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RESEARCH ARTICLE

A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes

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Abstract

Context Research on the impacts of anthropogenic habitat fragmentation has dominated landscape ecology for decades, yet our understanding of what drives species' distributions in naturally fragmented landscapes remains limited.

Objectives We aimed to (i) determine whether rocky patches embedded within a 'matrix' of fire prone grasslands act as naturally fragmented landscapes for an endangered marsupial predator, the northern quoll (*Dasyurus hallucatus*), and (ii) reveal the extent to which within-patch, patch, landscape variables, and matrix condition drive the occurrence of northern quolls.

Methods We deployed remote sensing cameras for a total of 200 nights, at 230 sites spanning rocky and grassland habitats across 6000 km^2 of the Pilbara bioregion of Western Australia. We examined the influence of within-patch, patch, landscape variables, and matrix condition on northern quolls using Generalised Linear Mixed Models.

Results We found strong evidence that northern quoll habitat is naturally fragmented, observing higher occurrence and abundance of quolls in rocky patches than the surrounding grassland matrix. Within rocky patches, quolls were more likely to use patches with higher vegetation cover and den availability (within-patch), lower amounts of edge habitat relative to patch area (patch), and larger amounts of surrounding rocky habitat (landscape). When quolls entered the matrix, they tended to remain in areas with high vegetation cover, close to rocky patches.

Conclusions Species occurrence in naturally fragmented landscapes is influenced by factors operating at multiple scales. Rocky habitats are naturally fragmented and vital to the conservation of a range of taxa around the world, including the northern quoll.

Supplementary Information The online version of this article (https://doi.org/10.1007/s10980-021-01207-9) contains supplementary material, which is available to authorized users.

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Introduction

Species frequently inhabit fragmented landscapes, where patches of suitable habitat are embedded within a hostile 'matrix' of unsuitable habitat (Fahrig 2003). Meta-population (Hanski 1994) and island biogeography theory (MacArthur and Wilson 2001) have shaped research on fragmented populations, whereby fragmented landscapes are viewed as consisting of habitat and non-habitat. 'Non-habitat' often arises in human modified landscapes through land clearing for agriculture and urbanisation (Hobbs and Saunders 1994). Landscapes that are naturally fragmented have habitat patches embedded in a relatively unmodified matrix that is nonetheless less suitable to a given species (Driscoll 2005). Examples of naturally fragmented landscapes include patches of humid high elevation forests surrounded by dryer vegetation at lower elevations for bird species in Mesoamerica (Watson and Peterson 1999), and isolated patches of suitable cliff habitat dispersed within an otherwise flat landscape for plant species in south-eastern Canada (Haig et al. 2000).

Within human-caused fragmented landscapes, habitat selection depends on variables operating at three spatial hierarchies: within-patch, patch, and landscape variables (Thornton et al. 2011). Within-patch variables are those that determine patch quality for a species, such as the abundance of food resources or the availability of shelter sites within the patch (Thornton et al. 2011). For example, tree hyraxes (*Dendrohyrax arboreus*) are less likely to occupy patches where high levels of wood removal has occurred, presumably due to a reduction in available denning hollows (Lawes et al. 2000). The size and shape of patches are characterised as patch variables (Thornton et al. 2011), each of which can influence species occurrence by limiting populations size (Bennett et al. 2006), and exposing patch-dependent species to edge effects (Andrén 1995). Finally, landscape variables relate to conditions surrounding a patch, such as the availability of further habitat and the condition of the matrix (Thornton et al. 2011; Driscoll et al. 2013).

While the amount of habitat in a landscape is a well-established predictor of species occurrence (Thornton et al. 2011), there is growing recognition of the important role of matrix condition in influencing species persistence within fragmented landscapes (Ricketts 2001; Eycott et al. 2012). For example, a meta-analysis of 1015 species comprising a range of taxa found the overall influence of patch area was significantly weaker in patches separated by a natural matrix when compared to an anthropogenic matrix (Prugh et al. 2008). Understanding processes influencing species use of the matrix can be vital for species conservation. 'For example, Changes in fire management can promote collared lizard movement (*Crotaphytus collaris collaris*) through woodland a matrix surrounded by rocky habitat, resulting in increased occupancy of rocky glades (Templeton et al. 2011).

