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

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

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

1 | INTRODUCTION

The scale of global habitat loss has rendered the protection of remaining habitat insufficient for maintaining biodiversity (Françoso et al., 2015), requiring active intervention for the restoration of lost and degraded habitats (Croak, Webb, & Shine, 2013). However, the replacement of natural habitat is rarely straightforward (Lawrence, Smith, Sullivan, & Mossman, 2018). Some refuges such as tree hollows and logs are renewable (sensu O’Connell & Keppel, 2016), often returning following restoration, but they can take decades to develop (Haslem et al., 2012).
The species is listed as endangered by the IUCN and has a poisoning by the introduced cane toad (Anderson, Hostetler, Sieving, & Johnson, 2016). Artificial refuges—such as artificial nests (Goldingay, Thomas, & Shanty, 2018), rock crevices (Croak, Pike, Webb, & Shine, 2012), and hibernacula (Zappalorti, 1994)—are human-made substitutes for natural refuges where wildlife can shelter, hibernate, and rear offspring in areas lacking natural refuges (Sherley, Barham, Barham, Leshoro, & Underhill, 2012). Artificial refuges have been used in many restoration efforts across the globe to provide shelter to animals where natural habitat has been altered or destroyed (e.g., Bolton, Medeiros, Hothersall, & Campos, 2004; Dervo et al., 2018; Keppers, Skoruppa, & Hickman, 2008). Yet, the science of artificial refuges is still in its infancy and artificial refuges can fail short, sometimes with perverse outcomes (Ebrahimi, Fenner, & Bull, 2012; Griffiths et al., 2017). Recreating habitable refuges requires not only the provision of a thermal and physical environment that replicates natural refuges (e.g., Griffiths et al., 2018), but also the array of resources that animals require, including a safe haven from predators (Anderson, Hostetler, Sieving, & Johnson, 2016).

The northern quoll (Dasyurus hallucatus) is an Australian marsupial mesopredator (~520 g) that has declined substantially over the past 200 years (Braithwaite & Griffiths, 1994; Moore et al., 2019). Range contractions of up to 75% have been recorded (Moore et al., 2019) due to habitat loss, introduced predators (namely the feral cat, Felis catus, and red fox, Vulpes vulpes), altered fire regimes, and poisoning by the introduced cane toad (Rhinella marina; Ibbett, Woinarski, & Oakwood, 2018; Moore et al., 2019). The species is listed as endangered by the IUCN and has a “decreasing” population trend (Oakwood, Woinarski, & Burnett, 2016). The Pilbara region of Western Australia is the last remaining stronghold for the northern quoll, likely due to the absence of cane toads (Moore et al., 2019; Woinarski, Burbidge, & Harrison, 2014). Yet, this stronghold is far from secure, with predation by feral cats threatening Pilbara quoll populations (Cramer et al., 2016; Hernandez-Santin, Goldizen, & Fisher, 2016), and >91% of the region under mining lease (Environmental Protection Authority, 2014). Conventional drill and blast mining in the Pilbara often destroys nonrenewable refuges and habitat (e.g., rocky outcrops), and is a primary driver of habitat loss for northern quolls (Cramer et al., 2016).

Rocky outcrops and mesas provide crucial denning sites for northern quolls (Burbidge & McKenzie, 1989; Hernandez-Santin et al., 2016), but are the focus of mining activities owing to their rich deposits of iron ore and gravel (Cramer et al., 2016; Ramanaidou & Morris, 2010). Mining companies are sometimes required to offset environmental damage by replacing or compensating for destroyed habitat (McGregor, Stokes, & Craig, 2014; Shackelford, Miller, & Erickson, 2018), and artificial refuges have been touted as one tool that could—along with other actions—help to offset the destruction of nonrenewable refuges (Cramer et al., 2016; Trulio, 1995). Artificial refuges comprised of rock, concrete, and gravel have been created by mining companies with the hope to rehabilitate previously destroyed habitat due to mining activities, as well as to provide off-site refuge for northern quolls during mining operations, particularly by trying to replace lost natal dens (i.e., crevices where female quolls raise their offspring; Cramer et al., 2016; Table S1). However, natural dens and their surroundings often have specific thermal, physical, and/or biotic characteristics, making their replacement difficult (Gallant, Reid, Slough, & Berteaux, 2014; Rowland, Briscoe, & Handsayde, 2017; White, Briers, Bouyer, Odden, & Linnell, 2015). Importantly, it is not known how artificial dens compare to natural dens.

