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Non-preferred habitat increases the activity area of the endangered northern quoll (Dasyurus hallucatus) in a semi-arid landscape

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1	Non-preferred habitat increases the activity area of the endangered
2	northern quoll (Dasyurus hallucatus) in a semi-arid landscape
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4	Running header: Northern quoll habitat selection
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6	Cowan, M. A. ^{1,2,*} , Moore, H. A. ³ , Hradsky, B. A. ⁴ , Jolly, C. J. ^{1,5} , Dunlop, J. A. ^{1,2,6} , Wysong,
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35	

36 Abstract

37 Animal conservation requires a sound understanding of the movement ecology and habitat selection of the species in question. A key component of this is identifying habitats that animals 38 actively seek or avoid. We quantified habitat selection and investigated the drivers of 39 variability in the short-term activity area of a small, endangered mesopredator, the northern 40 quoll (Dasyurus hallucatus), in the Pilbara region of Western Australia. We collated, 41 standardised, and analysed 14 northern quoll GPS tracking events from four studies conducted 42 between 2014 and 2018. Northern quolls selected activity areas in locations that were more 43 topographically rugged than the broader landscape, characterised by higher percentage cover 44 of rocky habitat and riverbed, and lower percentage cover of spinifex sandplain. The size of 45 46 their activity area also increased with higher percentage cover of non-preferred spinifex sandplain. Therefore, the destruction of habitats preferred by northern quolls—such as mining 47 of rocky habitat—and introduction of structurally simple habitat like spinifex sandplain, is 48 likely to negatively impact resource availability and lead to altered movement patterns that 49 could decrease survival. Future conservation planning should place emphasis on the protection 50 of rugged rocky habitat for northern quolls, as well as efficient movement pathways between 51 52 patches of this critical habitat.

53 Introduction

54 Effective conservation requires knowledge of the spatial and temporal use of preferred habitats by target species (Dellinger et al. 2020). Animal space use reflects resource availability in the 55 landscape (Michel et al. 2020; Wysong et al. 2020). If landscapes are resource-rich, animals 56 travel shorter distances (Doherty et al. 2019; Martin and Martin 2007; Viana et al. 2018). 57 Conversely, where resources are limited, animals travel further to access food, shelter, or mates 58 (Gardiner et al. 2019; Rus et al. 2020; Stobo-Wilson et al. 2021). In fragmented landscapes, 59 60 where an animal's preferred habitat is interspersed among non-preferred habitat, animals may need to acquire resources from multiple patches of the preferred habitat type (Dunning et al. 61 1992). The spatial extent and configuration of non-preferred habitat can affect the capacity of 62 animals to move between preferred habitat (Nimmo et al. 2019): large areas of non-preferred 63 habitat can lead to increased travel time (Beasley and Rhodes 2010), reducing foraging 64 efficiency while increasing predation risk and energy expenditure (Brown 1988; Haapakoski 65 et al. 2013). These behaviours are often influenced by predator interactions and the 'landscape 66 of fear', where animals perceive certain habitats as riskier than others (Bleicher 2017; Brown 67 1988). 68

69

70 One species which lacks information about its movement and habitat use is the northern quoll 71 (Dasyurus hallucatus)—an endangered, nocturnal mesopredator native to northern Australia (Moore et al. 2019). Over the past century, northern quolls have suffered substantial range 72 73 declines (Braithwaite and Griffiths 1994; Moore et al. 2019), presumably due to habitat loss, 74 introduced predators (namely the feral cat, *Felis catus*), altered fire regimes, and cane toads (Rhinella marina) (Ibbett et al. 2018; Moore et al. 2019; Woinarski et al. 2010). The Pilbara 75 76 region of Western Australia contains the last cane toad-free populations of northern quolls (Moore et al. 2019; Woinarski et al. 2014). Yet quolls in the Pilbara are far from secure (Cramer 77 78 et al. 2016; Moore et al. 2021a). Drill and blast mining operations often target the rocky habitat 79 that also provides crucial denning sites for northern quolls (Ramanaidou and Morris 2010), 80 because of their rich deposits of minerals such as iron ore, resulting in a structurally simplified landscape (Cramer et al. 2016; Henderson 2015). Based on previous research, we know 81 northern quolls are most likely to be found in rugged rocky outcrops but are less common in 82 spinifex sandplain habitats (Hernandez-Santin et al. 2016; Moore et al. 2021b). 83

While this research has informed much conservation work (Moore *et al.* 2021a), we know very little about how rocky habitat and spinifex sandplain influence northern quoll movement and space use, and even less about how northern quolls interact with other habitat types (Cramer *et al.* 2016). Understanding how northern quolls use different habitats, and how these habitats influence their movements, will allow greater protection of critical habitat and better inform rehabilitation projects which seek to reconnect remnant habitat or replicate northern quoll habitat that has been disturbed or destroyed (e.g., Cowan *et al.* 2020b).

