support,
510 and Allison Matthews and Ian Radford for their helpful comments. This study was funded by
511 the Department of Biodiversity, Conservation and Attractions (DBCA), Roy Hill, the Charles
512 Sturt University Faculty of Science, and the Institute for Land, Water and Society. All animal
513 capture and handling was undertaken with ethics approval from Charles Sturt University, and
514 research permits from the DBCA. This study took place primarily on Kariyarra and Nyamal
515 country.

516 **References**

- 517 Anderson, C. J., Hostetler, M. E., Sieving, K. E. & Johnson, S. A. (2016). Predation of
 518 artificial nests by introduced rhesus macaques (*Macaca mulatta*) in Florida, USA.
 519 *Biological Invasions*, 18, 2783-2789.
- 520 Bailey, R. L. & Bonter, D. N. (2017). Predator guards on nest boxes improve nesting success
 521 of birds. *Wildlife Society Bulletin*, 41, 434-441.
- 522 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects
 523 Models Using lme4. *Journal of Statistical Software*, 67, 1-48.
- 524 Battin, J. 2004. When Good Animals Love Bad Habitats: Ecological Traps and the
 525 Conservation of Animal Populations. *Conservation Biology*, 18, 1482-1491.
- 526 Begg, R. J. (1981). The Small Mammals of Little Nourlangie Rock, N.T IV. Ecology of
 527 *Zyzyomys woodwardi*, the Large Rock-rat, and *Z. argurus*, the Common Rock-rat,
 528 (Rodentia: Muridae). *Wildlife Research*, 8, 307-320.
- 529 Begg, R. J. & Dunlop, C. J. (1985). The Diets of the Large Rock-Rat, *Zyzyomys Woodwardi*,
 530 and the Common Rock-Rat, *Z. Argurus* (Rodentia: Muridae). *Wildlife Research*, 12,
 531 19-24.
- 532 Bhattacharyya, S., Dutta, S., Adhikari, B. S. & Rawat, G. S. (2015). Presence of a small
 533 mammalian prey species in open habitat is dependent on refuge availability. *Mammal*
 534 *Research*, 60, 293-300.
- 535 Bolton, M., Medeiros, R., Hothersall, B. & Campos, A. (2004). The use of artificial breeding
 536 chambers as a conservation measure for cavity-nesting procellariiform seabirds: a
 537 case study of the Madeiran storm petrel (*Oceanodroma castro*). *Biological*
 538 *Conservation*, 116, 73-80.
- 539 Braithwaite, R. W. & Griffiths, A. D. (1994). Demographic variation and range contraction in
 540 the northern quoll, *Dasyurus hallucatus*. *Wildlife Research*, 21, 203-217.
- 541 Bretscher, A., Dittel, J. W., Lambert, T. D. & Adler, G. H. (2018). Habitat structure
 542 influences refuge use by two sympatric species of Neotropical forest rodents. *Journal*
 543 *of Mammalogy*, 99, 1465-1471.
- 544 Briscoe, N. J., Handasyde, K. A., Griffiths, S., Porter, W. P., Krockenberger, A. & Kearney,
 545 M. R. (2014). Tree-hugging koalas demonstrate a novel thermoregulatory mechanism
 546 for arboreal mammals. *Biology Letters*, 10.
- 547 Brook, L. A., Johnson, C. N. & Ritchie, E. G. (2012). Effects of predator control on
 548 behaviour of an apex predator and indirect consequences for mesopredator
 549 suppression. *Journal of Applied Ecology*, 49, 1278-1286.
- 550 Burbidge, A. A. & McKenzie, N. L. (1989). Patterns in the modern decline of western
 551 Australia's vertebrate fauna: Causes and conservation implications. *Biological*
 552 *Conservation*, 50, 143-198.
- 553 Bureau of Meteorology. (2018). *Climate Data Online* [Online]. Available:
 554 http://www.bom.gov.au/climate/averages/tables/cw_004032.shtml [Accessed 30 July
 555 2018].
- 556 Burrows, N. D., Ward, B. & Robinson, A. (2009). Fuel dynamics and fire spread in spinifex
 557 grasslands of the Western Desert. *Proceedings of the Royal Society of Queensland*,
 558 *The*, 115, 69.
- 559 Cockle, K. L., Bodrati, A., Lammertink, M. & Martin, K. (2015). Cavity characteristics, but
 560 not habitat, influence nest survival of cavity-nesting birds along a gradient of human
 561 impact in the subtropical Atlantic Forest. *Biological Conservation*, 184, 193-200.
- 562 Cook, A. (2010). *Habitat use and home-range of the northern quoll, Dasyurus hallucatus:*
 563 *effects of fire*. The University of Western Australia.

564 Cooper, C. & Withers, P. (2010). Comparative physiology of Australian quolls (*Dasyurus*;
565 Marsupialia). *Journal of Comparative Physiology. B, Biochemical, Systemic, and*
566 *Environmental Physiology*, 180, 857-868.

567 Cramer, V. A., Dunlop, J., Davis, R. A., Ellis, R., Barnett, B., Cook, A., Morris, K. & Van
568 Leeuwen, S. (2016). Research priorities for the northern quoll (*Dasyurus hallucatus*)
569 in the Pilbara region of Western Australia. *Australian Mammalogy*, 38, 135-148.

570 Crawley, M. J. (2012). Proportion Data. *The R Book*.

571 Croak, B. M., Pike, D. A., Webb, J. K. & Shine, R. (2010). Using Artificial Rocks to Restore
572 Nonrenewable Shelter Sites in Human-Degraded Systems: Colonization by Fauna.
573 *Restoration Ecology*, 18, 428-438.