In this study, we:

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

First, we predict that, like other dasyurids (Matthews, Stawski, Körtner, Parker, & Geiser, 2017), quolls will select cool, deep dens that buffer extreme temperatures, particularly given that summer temperatures in the Pilbara regularly exceed temperatures at which quolls are prone to hyperthermia and dehydration (i.e., >36°C; Cooper & Withers, 2010). Second, we predict that quolls will select dens with specific physical dimensions that reduce predation risk, such as an opening that is large enough for quolls to enter, but small enough to exclude predators such as feral cats (Oakwood, 2000; O’Connell & Keppel, 2016). Finally, we predict that quolls will select dens in areas that minimize the likelihood of encountering larger predators (e.g., choosing areas with low feral cat activity and complex surrounding habitat structure; McGregor, Legge, Jones, & Johnson, 2015; Hernandez-Santin et al., 2016), as well as having ample small vertebrate prey (Dunlop, Rayner, & Doherty, 2017).

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

First, we predict that artificial refuges will experience more extreme thermal fluctuations compared to natural dens, as has been found in previous studies (e.g., Griffiths et al., 2018; Rowland et al., 2017). Second, we predict that artificial refuges will be shallower than natural dens,
owing to the selection of deep dens by quolls. Third, because artificial dens are located in previously disturbed areas, we predict that they will be surrounded by simpler habitat structure, and, partly because of this, will have more evidence of feral cat activity (as suggested by Hernandez-Santin et al., 2016). Finally, because of the simplified habitat surrounding artificial dens, we predict a lower availability of small vertebrate prey.

2 | METHODS

2.1 | Study area

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

**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 gray 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
2.2 | Experimental design

The experimental design included three treatments \((n = 10\) each) based on den type: occupied dens, unoccupied crevices, and artificial dens. Occupied dens were chosen as a natural baseline against which the other two den types could be compared (Figure 1b). Unoccupied crevices were used to determine whether northern quolls selected crevices with specific thermal, physical, and/or biotic characteristics. Artificial dens were created specifically for northern quolls by mining companies as part of rehabilitation works on previously developed land, as well as in areas outside existing mine works to mitigate damaged habitat. Most artificial dens were created between 2012 and 2015, with two dens created between 2015 and 2018. All artificial dens were constructed with a similar method—using large earthmoving vehicles to pile up rock/concrete and create crevices and cavities among the material. Two types of artificial dens were created: (a) large piles of variously sized waste rock (Figure 1d), and (b) smaller piles of concrete slabs and gravel (Figure 1e). Two artificial dens were selected from a railway rock armory where quoll activity had been previously recorded by Roy Hill (H. Davie, personal communication, October 12, 2018), and these were classed the same as the first den type (for further details on artificial dens, see Table S1).

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

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

2.3 | Den selection

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

2.4 | Data collection

2.4.1 | Thermal properties

We recorded temperature and relative humidity using DS1923 Hygrochron Temperature and Humidity Data Loggers (iButtons; Maxim Integrated Products). iButtons were placed inside small fiberglass mesh pouches \((5 \times 10 \text{ cm}^2)\) and programmed to record temperature \((\pm 0.5\,^\circ\text{C})\) and relative humidity \((\pm 0.6\%)\) hourly. Each den or crevice had one internal and one external iButton deployed from October 2018 to January 2019. Internal iButtons measured thermal properties of the den cavity. Placement was minimally invasive to quolls and we saw no den abandonment. External iButtons measured ambient conditions outside dens/crevices and were attached to the underside of the forward-facing camera trap to protect them from rain and direct sunlight. In total, 11.7% of all iButtons failed; of the 30 dens monitored, internal i Buttons failed at two occupied dens and two unoccupied crevices, while external iButtons failed at one occupied den, one unoccupied crevice, and one artificial den.
2.4.2 | Physical properties