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93 In this study, we investigate the movement ecology of northern quolls in a naturally fragmented landscape of rocky outcrops, spinifex sandplains, Acacia stands, and dry riverbeds in the 94 Pilbara, Western Australia. Riverbed in the Pilbara is often associated with rocky habitat, while 95 Acacia stands are patchily distributed amongst spinifex sandplain and rocky habitat (Van 96 Vreeswyk et al. 2004). Previous estimates of northern quoll movement are mostly derived from 97 Very High Frequency (VHF) tracking (e.g., Cook 2010; King 1989; Oakwood 2002)-a 98 technology now largely superseded by Global Positioning System (GPS) tracking (e.g., 99 Heiniger et al. 2020; Hernandez-Santin et al. 2020). We collated, standardised, and analysed 100 GPS data from four studies to investigate habitat selection, and the influence of habitat type on 101 102 movement, by northern quolls. We developed two predictions based on existing knowledge of northern quoll behaviour and ecology: 103

104

First, we predicted that northern quolls would select for habitats which are topographically rugged, such as rocky habitat and riverbed—which likely offer many resources required for survival. The landscape of fear also suggests that quolls would avoid simpler habitats like spinifex sandplain and *Acacia* stands. Rocky habitat is likely seen as safer by northern quolls, as feral cats, an agent of northern quoll decline—and a threat to other quoll species (Fancourt *et al.* 2015)—are more common and superior hunters in simpler habitats like spinifex sandplain (McGregor *et al.* 2015).

112

Second, we predicted that northern quoll activity areas (i.e., the movement footprint of northern quolls over seven nights) would be larger when containing higher percentages of presumably non-preferred habitat, such as spinifex sandplain, due to a lack of necessary resources for quolls, requiring them to travel further to access preferred habitat (e.g., rocky habitat).

Materials and methods

118 Study area

The Pilbara bioregion covers 179,000 km² of Western Australia and experiences a semi-arid 119 climate, with average maximum temperatures of 37°C during summer and 25°C during winter 120 (McKenzie et al. 2009). Annual rainfall is variable (250-500 mm), and falls predominately 121 between December and February (Bureau of Meteorology 2020). The Pilbara is characterised 122 by patches of rocky habitat with rugged hills, deep gorges, rough escarpments, and sandy plains 123 (Carwardine et al. 2014; Van Vreeswyk et al. 2004). The flora is diverse but is predominately 124 composed of Acacia, Triodia (spinifex), and Eucalyptus species, the composition of which is 125 largely influenced by local geology and fire history (Maslin and van Leeuwen 2008; Van 126 127 Vreeswyk et al. 2004).

128

We studied habitat selection of northern quolls at four sites in the Pilbara, using data from four 129 different studies conducted between 2014 and 2018 (Biologic 2016; Cowan et al. 2020b; 130 Hernandez-Santin et al. 2020; Moore, unpubl. data; Figure 1; Table S1 & S2). Studies occurred 131 primarily on Karriyarra, Ngarluma, and Nyamal country, and occupied a mixture of pastoral 132 leases, national parks, and mining tenements (Table S1). Study sites were broadly similar in 133 134 that they all contained rocky habitat, spinifex sandplain, and scattered Acacia stands. One site, Red Rock, also contained a sandy riverbed which flows seasonally and is closely associated 135 with rock (Van Vreeswyk et al. 2004; Figure 2). 136

137

138 Maps of habitat features

We used QGIS v3.12 (QGIS Development Team 2020) to create a map of habitat features for 139 140 each site. We applied semi-supervised classification of normalised difference vegetation index (NDVI) layers (Pandey and Kulhari 2018), derived from Sentinel-2 imagery (USGS 2020), to 141 map the six habitat types we considered likely to influence the spatial ecology of northern 142 quolls: rocky habitat, spinifex sandplain, Acacia midstory over spinifex understory (henceforth 143 Acacia stands), sandy dry riverbeds (henceforth riverbed), water, and disturbed ground (e.g., a 144 road or cleared land). Feature layers for the habitat maps were captured at a scale of 10 m for 145 each site during the year tracking took place-except for at Red Rock where we used a 146 consistent layer (2014) for each year. Red Rock had no fires between 2014 and 2018 and habitat 147 148 features remained relatively consistent across years. Habitat feature maps were cross-examined with the corresponding satellite imagery to ensure the accuracy of habitat feature classification 149

(as per Tilahun and Teferie 2015). During analysis, we did not investigate northern quollselection of water or disturbed ground due to a lack of representation among sites.