574 Croak, B. M., Pike, D. A., Webb, J. K. & Shine, R. (2012). Habitat Selection in a Rocky
575 Landscape: Experimentally Decoupling the Influence of Retreat Site Attributes from
576 That of Landscape Features. *PLOS ONE*, 7.

577 Croak, B. M., Webb, J. K. & Shine, R. (2013). The benefits of habitat restoration for rock-
578 dwelling velvet geckos *Oedura lesueurii*. *Journal of Applied Ecology*, 50, 432-439.

579 Dervo, K. B., Museth, J. & Skurdal, J. (2018). Assessing the Use of Artificial Hibernacula by
580 the Great Crested Newt (*Triturus cristatus*) and Smooth Newt (*Lissotriton vulgaris*) in
581 Cold Climate in Southeast Norway. *Diversity*, 10.

582 Diete, R. L., Meek, P. D., Dixon, K. M., Dickman, C. R. & Leung, L. K. P. (2016). Best bait
583 for your buck: bait preference for camera trapping north Australian mammals.
584 *Australian Journal of Zoology*, 63, 376-382.

585 Dunlop, J., Rayner, K. & Doherty, T. S. (2017). Dietary flexibility in small carnivores: a case
586 study on the endangered northern quoll, *Dasyurus hallucatus*. *Journal of Mammalogy*,
587 98, 858.

588 Ebrahimi, M., Fenner, A. & Bull, C. (2012). Lizard behaviour suggests a new design for
589 artificial burrows. *Wildlife Research*, 39, 295-300.

590 Environmental Protection Authority (2014). Cumulative environmental impacts of
591 development in the Pilbara region.

592 Fancourt, B. A., Hawkins, C. E., Cameron, E. Z., Jones, M. E. & Nicol, S. C. (2015). Devil
593 Declines and Catastrophic Cascades: Is Mesopredator Release of Feral Cats Inhibiting
594 Recovery of the Eastern Quoll? *PLOS ONE*, 10.

595 Frafjord, K. (2003). Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition
596 overtaken by interspecific competition? *Biological Conservation*, 111, 445-453.

597 Françoso, R. D., Brandão, R., Nogueira, C. C., Salmons, Y. B., Machado, R. B. & Colli, G.
598 R. (2015). Habitat loss and the effectiveness of protected areas in the Cerrado
599 Biodiversity Hotspot. *Natureza & Conservação*, 13, 35-40.

600 Gallant, D., Reid, D. G., Slough, B. G. & Berteaux, D. (2014). Natal den selection by
601 sympatric arctic and red foxes on Herschel Island, Yukon, Canada. *Polar Biology*, 37,
602 333-345.

603 Gardner, J. L., Amano, T., Sutherland, W. J., Clayton, M. & Peters, A. (2015). Individual and
604 demographic consequences of reduced body condition following repeated exposure to
605 high temperatures. *Ecology*.

606 Gaylard, A. & Kerley, G. I. H. (2001). Habitat assessment for a rare, arboreal forest mammal,
607 the tree hyrax *Dendrohyrax arboreus*. *African Journal of Ecology*, 39, 205-212.

608 Goldingay, R. L., Thomas, K. J. & Shanty, D. (2018). Outcomes of decades long installation
609 of nest boxes for arboreal mammals in southern Australia. *Ecological Management &*
610 *Restoration*, 19, 204-211.

611 Griffiths, S., Lentini, P., Semmens, K., Watson, S., Lumsden, L. & Robert, K. (2018).
612 Chainsaw-Carved Cavities Better Mimic the Thermal Properties of Natural Tree
613 Hollows than Nest Boxes and Log Hollows. *Forests*, 9.