We measured the physical properties of dens, crevices, and their immediate surroundings including counting the number of entrances to the internal cavity, and measuring the width and height of the largest entrance with a tape measure. Den or crevice depth was measured using a 1.8 m long, PVC-coated metal garden stake pushed in from the entrance to where it could go no further. For dens deeper than 1.8 m, garden stakes were cable tied together, end on end. By using a straight pole to measure depth, it is possible that we at times underestimated den depth if dens continued after sharp bends. To quantify habitat immediately surrounding each den or crevice, we measured ground cover at 1 m intervals along two perpendicular 25-m transects, centered on each den or crevice (n = 50 points per den/crevice). Ground cover was classified as rock, bare ground, Triodia spp., or grass/herb. Within a 50 × 50 m grid, we visually assessed the percent cover of rocks within four different size classes (embedded rock or individual rock diameters of <0.5 m, 0.5–2 m, and >2 m). Embedded rock was part of a rock formation fixed to the ground (i.e., inselbergs).

2.4.3 | Quoll interactions with predators and prey

We used forward-facing camera traps to measure the activity of feral cats, northern quolls, and their prey. We installed an unbaited, forward facing Reconyx PC900 Hyperfire covert cameras (camera traps) (Reconyx, WI) on a 0.5-m high wooden stake, 1–3 m from each den or crevice (n = 30 in total), facing the entrance. Cameras were set on high sensitivity to take three shots per trigger at 1 s intervals, and remained in place from October 2018 to January 2019. To detect potential vertebrate prey species, one baited (rolled oats, peanut butter, and sardines) camera trap was installed within 10 m of each den and crevice, mounted 1.5 m above the ground, facing downward. Both camera trap types were deployed at each den or crevice from October 2018 to January 2019. When forward-facing cameras also detected prey species, these data were included in estimates of prey availability; however, predators were only included in visitation analysis when detected by forward-facing cameras. Potential prey were animals that could be depredated by northern quolls, based on their diet in the Pilbara (Dunlop et al., 2017; Pollock, 1999). To avoid repeatedly counting single individuals over short period of time, we defined an “independent detection” as any triggers of the same species separated by more than 15 min (Diete, Meek, Dixon, Dickman, & Leung, 2016; Hofmeester, Rowcliffe, & Jansen, 2017; Rendall, Sutherland, Cooke, & White, 2014). Visitation was defined as the number of independent detections of a given species over the duration of sampling (excluding cameras that failed), which was corrected for trap nights. For potential prey species, visitation data was pooled into three groups: “mammal,” “reptile,” and “bird” prey (Table S3).

2.5 | Data analysis

We used R version 2.15.3 for our analyses (R Core Team, 2013), and first examined whether northern quoll visitation differed among den types using generalized linear models (GLMs) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The response variable was northern quoll visitation, and den type was included as a categorical predictor variable with three levels (occupied den, unoccupied crevice, artificial den). Because the response variable was a count, a Poisson distribution was initially specified, but showed evidence of over dispersion. Therefore, the model was refit specifying a negative binomial distribution (Zuur et al., 2009). Occupied dens were specified in this, and all GLMs, as the reference category (Crawley, 2012).

2.5.1 | Thermal properties

To compare thermal properties of dens, we fitted generalized additive mixed models (GAMMs) (Zuur et al., 2009), with temperature and humidity as response variables. Predictor variables were time of day (continuous variable), and a six-level categorical variable that concatenated den type (occupied den, unoccupied crevice, artificial den) and iButton location (internal or external). Site was included as a random effect to account for repeated measures (Zuur et al., 2009). We included an interaction between time of day and the concatenated predictor using the “by” function to allow a separate curve of internal and external temperature and humidity with time of day for each den type (Zuur et al., 2009). Separate models were constructed for spring and summer. GAMMs were fitted using the “gamm4” package (Wood & Scheipl, 2017). Predictions from GAMMs were plotted in relation to the northern quoll’s “thermal stress range,” which is the range of temperatures within which quolls are likely to experience thermal stress, defined by two thresholds: (a) 36°C, the ambient temperature where quolls significantly increase physiological cooling via evaporative water loss, resulting in thermal stress (Cooper & Withers, 2010), and (b) 41°C, the lethal body temperature of other marsupials, including green ringtail possums (Pseudochirops archeri) and quokkas (Setonix brachyurus) (Krockenberger, Edwards, & Kanowski, 2012; Robinson & Morrison, 1957).
2.5.2 | Physical properties