152

153 Animal capture and data acquisition

Trapping effort varied slightly between the studies, however, the same broad method was 154 applied, and all live animal research was approved by the respective institutional animal ethics 155 committees (see Acknowledgements). Wire cage traps ($45 \text{ cm} \times 17 \text{ cm} \times 17 \text{ cm}$, Sheffield Wire 156 Co., Welshpool, WA) were deployed in transects during autumn, winter, or spring between 157 158 2014 and 2018 (see Biologic 2016; Cowan et al. 2020b; Hernandez-Santin et al. 2019). Trapping did not occur during summer to avoid trapping females raising young during this time 159 (Dunlop et al. 2014). Traps were placed in rocky and riparian habitats because these are the 160 areas in which northern quolls locate their dens in the Pilbara (Hernandez-Santin et al. 2022), 161 resulting in an increased likelihood of trap success. Traps were baited with universal bait (oats 162 and peanut butter) or a mixture of the universal bait and sardines (as per Dunlop et al. 2014). 163 Traps were opened in the evening and checked the following morning. All individuals were 164 processed at the site of trapping, which involved taking a series of morphological 165 measurements, recording sex and weight, and attaching a GPS unit (provided the unit did not 166 167 exceed five percent of the animal's bodyweight). GPS units were deployed on 25 individuals for up to 37 days before animals were re-trapped and the GPS unit was removed. GPS units 168 169 were fitted as collars or backpacks; brands and tracking methods differed slightly between studies due to limitations of battery life, data storage, and study time (Table S2). 170

171

172 Data screening and processing

173 To eliminate errors and reduce bias due to variation in study methods, data were screened prior to being included in analysis. Data contributed by Biologic (2016) had been pre-screened by 174 175 the authors to discard all locations not recording elevation, as well as those with low GPS accuracy (horizontal dilution of precision greater than 5). We screened all datasets further by 176 discarding GPS points before 12:00 pm on the day of collaring, as well as all those after 12:00 177 pm on the date before collar retrieval, as GPS fixes may have been affected by quolls being in 178 a trap. Unrealistic GPS fixes were removed based on the average sprinting speed of northern 179 quolls (4.5 m s⁻¹) (Wynn *et al.* 2015), where points too far to be reached in the time between 180 fixes were excluded (Bjørneraas et al. 2010). 181

To ensure that GPS locations reflected the times when northern quolls were active, we only 183 included GPS locations recorded between 6:00 pm and 6:00 am. Individuals with fewer than 184 30 fixes, as well as individuals whose GPS units failed within the first day, were removed 185 because there was unlikely sufficient data to accurately measure activity areas (Girard et al. 186 2002; Seaman et al. 1999). We did not standardise fix rates among datasets because doing so 187 resulted in many unusable individuals with too few GPS locations, and differences in fix rate 188 are often negligible when applying kernel density estimation (Huck et al. 2008; Mitchell et al. 189 2019; Peris et al. 2020). 190

191

192 Activity area size

Many tracking events did not represent complete home ranges of each individual and instead 193 represented a sample of each individual's home range. This is because they did not reach an 194 asymptote with fixes added sequentially (i.e., over time) at 10-fix intervals. An asymptote is 195 196 calculated by plotting activity area with the number of fixes—with 10 sequential fixes added in each iteration in this case—and is reached when adding additional fixes has little to no effect 197 198 on the size of the activity area, thus representing a true home range (Harris et al. 1990). Instead, to account for differing tracking durations among individuals, we standardised each dataset to 199 200 a total period of seven nights (one week) and refer to the area used by northern quolls during this time as their 'short-term activity area' (henceforth activity area) (Doherty et al. 2019). 201 202 Some individuals were tracked for one week, but GPS tracking ceased before seven nights of data could be reached (likely due to battery failure or memory limitations). Therefore, six 203 individuals were tracked for less than seven nights, and six individuals were tracked for seven 204 nights (n = 12). The shorter tracking duration for these individuals is accounted for in further 205 analyses (see below). For one individual (E6CA67) tracked for 29 nights, we isolated each 206 seven-night period (hereafter referred to as a 'tracking event'), separated by a buffer of one 207 night between each. Each tracking event was treated as an individual event, and therefore the 208 individual quoll appears in the data three times. We accounted for this by including 'individual' 209 210 as a random effect in all analyses (Bates et al. 2015).