- 614 Griffiths, S., Rowland, J. A., Briscoe, N. J., Lentini, P., Handasyde, K. A., Lumsden, L. F. &
615 Robert, K. A. (2017). Surface reflectance drives nest box temperature profiles and
616 thermal suitability for target wildlife. *PLOS ONE*, 12
- 617 Haslem, A., Avitabile, S. C., Taylor, R. S., Kelly, L. T., Watson, S., Nimmo, D. G., Kenny,
618 S. A., Callister, K. E., Spence-Bailey, L. M., Bennett, A. F. & Clarke, M. F. (2012).
619 Time-since-fire and inter-fire interval influence hollow availability for fauna in a fire-
620 prone system. *Biological Conservation*, 152, 212-221.
- 621 Henneron, L., Sarthou, C., De Massary, J.C. & Ponge, J.F. (2019). Habitat diversity
622 associated to island size and environmental filtering control the species richness of
623 rock-savanna plants in neotropical inselbergs. *Ecography*.
- 624 Hernandez-Santin, L., Goldizen, A. W. & Fisher, D. O. (2016). Introduced predators and
625 habitat structure influence range contraction of an endangered native predator, the
626 northern quoll. *Biological Conservation*, 203, 160-167.
- 627 Hofmeester, T. R., Rowcliffe, J. M. & Jansen, P. A. (2017). A simple method for estimating
628 the effective detection distance of camera traps. *Remote Sensing in Ecology and
629 Conservation*, 3, 81-89.
- 630 Hohnen, R., Tuft, K., Legge, S., Walters, N., Johanson, L., Carver, S., Radford, I. J. &
631 Johnson, C. N. (2016). The significance of topographic complexity in habitat
632 selection and persistence of a declining marsupial in the Kimberley region of Western
633 Australia. *Australian Journal of Zoology*, 64, 198-216.
- 634 Ibbett, M., Woinarski, J. C. Z. & Oakwood, M. (2018). Declines in the mammal assemblage
635 of a rugged sandstone environment in Kakadu National Park, Northern Territory,
636 Australia. *Australian Mammalogy*, 40, 181-187.
- 637 Isaac, J. L., De Gabriel, J. L. & Goodman, B. A. (2008). Microclimate of daytime den sites in
638 a tropical possum: implications for the conservation of tropical arboreal marsupials.
639 *Animal Conservation*, 11, 281-287.
- 640 Keppers, J. L., Skoruppa, M. K. & Hickman, G. C. (2008). Use of artificial burrows by
641 Western Burrowing Owls and other vertebrates during winter in southern Texas.
642 *Bulletin of the Texas Ornithological Society*, 41, 59-64.
- 643 Khalatbari, L., Yusefi, G. H., Martínez-Freiría, F., Jowkar, H. & Brito, J. C. (2018).
644 Availability of prey and natural habitats are related with temporal dynamics in range
645 and habitat suitability for Asiatic Cheetah. *Hystrix, the Italian Journal of
646 Mammalogy*, 29, 145-151.
- 647 Krockenberger, A. K., Edwards, W. & Kanowski, J. (2012). The limit to the distribution of a
648 rainforest marsupial folivore is consistent with the thermal intolerance hypothesis.
649 *Oecologia*, 168, 889-899.
- 650 Lalas, C., Jones, P. & Jones, J. (1999). The design and use of a nest box for Yellow-eyed
651 Penguins *Megadyptes antipodes* - a response to a conservation need. In: Lalas, C.,
652 Brossy, J. J., Cooper, J., Crawford, R., Klages, N. & Shannon, L. (eds.).
- 653 Lawrence, P. J., Smith, G. R., Sullivan, M. J. P. & Mossman, H. L. (2018). Restored
654 saltmarshes lack the topographic diversity found in natural habitat. *Ecological
655 Engineering*, 115, 58-66.
- 656 Le Roux, D. S., Ikin, K., Lindenmayer, D., Bistricher, G., Manning, A. D. & Gibbons, P.
657 (2016). Effects of entrance size, tree size and landscape context on nest box
658 occupancy: Considerations for management and biodiversity offsets. *Forest Ecology
659 and Management*, 366, 135-142.
- 660 Lindenmayer, D., Crane, M., Evans, M., Maron, M., Gibbons, P., Bekessy, S. & Blanchard,
661 W. (2017). The anatomy of a failed offset. *Biological Conservation*, 210, 286-292.
- 662 Maron, M., Hobbs, R. J., Moilanen, A., Matthews, J. W., Christie, K., Gardner, T. A., Keith,
663 D. A., Lindenmayer, D. & Mcalpine, C. A. (2012). Faustian bargains? Restoration

- 664 realities in the context of biodiversity offset policies. *Biological Conservation*, 155,
665 141-148.
- 666 Matthews, J. K., Stawski, C., Körtner, G., Parker, C. A. & Geiser, F. (2017). Torpor and
667 basking after a severe wildfire: mammalian survival strategies in a scorched
668 landscape. *Journal of comparative physiology.*, 187, 385-393.
- 669 McDonald, P. J., Stewart, A., Schubert, A. T., Nano, C. E. M., Dickman, C. R. & Luck, G.
670 W. (2016). Fire and grass cover influence occupancy patterns of rare rodents and feral
671 cats in a mountain refuge: implications for management. *Wildlife Research*, 43, 121-
672 129.
- 673 McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2006). Fauna-habitat relationships: a
674 basis for identifying key stand structural attributes in temperate Australian eucalypt
675 forests and woodlands. *Pacific Conservation Biology*, 12, 89-110.
- 676 McGregor, H. W., Legge, S., Jones, M. E. & Johnson, C. N. (2015). Feral Cats Are Better
677 Killers in Open Habitats, Revealed by Animal-Borne Video. *PloS one*, 10.
- 678 McGregor, R. A., Stokes, V. L. & Craig, M. D. (2014). Does forest restoration in fragmented
679 landscapes provide habitat for a wide-ranging carnivore? *Animal Conservation*, 17,
680 467-475.
- 681 McKenzie, N. L., Van Leeuwen, S. & Pinder, A. M. (2009). Introduction to the Pilbara
682 Biodiversity Survey, 2002–2007. *Records of the Western Australian Museum*,
683 *Supplement*, 78.
- 684 Meredith, M. & Ridout, M. (2018). Overview of the overlap package.
- 685 Miller, K. L., Trezise, J. A., Kraus, S., Dripps, K., Evans, M. C., Gibbons, P., Possingham, H.
686 P. & Maron, M. (2015). The development of the Australian environmental offsets
687 policy: from theory to practice. *Environmental Conservation*, 42, 306-314.
- 688 Moore, H. A., Dunlop, J. A., Valentine, L. E., Woinarski, J. C. Z., Ritchie, E. G., Watson, D.
689 M. & Nimmo, D. G. (2019). Topographic ruggedness and rainfall mediate geographic
690 range contraction of a threatened marsupial predator. *Diversity and Distributions*,
691 10.1111/ddi.12982.
- 692 Murphy, B. P., Wooley, L.-A., Geyle, H. M., Legge, S. M., Palmer, R., Dickman, C. R.,
693 Augusteyn, J., Brown, S. C., Comer, S., Doherty, T. S., Eager, C., Edwards, G.,
694 Fordham, D. A., Harley, D., McDonald, P. J., McGregor, H., Moseby, K. E., Myers,
695 C., Read, J., Riley, J., Stokeld, D., Trewella, G. J., Turpin, J. M. & Woinarski, J. C. Z.
696 (2019). Introduced cats (*Felis catus*) eating a continental fauna: The number of
697 mammals killed in Australia. *Biological Conservation*, 237, 28-40.
- 698 Nano, T. J., Smith, C. M. & Jefferys, E. (2003). Investigation into the diet of the central rock-
699 rat (*Zyomys pedunculatus*). *Wildlife Research*, 30, 513-518.
- 700 Nichols, O. G. & Nichols, F. M. (2003). Long-Term Trends in Faunal Recolonization After
701 Bauxite Mining in the Jarrah Forest of Southwestern Australia. *Restoration Ecology*,
702 11, 261-272.
- 703 O'Connell, C. & Keppel, G. (2016). Deep tree hollows: important refuges from extreme
704 temperatures. *Wildlife Biology*, 22, 305-310.
- 705 Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus*
706 *hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of*
707 *Zoology*, 48, 519-539.
- 708 Oakwood, M. (2002). Spatial and social organization of a carnivorous marsupial *Dasyurus*
709 *hallucatus*. *Journal of Zoology*, 257, 237-248.
- 710 Oakwood, M. (2008). Northern Quoll *Dasyurus hallucatus*. In: VAN DYCK, S. &
711 STRAHAN, R. (eds.) *The Mammals of Australia*. 3 ed. Sydney: New Holland
712 Publishers (Australia) Pty Ltd.