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

2.5.3 | Quoll interactions with predators and prey

GLMs were used to examine whether predator visitation and prey availability differed among den types. The response variable was the relative visitation rates of feral cats and prey (pooled into mammals, reptiles, birds) corrected for the number of trap nights. A negative binomial distribution was specified in all models and den type was included as a categorical predictor. In addition to spatial avoidance, smaller predators are known to temporally avoid larger predators (Brook, Johnson, & Ritchie, 2012). Therefore, we measured activity overlap of quolls and feral cats at each den type. We fit kernel density curves of activity based on the timing of observations of each species from camera traps using the “Overlap” package (Fancourt, Hawkins, Cameron, Jones, & Nicol, 2015; Ridout & Linkie, 2009). A coefficient of overlap between quolls and cats was then calculated for each den type. This coefficient is a quantitative measure of overlap in activity time, ranging from 0 (no overlap) to 1 (complete overlap in activity). We used the Δ1 estimator (appropriate for datasets with a small number of observations (Ridout & Linkie, 2009)) to measure activity overlap for occupied dens and unoccupied crevices, owing to feral cats having fewer than 75 individual detections. The same was used for artificial dens, with northern quolls having less than 75 individual detections (Meredith & Ridout, 2018). Relative visitation rates of northern quolls were corrected for trap nights.

3 | RESULTS

Camera traps were deployed for a total of 2,526 trap nights, during which, we detected northern quolls at all occupied dens and unoccupied crevices, and at five artificial dens. There was a total of 459 independent detection events—at least 15 min apart—of northern quolls across all dens and crevices over the 2,526 trap nights, ranging from 2 to 108 at occupied dens, 0 to 28 at unoccupied crevices, and 0 to 40 at artificial dens. There was no significant difference in the number of quoll detections between occupied dens and unoccupied crevices (Figure S1), whereas occupied dens had more detections compared to artificial dens (p < .05, CI95%: −2.71, −0.12) (Figure S1). There was also no significant difference in the number of quoll detections between unoccupied crevices and artificial dens. Quolls at occupied dens were regularly pictured entering and leaving the den cavity, often with young, whilst quolls at unoccupied crevices and artificial dens were usually moving past or briefly inspecting the crevice. Failed camera traps were removed from analysis, with one each at occupied dens and unoccupied crevices, and three at artificial dens. Rock style artificial dens had one site that detected northern quolls and three sites that detected feral cats, while concrete style artificial dens had three sites that detected northern quolls and one site that detected feral cats.

3.1 | Thermal properties

Temperatures outside all den types fluctuated more widely than inside (Figure 2a,b). During spring, there were higher peak mean temperatures of ~42–45°C externally, compared to ~33–36°C internally, and lower mean temperatures of ~22–24°C externally, compared to ~29–32°C internally (Figure 2a). Occupied dens were on average significantly cooler internally and externally compared to unoccupied crevices, but did not differ significantly from artificial dens (Table S4). Trends during summer showed similar patterns to spring, albeit at higher temperatures (Figure 2b). Unoccupied crevices were significantly warmer than occupied dens, while artificial dens resembled occupied den temperatures internally throughout the day, with no significant differences in average temperature (Table S4; Figure 2a,b). Humidity at all den types was also less variable inside the cavity than outside (Figure 2c). External humidity was higher during the night (~60%) than internal humidity (~40%) (Figure 2c). Internal and external humidity did not differ significantly among den types (Table S4). Time of day was a significant predictor of temperature and humidity at all den types and in all seasons (Table S5).

3.2 | Physical properties

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

### 3.3 Quoll interactions with predators and prey

Over 2,526 total trap nights, there were 150 independent feral cat detections on 87 trap nights at five occupied dens, three unoccupied crevices, and four artificial dens. Of the dens and crevices visited by feral cats, occupied dens and unoccupied crevices had a range of 1–2 and an average of 1 individual cat per den, while artificial dens had a range of 1–3 and an average of 2 individual cats per den. Feral cats were recorded exploring the entrances of two occupied dens and one artificial den at similar times to which northern quolls were using it (Figure S2). Relative feral cat visitation (corrected for trap nights) did not differ between occupied dens and unoccupied crevices;
however, feral cat visitation was significantly lower at occupied dens than at artificial dens (Table S7; Figure 4a). This difference, however, was driven by an outlier: an artificial den with >100 independent detections. Images showed a feral cat entering and existing the den with kittens, suggesting that the den may have been used for rearing young (Figure S2). Northern quolls were most active at night and feral cats were most active in the early morning. At occupied dens, feral cats were active for longer, with activity only decreasing between approximately 9:00 a.m. and 12:00 p.m. (Figure 5b). Northern quolls and feral cats were more likely to be active at similar times at occupied dens, compared to unoccupied crevices (Figure 5c) and artificial dens (Figure 5d): activity overlap was highest at occupied dens (0.69, CI95%:0.46, 0.82), followed by unoccupied crevices (0.53, CI95%:0.19, 0.69), and artificial dens (0.20, CI95%:0.17, 0.36) (Figure 5a).