211

We estimated northern quoll activity area from utilisation distributions (UDs) at the 95% isopleth using fixed kernel density estimation (KDE). Kernel density estimation uses a smoothing parameter or bandwidth (*h*) to smooth GPS points, creating a probability density estimate which reflects the intensity of use within an animal's activity area (Signer *et al.* 2015). We used the *ad hoc* method ($h_{ad hoc}$) (referred to as 'reference scaled' in the R package; see 217 below) to determine *h* because $h_{ad\ hoc}$ is robust to sample size, accurately reflects the true 218 activity area, and is consistent and repeatable (Kie 2013). We used fixed KDE (where the kernel 219 width remains the same regardless of the distance between points) instead of adaptive KDE 220 (where the kernel width increases with increasing distance between points) because adaptive 221 KDE can sometimes over-estimate activity area size (Blundell *et al.* 2001; Kernohan *et al.* 222 2001; Powell 2000). We used the package "rhr" (Table S3, Signer and Balkenhol 2015) in R 223 version 1.3.959 to estimate activity area (R Core Team 2020).

224

225 Habitat selection

To analyse northern quoll habitat selection, we quantified the percentage of habitat types in 226 each "used" short-term activity area (n = 14) and 10 randomly placed circular "available" 227 activity areas per individual (n = 140), equal in size to the activity area of the individual being 228 measured and randomly placed within the available landscape (Squires et al. 2013; Wysong et 229 230 al. 2020). Due to the fragmented nature of northern quoll habitat in the Pilbara (Moore et al. 2021b), available activity areas for each individual were sampled within habitat considered 231 232 accessible by that individual (Hazen et al. 2021). To define the boundaries for the available landscape for each individual, we followed a similar method to Wysong et al. (2020). We fitted 233 234 a 100% minimum convex polygon (MCP) to the GPS data of each individual tracking event. We then placed a buffer around each MCP equal to the radius of the largest northern quoll 235 activity area if assumed to be circular (897 m). We then subtracted the radius of the activity 236 area being measured. We used the "extract" function in the "raster" package to determine the 237 proportion cover of each habitat type within each "used" and "available" activity area in R 238 (Hijmans et al. 2015). 239

240

To test our predictions about selection and avoidance of the four habitat types, we used Beta-241 Binomial Mixed Models (BBMMs) to evaluate if the proportion cover of each habitat type 242 differed between "used" and "available" activity areas. BBMMs allow for the analysis of 243 244 proportion data-including over-dispersed proportion data-and random effects (Douma and Weedon 2019). We did not account for tracking duration in BBMMs because the data were 245 proportion data which was relative to each individual tracking event. A separate BBMM was 246 fitted for each habitat type. The response variable was the proportional cover of the habitat type 247 (rocky habitat, riverbed, spinifex sandplain, Acacia stands) within an activity area, and the 248 predictor variable was the "used" or "available" activity area. The reference category 249 (intercept) was the "available" activity area category. Selection (or avoidance) was evaluated 250

using a *p*-value statistical significance approach. We included 'individual' and 'site' as random
effects (Muff *et al.* 2020). BBMMs were fitted using the package "PROreg" in R (NajeraZuloaga *et al.* 2020).

254

We also investigated whether northern quolls selected for highly topographically rugged areas. 255 256 The topographic ruggedness index (TRI) is defined as the difference in elevation between a cell and the eight cells surrounding it (Riley et al. 1999). To create topographic ruggedness 257 index maps for each site, we sourced Digital Elevation Models (30 m scale) (Gallant et al. 258 259 2009), and used the "Terrain Ruggedness Index" function in QGIS (QGIS Development Team 2020). We overlaid the "used" and "available" northern quoll activity areas onto topographic 260 ruggedness maps and identified the median topographic ruggedness index for each activity 261 area. To evaluate if northern quolls used activity areas with a higher median topographic 262 ruggedness index compared to the broader landscape, we fitted a Generalised Linear Mixed 263 Model (GLMM) with 'individual' as a random effect, and median topographic ruggedness as 264 a continuous response variable (Bates et al. 2015). We could not include site as a random effect 265 266 due to small sample size. The categorical predictor variable was either the "used" or "available" (intercept) activity area. GLMMs were fitted using the package "ImerTest" in R (Kuznetsova 267 268 et al. 2015).