713 Oakwood, M., Woinarski, J. C. Z. & Burnett, S. (2016). *Dasyurus hallucatus*. *The IUCN Red*
714 *List of Threatened Species 2016* [Online]. Available:
715 <http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T6295A21947321> [Accessed 13
716 January 2020].

717 Patterson, L., Kalle, R. & Downs, C. (2016). Predation of artificial bird nests in suburban
718 gardens of KwaZulu-Natal, South Africa. *Urban Ecosystems*, 19, 615-630.

719 Pavey, C. R., Addison, J., Brandle, R., Dickman, C. R., McDonald, P. J., Moseby, K. E. &
720 Young, L. I. (2017). The role of refuges in the persistence of Australian dryland
721 mammals. *Biological Reviews*, 92, 647-664.

722 Pollock, A. B. (1999). Notes on status, distribution and diet of Northern Quoll *Dasyurus*
723 *hallucatus* in the Mackay-Bowen area, mideastern Queensland. *Australian Zoologist*,
724 31, 388-395.

725 R Core Development Team (2013). R: A language and environment for statistical computing.

726 Rabelo, R. M., Aragon, S. & Bicca-Marques, J. C. (2019). Prey abundance drives habitat
727 occupancy by jaguars in Amazonian floodplain fluvial islands. *bioRxiv*.

728 Radford, I. J. (2012). Threatened mammals become more predatory after small-scale
729 prescribed fires in a high-rainfall rocky savanna. *Austral Ecology*, 37, 926-935.

730 Radford, I. J., Gibson, L. A., Corey, B., Carnes, K. & Fairman, R. (2015). Influence of Fire
731 Mosaics, Habitat Characteristics and Cattle Disturbance on Mammals in Fire-Prone
732 Savanna Landscapes of the Northern Kimberley. *PLOS ONE*, 10.

733 Ramanaidou, E. R. & Morris, R. C. (2010). A synopsis of the channel iron deposits of the
734 Hamersley Province, Western Australia. *Applied Earth Science*, 119, 56-59.

735 Rendall, A. R., Sutherland, D. R., Cooke, R. & White, J. (2014). Camera trapping: a
736 contemporary approach to monitoring invasive rodents in high conservation priority
737 ecosystems. *PloS one*, 9.

738 Reside, A. E., Briscoe, N. J., Dickman, C. R., Greenville, A. C., Hradsky, B. A., Kark, S.,
739 Kearney, M. R., Kutt, A. S., Nimmo, D. G., Pavey, C. R., Read, J. L., Ritchie, E. G.,
740 Roshier, D., Skroblin, A., Stone, Z., West, M. & Fisher, D. O. (2019). Persistence
741 through tough times: fixed and shifting refuges in threatened species conservation.
742 *Biodiversity and Conservation*, 28, 1303-1330.

743 Ridout, M. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera
744 trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322-
745 337.

746 Robinson, K. W. & Morrison, P. R. (1957). The reaction to hot atmospheres of various
747 species of Australian marsupial and placental animals. *J Cell Comp Physiol*, 49, 455-
748 478.

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

752 Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. & Evans, T. A. (2014).
753 Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*,
754 20, 495-503.

755 Shackelford, N., Miller, B. P. & Erickson, T. E. (2018). Restoration of Open-Cut Mining in
756 Semi-Arid Systems: A Synthesis of Long-Term Monitoring Data and Implications for
757 Management. *Land Degradation & Development*, 29, 994-1004.

758 Sherley, R. B., Barham, B. J., Barham, P. J., Leshoro, T. M. & Underhill, L. G. (2012).
759 Artificial nests enhance the breeding productivity of African Penguins (*Spheniscus*
760 *demersus*) on Robben Island, South Africa AU. *Emu - Austral Ornithology*, 112, 97-
761 106.