Mammal prey detections did not differ significantly between occupied dens and unoccupied crevices, but there were significantly more mammal prey detections at occupied dens compared to artificial dens (Table S7; Figure 4b). Over 5,631 total trap nights, the common rock rat (*Zyzomys argurus*) was the most common mammal prey detected (93 detections; Table S3). Reptile prey detections were significantly lower at occupied dens compared to unoccupied crevices, with no difference at artificial dens (Table S7; Figure 4c). There were 614 detections of birds across all den types (Table S3), with significantly more bird prey detections at occupied dens, compared to

![Figure 3](image URL)  
**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, gray dots represent suspected outliers, and red asterisks denote a significant difference from the intercept (occupied dens).
unoccupied crevices, and no difference compared to artificial dens (Table S7; Figure 4d).

4 | DISCUSSION

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

4.1 | Thermal properties

A key challenge in the construction of artificial refuges is to closely replicate the thermal environments of natural refuges (Griffiths et al., 2018; Rowland et al., 2017), because natural refuges often have specific thermal properties that are critical for their inhabitants, such as internal temperatures that are more stable than the external climate (O’Connell & Keppel, 2016). Artificial refuges that fail to replicate natural conditions can expose animals to thermal stress (Griffiths et al., 2018). For instance, evaporative heat loss of arboreal mammals needs to be 1.5–2.4 times higher in nest boxes than natural hollows during summer to avoid overheating, which could lead to dehydration (Rowland et al., 2017). In arid and semiarid regions, it is particularly important for refuges to buffer high external temperatures and maintain
humidity to avoid mortality of the animals inside (Gardner, Amano, Sutherland, Clayton, & Peters, 2015). Ambient temperatures near dens and crevices far exceeded the temperatures at which quolls must increase physiological cooling through evaporative heat loss (~36°C), and regularly reached lethal temperatures (i.e., >41°C) (Cooper & Withers, 2010). In our study, temperatures inside crevices of all types were cooler and all den types had more stable internal temperature and humidity profiles compared to the outside air. However, occupied northern quoll dens were cooler-still compared to nearby, unoccupied crevices, suggesting that they—like many animals (Isaac, De Gabriel, & Goodman, 2008; Reside et al., 2019; Scheffers, Edwards, Diesmos, Williams, & Evans, 2014)—select dens that offer additional thermal buffering, presumably to reduce the time spent at stressful temperatures within the refuge (O’Connell & Keppel, 2016). In contrast to unoccupied crevices, artificial dens closely matched the thermal properties of occupied dens. Like occupied dens, artificial dens remained below the thermal stress range for longer and during a greater range of ambient temperatures. This finding is important and implies that—contrary to our predictions, and despite quite specific den selection by northern quolls—artificial dens can provide a suitable thermal environment, potentially allowing quolls to survive and rear young in areas they otherwise could not.

### 4.2 Physical properties

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

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

The environmental context surrounding potential refuges can also influence whether they will be used or not (Bhattacharyya, Dutta, Adhikari, & Rawat, 2015; McElhinny, Gibbons, Brack, & Bauhus, 2006; Reside et al., 2019). Many animals often select natural refuges close to important resources that provide protection, temperature regulation, or food (Bretscher, Dittel, Lambert, & Adler, 2018; Croak et al., 2012). Northern quolls in the Pilbara often inhabit complex rocky habitat, likely because it provides protection from predation (Cook, 2010; Hernandez-Santin et al., 2016) and fire (Burrows, Ward, & Robinson, 2009), and often contains temporary ponds and sheltered crevices (Henneron, Sarthou, De Massary, & Ponge, 2019; Radford, Gibson, Corey, Carnes, & Fairman, 2015). Artificial dens in our study area were usually placed in open, flat landscapes, with a history of disturbance—characteristics that have been shown to negatively affect refuge use in other species (Lalas, Jones, & Jones, 1999; McGregor et al., 2014). As predicted, we found areas surrounding artificial dens lacked important habitat complexity; they were characterized by less embedded rock, Triodia cover, and herbaceous vegetation, and had more small rocks and bare ground. To improve environmental context surrounding artificial dens, further long-term research should focus on the capacity of artificial landscapes to recover over time through both active and passive restoration, to avoid placing dens in habitat that may never be suitable.