269

270 **Determinants of activity area**

To test our prediction that northern quoll activity areas would increase in size with an 271 increasing percentage cover of spinifex sandplain, we developed Linear Mixed Models 272 (LMMs) in which the response variable was the "used" activity area size, and the predictor 273 variable was one of: median topographic ruggedness index (median TRI), sex, weight, or the 274 proportional cover of rocky habitat, spinifex sandplain, or riverbed. We included only 275 276 univariate models to simplify model selection and preclude overfitting, due to our small sample size. We also only considered habitat variables that northern quolls either selected or avoided 277 278 disproportionately more than what was available in the broader landscape (i.e., rocky habitat, spinifex sandplain, and riverbed), therefore, Acacia stands were excluded. The response 279 280 variable was log₁₀ transformed because predictor variables had non-linear relationships, and 'individual' was included as a random effect to account for the repeat sampling of the same 281 individual (Bates 2010). We could not include 'site' as a random effect due to small sample 282 size (Bates et al. 2015; Stratmann et al. 2021). To account for some individuals having less 283 284 than seven nights of data, we included 'nights' as an offset in the model, which was the number

- of nights each individual was tracked (Stobo-Wilson *et al.* 2021). This variable was also \log_{10}
- transformed. GLMs were fitted using the package "lme4" in R (Bates *et al.* 2020).
- 287
- 288 We applied second order Akaike's Information Criterion (AICc) ranking to determine the best
- model explaining variation in activity area size. We determined the goodness of fit (r^2) for all
- 290 models and acknowledged models as having substantial support when Δ AICc <2 (Burnham
- and Anderson 2001; Mac Nally et al. 2018). We used the "AICcmodavg" package in R to
- conduct model selection (Mazerolle and Mazerolle 2017).

293 **Results**

294 Of the 25 northern quolls collared in the four studies, data for eight female and four male northern quolls met our study criteria (n = 12), resulting in 14 tracking events (Figure S1). 295 Three of these tracking events occurred during autumn, seven during winter, and four during 296 spring (Table S4). Nine tracking events occurred at Red Rock, three at Cattle Gorge, and one 297 each at De Grey Ridge and Python Pool. After data were trimmed to the relevant diel period, 298 five location errors were removed from the datasets of three northern quolls in total. The mean 299 300 number of GPS fixes for all weekly (seven-night) short-term activity areas was 267 ± 57 fixes (mean \pm SE) while the minimum was 69 fixes, and the maximum was 418 fixes (Table 1; Table 301 S4). 302

303

304 Activity area size

For weekly short-term tracking events, the mean activity area for females and males combined was 153.42 ± 38.69 ha (Table 1). The mean weekly activity area for females was 91.24 ± 24.39 ha (min = 22.96 ha, max = 128.62 ha), while the mean weekly activity area for males was 215.61 ± 61.75 ha (min = 53.84 ha, max = 340.54 ha) (Table 1; Table S4).

309

310 Habitat selection

Northern quolls selected activity areas in locations with significantly higher percentage cover of rocky habitat and riverbed, and significantly lower percentage cover of spinifex sandplain, compared to the available landscape (Figure 3, Table 2). Their activity areas had a similar percentage of *Acacia* stands compared to the available landscape (Figure S2; Table 2). Finally, northern quolls selected activity areas in locations with significantly higher topographic ruggedness compared to the available landscape (Figure 3, Table 2).

317

Some northern quolls primarily used rocky habitat connected by riverbed and spinifex sandplain; riverbed was often associated with rocky habitat at Red Rock (Figure 4a). One male northern quoll used an activity area covering large areas of spinifex sandplain at Python Pool to access patches of rocky habitat (Figure 4b). Others used mainly rocky habitat like at Cattle Gorge (Figure 4c), while one female had an activity area with high cover of *Acacia* stands at De Grey Ridge (Figure 4d, Table S4).

324

325 Determinants of activity area size

- 326 The model "spinifex sandplain" was the top-ranked model ($_{wi}$ AICc = 0.56) and explained 20%
- 327 of the variability in activity area size (Table 3). This model showed that northern quoll activity
- area increased in size when the percentage cover of spinifex sandplain was higher (Figure 5).

329 **Discussion**

330 We investigated the movement ecology of the endangered northern quoll in an arid landscape to identify their preferred habitat and drivers of activity area size. As predicted, northern quolls 331 located their short-term activity areas in habitats that were more rugged, characterised by 332 higher percentage cover of rocky habitat and riverbed than the available landscape. Northern 333 quolls also selected activity areas in locations with a lower percentage cover of spinifex 334 sandplain than the available landscape, and activity areas increased in size when they contained 335 336 a higher percentage cover of spinifex sandplain. Our findings support those of previous studies which suggest rugged rocky areas provide critical habitat for the Pilbara northern quoll (Moore 337 et al. 2021a), and are likely rich in key resources compared to spinifex sandplain. Together 338 339 these results have important implications for the conservation of this species, particularly in 340 terms of the loss of rugged rocky habitat.