- 762 Trainor, C., Fisher, A., Woinarski, J. C. Z. & Churchill, S. (2000). Multiscale patterns of
763 habitat use by the Carpenterian rock-rat (*Zyzomys palatalis*) and the common rock-rat
764 (*Z. argurus*). *Wildlife Research*, 27, 319-332.
- 765 Trulio, A. T. (1995). Passive Relocation: A Method to Preserve Burrowing Owls on
766 Disturbed Sites. *Journal of Field Ornithology*, 66, 99-106.
- 767 Van Vreeswyk, A. M. E., Leighton, K. A., Payne, A. L. & Hennig, P. (2004). An inventory
768 and condition survey of the Pilbara region, Western Australia.
- 769 White, S., Briers, R. A., Bouyer, Y., Odden, J. & Linnell, J. D. C. (2015). Eurasian lynx natal
770 den site and maternal home-range selection in multi-use landscapes of Norway.
771 *Journal of Zoology*, 297, 87-98.
- 772 Woinarski, J. C. Z., Burbidge, A. & Harrison, P. (2014). *The action plan for Australian*
773 *mammals 2012*, CSIRO publishing.
- 774 Wood, S. & Scheipl, F. (2017). gamm4: Generalized Additive Mixed Models using ‘mgcv’
775 and ‘lme4’.
- 776 Zappalorti, R. (1994). Artificial refuge as a habitat improvement strategy for snake
777 conservation. In: Murphy, J. B., Collins, J. T. & Adler, K. (eds.) *Captive Management*
778 *and Conservation of Amphibians and Reptiles*. New York: Ithaca.
- 779 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects*
780 *models and extensions in ecology with R*, New York, Springer.

Figure legends

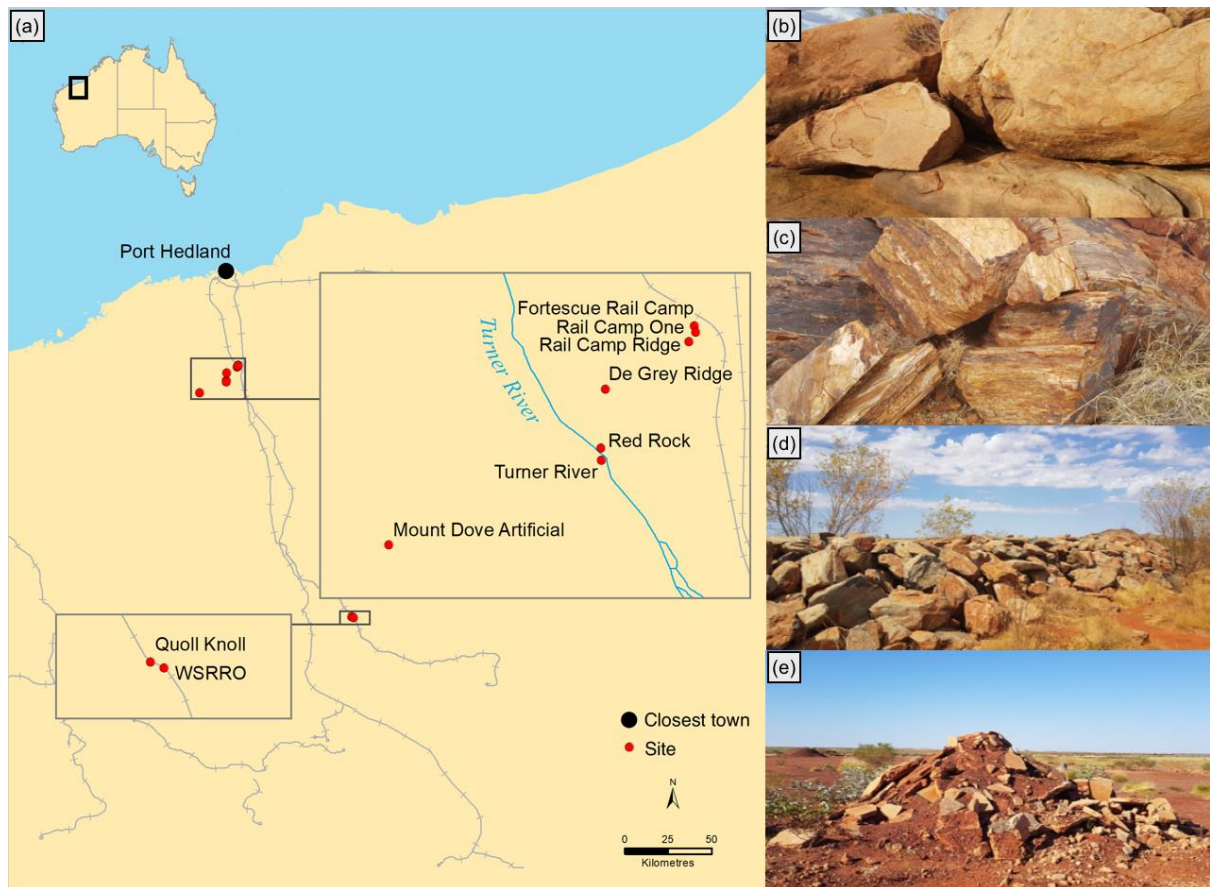


Figure 1: A map of the study sites (red dots) and the closest town (black dot) (a). The Turner River is shown in blue running between the Red Rock and Turner River sites and railways are grey lines. Den type examples: (b) occupied den at Turner River, (c) unoccupied crevice at De Grey Ridge, (d) rock-style artificial habitat at Mount Dove Artificial and (e) concrete and gravel style artificial habitat at Fortescue Rail Camp.