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

### 4.3 Quoll interactions with predators and prey

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

It is possible that, in some instances, artificial dens could act as ecological traps for northern quolls: habitats that are selected by animals because they appear high quality (e.g., having thermally suitable crevices) but are in fact maladaptive as they decrease fitness or increase mortality risk (Battin, 2004). This reinforces the importance of creating (or maintaining) structurally complex habitats around artificial dens, to create less preferable habitat for cats. These findings, including observations of feral cat breeding within an artificial den, also highlight the importance of tailoring den dimensions (e.g., depth, entrance width) such that they exclude predators both from predating upon quolls within dens and using dens for their own recruitment (e.g., Bailey & Bonter, 2017). One possible reprieve for quolls is that cat and quoll activity overlap was lowest at artificial dens,
suggesting a reduced probability of animals encountering one another outside of the den. However, high overlap at occupied dens may indicate cats are tracking quolls to their dens and synchronizing their activity to increase the probability of an encounter: dasyurids are most abundant in feral cat diet throughout the Pilbara region and adjacent deserts (Murphy et al., 2019). We cannot discount that—should artificial dens become regularly occupied by quolls—it is possible that such temporal tracking of quolls by cats could occur at artificial dens as well.

The lack of potential mammal prey at artificial dens is important, as small marsupials and rodents can make up a large portion of northern quoll diet (Dunlop et al., 2017), and predators often use habitat based on the availability of prey (Gallant et al., 2014; Khalatbari, Yusefi, Martínez-Freiría, Jowkar, & Brito, 2018; Rabelo, Aragon, & Bicca-Marques, 2019). The most commonly recorded mammal prey in this study was the common rock-rat (Z. argurus), which is a favored food item for northern quolls (Dunlop et al., 2017). Rock-rats feed mainly on seeds, stems, leaves, and fruit of Ficus spp. (Begg & Dunlop, 1985; Nano, Smith, & Jefferys, 2003), and are often associated with rock complexity, grasses, and plants that produce seeds (e.g., Triodia spp.) (Begg, 1981; Radford, 2012; Trainor, Fisher, Woinarski, & Churchill, 2000). A lack of appropriate habitat in the form of rocky cover, Triodia cover, and other herbaceous plants may therefore explain rock-rat absences at artificial dens. Restoring habitat complexity and vegetation around artificial dens may help to attract small mammals like common rock-rats and increase the availability of mammal prey for northern quolls. There is scope for future research to focus on the best practice of restoring habitat complexity for the benefit of northern quolls and their prey, particularly revegetation.

5 | IMPLICATIONS AND CONCLUSION

The role of artificial refuges in conservation has expanded with the need to “offset” environmental damage caused by industry (Maron et al., 2012). Offsets seek to compensate for the environmental costs of human actions, such as mining or urban development, by creating equivalent environmental gains elsewhere (Miller et al., 2015). If artificial refuges do not closely replicate natural refuges, and are therefore not used by target species, they are likely to fail to offset ecological damage (Lindemayer et al., 2017).

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

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Judy A. Dunlop, Dale G. Nimmo, and Mitchell A. Cowan conceived the ideas; Mitchell A. Cowan, Judy A. Dunlop, and Harry A. Moore collected the data; Mitchell A. Cowan and Dale G. Nimmo analyzed the data with input from Judy A. Dunlop, James M. Turner, and H.A. M; and Mitchell A. Cowan and Dale G. Nimmo led the writing with input from Judy A. Dunlop, James M. Turner, and Harry A. Moore.
DATA ACCESSIBILITY STATEMENT
Data supporting this study can be found on the Dryad Digital Repository, doi: 10.5061/dryad.0gb5mkxxt.

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