341

As predicted, northern quolls selected activity areas in locations with higher percentage cover 342 of rocky habitat and in areas which were more topographically rugged than the available 343 landscape. This supports findings from other studies and confirms that northern quolls and 344 many other critical weight range mammals (CWR, 35–5500 g) (Murphy and Davies 2014) 345 346 persist in rugged, rocky habitat at a landscape scale (Burbidge and McKenzie 1989; Hernandez-Santin and Fisher 2022; McDonald et al. 2017; Molloy et al. 2017; Moore et al. 2019; 347 Oakwood 2002). Structurally complex rocky habitats in the Pilbara provide several resources 348 349 and functions to northern quolls which are critical for survival. These include thermally stable 350 denning habitat (Cowan et al. 2020b), protection from predators (Hernandez-Santin et al. 2016), and abundant prey (Dunlop et al. 2017). Rocky habitat also protects CWR mammals 351 352 from fire, grazing, and extreme temperatures (Fitzsimons and Michael 2017; McDonald et al. 2017). The availability of rugged rocky habitat therefore appears critical for northern quoll 353 persistence, and potential removal of rugged rocky habitat due to human disturbance (e.g., 354 mining) is likely to heavily impact their persistence (Cramer et al. 2016). 355

356

Some habitat types may be avoided because they lack crucial resources or contain risks which animals prefer to avoid (Aldridge and Boyce 2007; Polfus *et al.* 2011). Here, the apparent avoidance of spinifex sandplain by northern quolls is likely explained by increased predation risk in this habitat type and the landscape of fear, which suggests that animals move between resource patches more regularly in areas close to shelter, due to greater perceived safety

(Bleicher and Dickman 2020; Laundré et al. 2001). For example, feral cats are most successful 362 at hunting in open habitats, where prey is more exposed (McGregor et al. 2015; Moseby et al. 363 2021; Stobo-Wilson et al. 2020), such as spinifex sandplain. Hernandez-Santin et al. (2016) 364 showed that feral cats frequently used flat, open spinifex sandplain in their Pilbara ranges and 365 northern quolls avoided areas used by cats spatially and temporally. Moving through spinifex 366 sandplain is likely risky for the smaller quoll, due to the increased chance of intraguild 367 predation (Virgós et al. 2020). Reducing the predation risk by feral cats through control 368 programs could benefit quolls by enabling them to make greater use of spinifex sandplains and 369 370 reducing their reliance on fragmented rocky habitat. For example, after feral cat baiting in the Pilbara, northern quolls were detected using lowland habitats most frequently used by feral 371 cats, likely due to reduced predation pressure (Palmer et al. 2021). Similarly, on Groote 372 Eylandt-an island in the Northern Territory with a low abundance of northern quoll 373 predators-northern quolls occupied, had better body condition, and fed within a broader 374 dietary niche within savanna woodland compared to rocky habitat (Thomas et al. 2021). 375

376

The rocky habitat preferred by northern quolls [in the presence of feral cats] in the Pilbara is 377 naturally fragmented by spinifex sandplain and (sometimes) by riverbed (Moore et al. 2021b; 378 379 Van Vreeswyk et al. 2004). Therefore, northern quolls must travel through these habitats to reach isolated rocky habitat patches. When present, northern quolls selected activity areas in 380 381 locations with higher percentage cover of riverbed. Conversely, activity areas were larger when they contained higher percentage cover of spinifex sandplain. Spinifex sandplain covers great 382 383 expanses between rocky habitat and does not offer much protection to northern quolls, with a lack of denning structures or shelter due to low habitat complexity (Hernandez-Santin et al. 384 2022; Moore et al. 2021b). The increased travel time caused by having large amounts of 385 spinifex sandplain within their activity areas likely exacerbates the already increased risk of 386 387 predation for northern quolls in this habitat, and may negatively affect their foraging efficiency or fitness (Perry and Pianka 1997). This is supported by the fact that northern quolls in the 388 Pilbara are less abundant in landscapes where rocky habitat is more fragmented (Moore et al. 389 2022). A return to landscape management techniques, such as traditional mosaic burning, may 390 391 reduce the large-scale burning of spinifex sandplain, creating increased habitat complexity (Greenwood et al. 2021). When coupled with effective feral cat management (Cowan et al. 392 2020a), this may decrease feral cat success in spinifex sandplain and increase the usability of 393 this habitat by northern quolls (Doherty et al. 2015)—like mosaic burning has done for other 394

small Australian species (Bliege Bird *et al.* 2013; Holland and Bennett 2007; McDonald *et al.*2016).