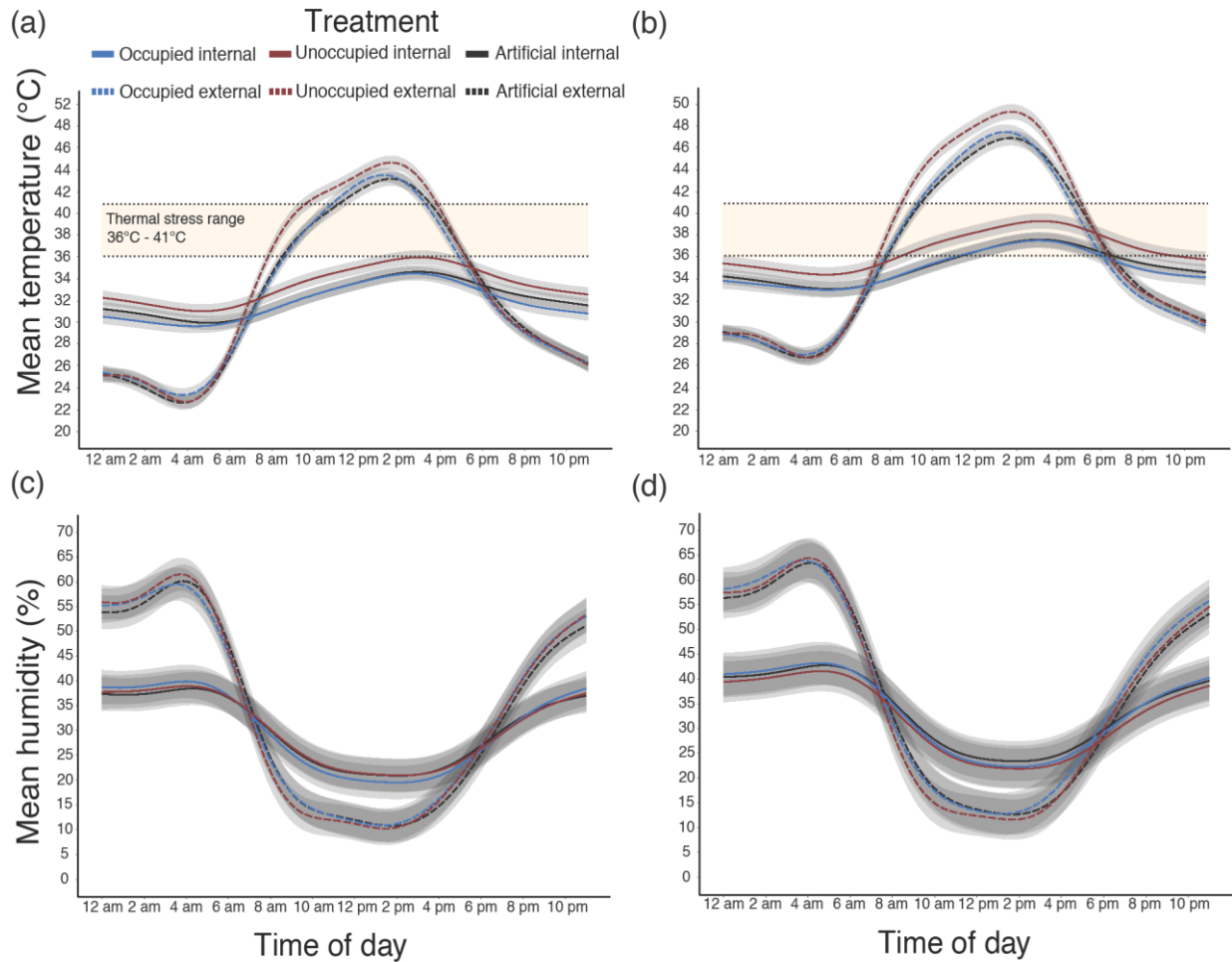


Figure 2: Predictions from Generalised Additive Mixed Models of internal and external daily temperature (°C) patterns for den types during (a) spring (October 2018 to November 2018) and (b) summer (December 2018 to January 2019), and internal and external daily relative humidity (%) patterns for den types during (c) spring and (d) summer. Blue lines represent occupied dens, maroon lines represent unoccupied crevices, black lines represent artificial dens, solid lines represent internal temperature or humidity, dashed lines represent external temperature or humidity, the thermal stress range is shown by the yellow bar with black dotted boundaries, grey shaded areas around treatment lines define 95% confidence intervals.

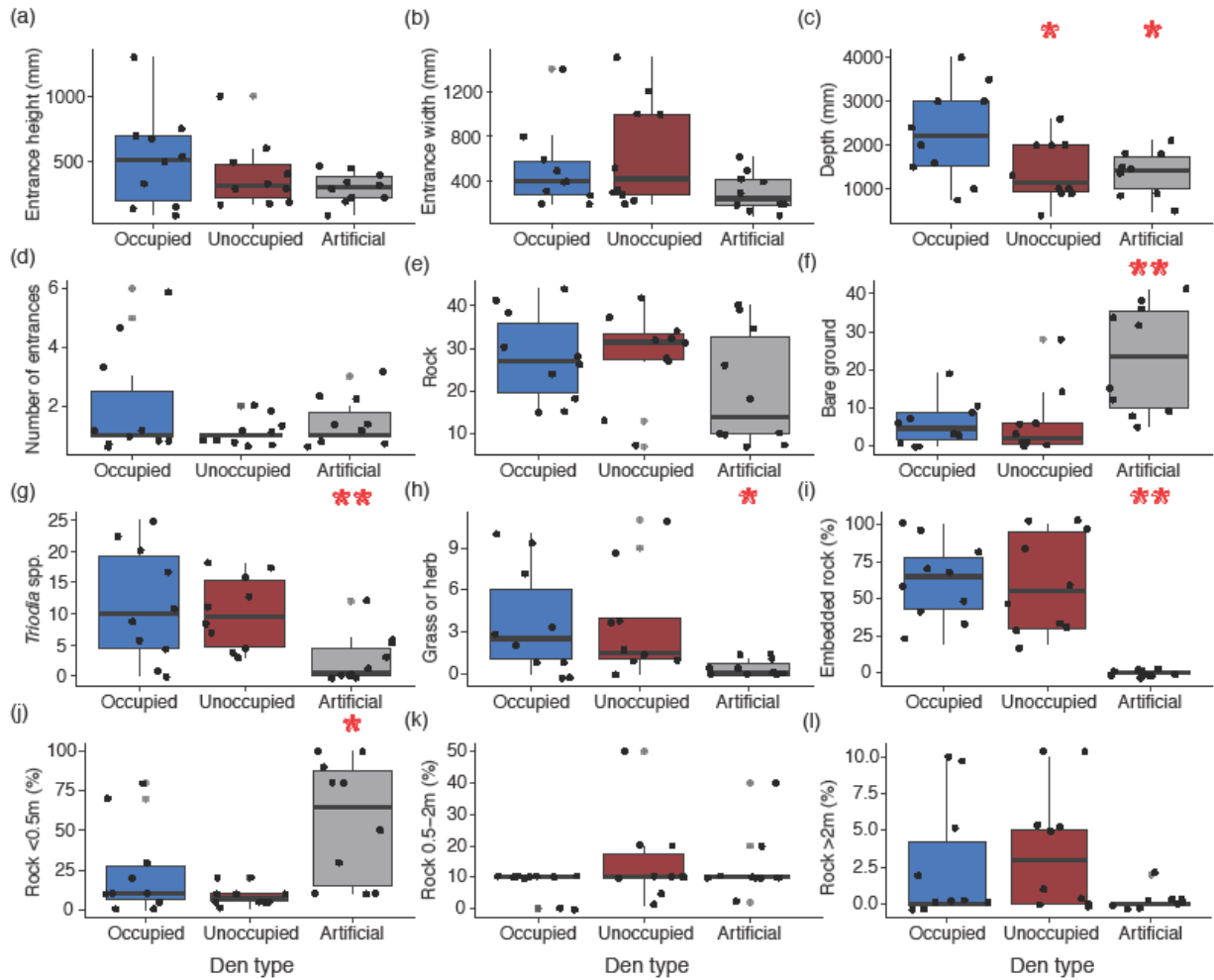


Figure 3: Physical and environmental properties of each den type, specifically: (a) entrance height (mm), (b) entrance width (mm), (c) depth (mm), (d) number of entrances, and cover of (e) rock, (f) bare ground, (g) *Triodia* spp., (h) grass/herb, (i) embedded rock, (j) rock < 0.5 m in diameter, (k) rock 0.5 - 2 m, and (l) rock > 2 m. Black dots represent data values, grey dots represent suspected outliers and red asterisks denote a significant difference from the intercept (occupied dens).