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The selection of areas with increased cover of riverbed by northern quolls is likely because 398 riverbed is often associated with rocky habitat and may facilitate movement and foraging 399 400 opportunities (Ruprecht 1996). Hernandez-Santin et al. (2016) found that the distribution of northern quolls in the Pilbara was positively associated with creek lines, but the distribution of 401 402 feral cats was not, highlighting potential benefits of using this habitat for quolls, as for many 403 small terrestrial vertebrates (Sánchez-Montoya et al. 2016). However, this habitat is also likely 404 important for the dispersal of larger predators of the northern quoll in some instances, including feral cats and dingoes (Canis dingo) (Williamson et al. 2021; Wysong et al. 2020). Riverbeds 405 may also offer food for northern quolls. Here, riverbeds were dry, but often hold surface water 406 in the form of puddles for much longer than the surrounding landscape (Smit and Grant 2009). 407 408 In a mesic environment in Queensland, Pollock (1999) found that ~60% of northern quoll locations were less than 200 m from permanent water, while Hill and Ward (2010) noted that 409 410 in the Northern Territory there was higher prey availability for northern quolls near water sources. Therefore, riverbeds may facilitate a form of landscape complementation for northern 411 412 quolls, where quolls benefit from the resources available within two key habitats (i.e., rocky habitat and riverbed) (Dunning et al. 1992; Nimmo et al. 2019). Previously, emphasis has been 413 414 placed on protecting or attempting to replicate only rocky habitat for northern quolls (Cowan et al. 2020b). However, this emphasises the importance of considering potential dispersal 415 416 routes and supplemental foraging habitats when planning for northern quoll conservation and 417 management (Bennett 1990; Doherty and Driscoll 2018).

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419 Our study adds to the growing body of knowledge that suggests that northern quolls require rugged, rocky habitat for survival in the Pilbara, and that their space use is driven by selection 420 for habitats which provide shelter from larger predators such as feral cats. This study also 421 422 provides a baseline for future studies to investigate how human disturbances such as fire, mining, and agriculture influence northern quoll movement and space use (Moore et al. 2021a). 423 424 The destruction of complex rugged habitat or efficient movement corridors, and replacement with simple habitat—such as cleared land or spinifex sandplain—will likely have dramatically 425 negative effects on northern quolls, including expulsing local populations, or having 426 cumulative impacts on the broader population by limiting movement or causing populations to 427 428 become isolated. Alternatively, it may force northern quolls to travel longer distances to gain

429 the resources needed for survival, potentially decreasing individual body condition and leaving quolls exposed to increased predation, risk of fire, and grazing pressures. The conservation of 430 431 northern quolls in the Pilbara should value existing rugged, rocky habitat which provides important food resources and protection from predation, as well as efficient movement 432 pathways such as riverbeds that facilitate dispersal. Spinifex sandplain may also offer foraging 433 resources for northern quolls in the Pilbara, but currently, predation risk is likely driving its' 434 435 avoidance. Management actions to increase complexity of spinifex sandplain may drive higher use of this habitat by northern quolls, and all conservation actions should be coupled with 436 437 effective management of invasive predators such as feral cats.

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450 Data availability statement

451 Data used in this study have not been published publicly to protect this cryptic, endangered
452 species. Each dataset is managed by separate authors and organisations; therefore, data can be
453 requested by contacting the respective authors of this study.

454

455 **Conflict of interest**

456 The authors declare no conflict of interest.

457

458 **Declaration of funding**

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853 **Figure legends**

Figure 1. A map of the locations of the four sites in the Pilbara region of Western Australia where northern quolls were tracked between 2014 and 2018. Black points represent study sites and white points represent major towns close to study sites. The satellite base map was sourced from ESRI (2021).

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Figure 2: Examples of the dominant habitat types at our study sites in the Pilbara region of Western Australia: a) rocky habitat, which often rises above the landscape to form outcrops; b) spinifex sandplain, which fragments rocky habitat and can stretch for kilometres; c) *Acacia* stands, which can form thick patches throughout the rocky spinifex matrix; and d) riverbed, which consists of a sandy base between rocky habitat and vegetation. Photographs: Cowan, M.

Figure 3. Habitat variables significantly selected or avoided by northern quolls were: the proportional cover of a) rocky habitat, b) riverbed, and c) spinifex sandplain, and d) the median topographic ruggedness index (median TRI), Black points represent data values within 'available' and 'used' northern quoll activity areas., grey points represent outliers, and red asterisks signify a significant difference between 'used' and 'available' activity areas. Boxplots show the distribution of the data for available and used activity areas.