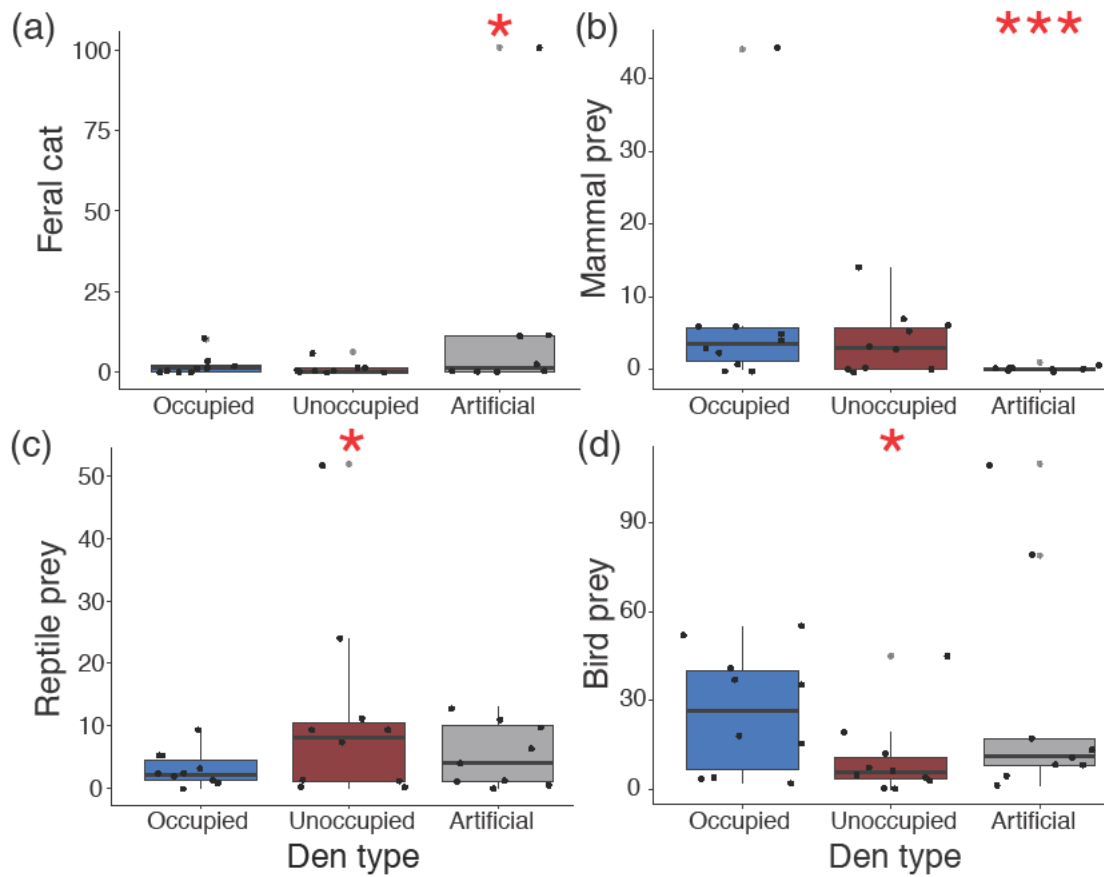


Figure 4: Relative visitation of (a) feral cats, (b) mammal prey, (c) reptile prey, and (d) bird prey corrected for trap nights at occupied dens (blue), unoccupied crevices (maroon) and artificial dens (grey), from October 2018 to January 2019. Black dots represent data values, grey dots represent suspected outliers and red asterisks denote a significant difference from the intercept (occupied dens).

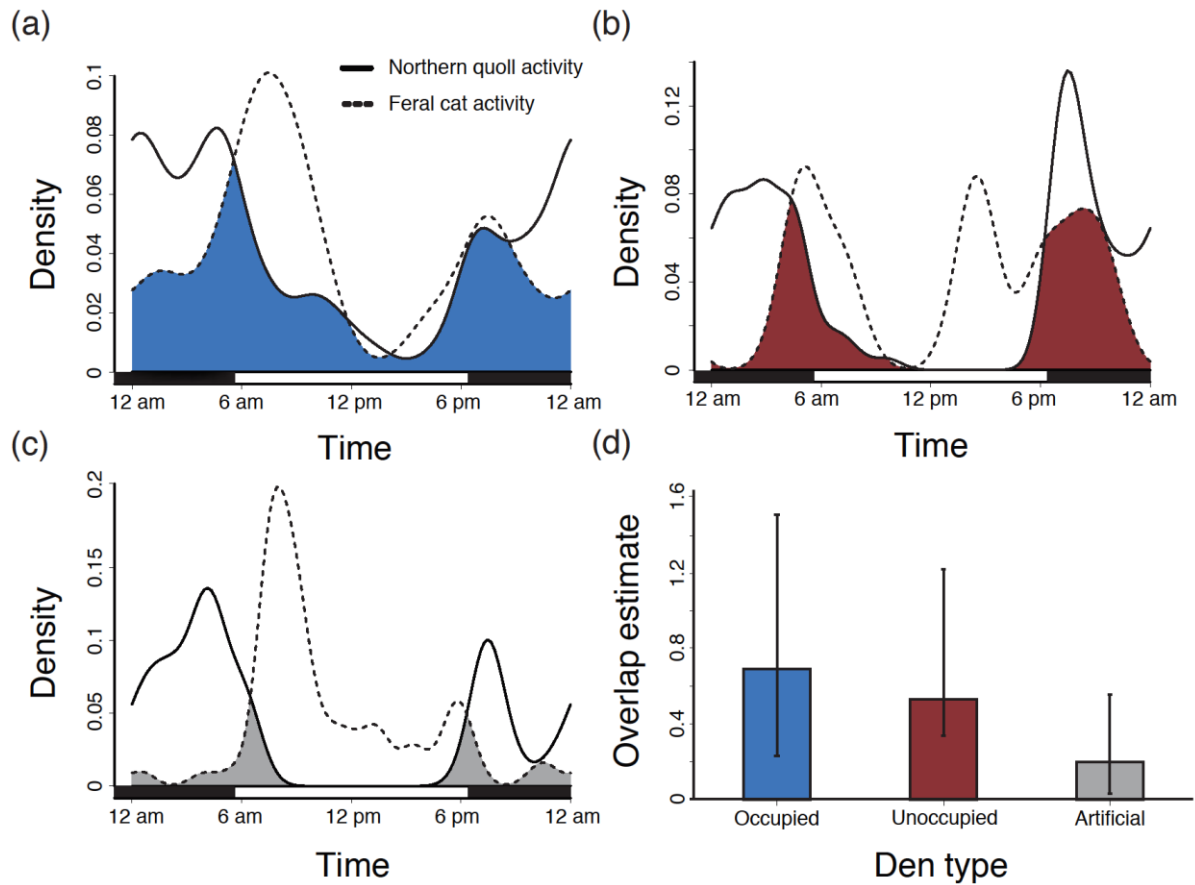


Figure 5: Activity patterns of northern quoll and feral cat activity (0=no overlap and 1=complete overlap), plotted against time of day at (b) occupied dens (blue), (c) unoccupied crevices (maroon) and (d) artificial dens (grey), from October 2018 to January 2019, as well as (d) temporal overlap estimates. Solid and dashed lines represent northern quoll and feral cat activity, respectively. For line graphs, coloured areas represent activity overlap between northern quolls and feral cats and black bars indicate the scotophase, and for bar graphs, error bars represent 95% confidence intervals.