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Figure 4. Habitat maps of the four sites in the Pilbara region of Western Australia with examples of a) two female northern quoll activity areas at Red Rock showing use of rocky habitat, riverbed, and spinifex sandplain; b) a male northern quoll activity area at Python Pool covering rocky habitat and *Acacia* stands but also large amounts of spinifex sandplain; c) a female northern quoll activity area at Cattle Gorge primarily using rocky habitat; and d) a female northern quoll activity area at De Grey Ridge using primarily rocky habitat and *Acacia* stands. Habitat maps were derived from Sentinel-2 imagery (USGS 2020).

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Figure 5. The a) coefficients, and b) predicted effects of the top-ranked model (spinifex sandplain) determining northern quoll activity area. Northern quoll activity area was log₁₀ transformed to increase normality. In plot a), points reflect coefficients, thick bars represent the standard error, thin bars represent 95% confidence intervals, and the red dashed line represents the zero line (zero difference from the intercept). All bars which do not touch the zero line are significant. The intercept reflects the reference level: 0% cover of spinifex
sandplain. For plot b), the black line represents the predicted effects, and the red band
represents the 95% confidence interval.

889 Tables

Table 1. The mean and standard error (SE) of short-term activity area size and percentage cover of each habitat type for all northern quolls, female northern quolls, and male northern quolls. Means and SE for habitat cover (%) reflect all short-term activity areas (i.e., including those tracked for less than seven nights). However, short-term activity area size (ha) marked with an asterisk (*) reflects only activity areas which reached seven nights. Individual characteristics for each tracking event can be found in Table S4.

Measure	Sex	Short-term activity area size (ha)*	Rocky habitat (%)	Spinifex sandplain (%)	Acacia stands (%)	Riverbed (%)
Mean	All	153.42	23.14	57.09	12.68	4.86
	Female	91.24	27.07	50.95	13.89	4.98
	Male	215.61	13.33	72.44	9.66	4.57
SE	All	38.69	3.12	3.86	3.94	1.27
	Female	24.39	0.03	0.04	0.05	0.02
	Male	61.75	5.97	4.55	2.74	1.78

Table 2. Outputs from BBMMs and GLMMs for northern quoll habitat selection. Habitat types
in bold denote that used activity areas differed significantly to the intercept (available activity
areas). SE represents the standard error.

Habitat variable	Activity area type	Coefficient	SE	t value	p value
Rocky habitat	Intercept	-2.48	0.09	-27.88	< 0.001
	Used	1.08	0.25	4.32	<0.001
Riverbed	Intercept	-9.55	0.12	-81.62	< 0.001
	Used	0.92	0.31	2.92	0.004
Spinifex sandplain	Intercept	0.87	0.07	11.69	< 0.001
	Used	-0.79	0.23	-3.41	<0.001
Acacia stands	Intercept	-2.44	0.06	-41.68	< 0.001
	Used	0.19	0.18	1.03	0.302
Median TRI	Intercept	0.63	0.31	2.00	0.140
	Used	0.79	0.18	4.48	<0.001

902 Table 3. Model selection outputs for possible determinants of northern quoll activity area size, offset for the number of nights tracked. Rocky habitat, riverbed, and spinifex sandplain are the 903 904 proportion of the activity area comprising that habitat type, median TRI is the median topographic ruggedness index of the activity area, sex is whether the quoll was male or female, 905 and weight is the body weight of the individual. Models are ranked in descending order from 906 best to least supported. K represents the number of estimated parameters for each model, AICc 907 908 represents the Akaike's Information Criterion, \triangle AICc indicates the delta AIC value, and wi AICc indicates the level of support for each model. Log-likelihood and model fit are also 909 provided for each model. Models in bold are those which had substantial support (Δ AICc <2, 910 Burnham and Anderson 2001; Mac Nally et al. 2018). 911

Rank	Model	Κ	AICc	Δ AICc	wi AICc	Log-likelihood	r^2
1	spinifex sandplain	4	43.05	0	0.56	-15.3	0.20
2	median TRI	4	45.84	2.79	0.14	-16.7	0.02
3	riverbed	4	46.5	3.45	0.1	-17.03	0.13
4	rocky habitat	4	46.98	3.93	0.08	-17.27	0.03
5	weight	4	47.47	4.42	0.06	-17.51	0.04
6	sex	4	47.74	4.7	0.05	-17.65	0.01

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914 Short summary for online Table of Contents

To effectively conserve species, we must have a good understanding of the key habitats that they use or avoid. We investigated the habitat use of the endangered northern quoll and found that they primarily selected areas with higher proportions of rugged, rocky habitat and riverbed, and avoided areas with higher proportions of spinifex sandplain—a habitat which caused quolls to have larger activity areas. These findings will inform conservation efforts to increase protection of key habitats for the endangered northern quoll.