In our study, we test if rocky patches embedded within fire prone grasslands act as naturally occurring fragmented landscapes for the largest marsupial predator in north-west Australia, the endangered northern quoll (*Dasyurus hallucatus*). We then test how habitat variables measured at the within-patch, patch, and landscape scale drive northern quoll occurrence and abundance. Northern quolls previously occurred widely in northern Australia, but have since undergone substantial declines (Braithwaite and Griffiths 1994; Moore et al. 2019), likely due to a combination of threats including altered fire regimes (Woinarski et al. 2011), predation by feral predators (Oakwood 1997), and most recently, the arrival of cane toads; an invasive amphibian that can be fatally toxic when consumed by quolls (Oakwood 2004). The Pilbara bioregion in north-west Western Australia is the only mainland section of the northern quoll's range yet to be impacted by cane toads, and as such is regarded as a critical population for the species (Cramer et al. 2016). Here, quolls are known to occur on large, continuous rocky mesas, but less is known about their patterns of occurrence in naturally fragmented rocky landscapes, typically comprising patches of smaller to medium-sized granite outcrops.

Within these landscapes, a range of factors have the potential to be important predictors of quoll patch suitability, yet few have been formally tested. For example, at the within-patch scale, an important predictor may be the availability of denning habitat (small caves, crevices), used for sheltering in during the day (northern quolls are nocturnal) and storing young inside during the breeding season (Oakwood 2000; Cowan et al. 2020). At the patch scale, habitat suitability may be enhanced or reduced by factors such as the size and shape of rocky outcrops, as well as patch geomorphology, such has been demonstrated in other rock dependent species (Michael et al. 2008; Do Carmo and Jacobi 2016).

Further, given northern quolls use large home ranges that can exceed the size of a single rocky patch (Hernandez-Santin et al. 2020), the extent of rocky habitat surrounding patches may also be a determining factor in patch suitability. However, for quolls to access this additional rocky habitat they may be forced to traverse through a non-habitat matrix of spinifex grasslands, where they may be more likely to encounter predators (Hernandez-Santin et al. 2016), thus potentially creating a 'landscape of fear' (Laundré et al. 2001). The age and structure of spinifex vegetation is mostly determined by fire in northern Australia (Allan and Southgate 2002) and—— is therefore likely to be important in mitigating the risk of lethal encounters with predators such as dingoes and feral cats, with the latter known to hunt more efficiently in open landscapes (McGregor et al. 2015). Understanding the multi-scaled habitat requirements and constraints for northern quolls is particularly important in the Pilbara, as rocky habitats are increasingly being degraded or removed from the landscape as part of expanding mining activity (Majer 2014). Indeed, identifying patches of critical habitat that support northern quoll persistence has been identified as a key research and conservation priority (Cramer et al. 2016).

Materials and methods

Study area

This study was carried out across four properties situated within the Pilbara bioregion in north-west Western Australia. These were Indee Station, Mallina Station, Pippingarra Station and Yandeyarra Indigenous Reserve. Yandeyarra Indigenous Reserve is also a working cattle station. The study area encompassed the Karayarra and Nyamal Indigenous language groups. Vegetation across all study sites is dominated by hummock grasslands (*Triodia* spp.) that cover roughly 30 – 50% of the ground surface, with varying time since fire. Tree cover is sparse to non-existent across the study area, and is mostly comprised of mulga (*Acacia aneura*), snakewood (*Acacia xiphophylla*) and snappy gum (*Eucalyptus leucophloia*). Geology is characterised by largely flat sand plains scattered with greenstone ridges and granite. Climate within the study region is characterized by high temperatures and low annual rainfall. Average daily temperature maximums across the study period ranged from 28.4 °C (August 2017) to 44.1 °C (December 2018) (Australian Bureau of Meteorology 2020).

Study design

We employed a nested experimental design by establishing a total of 230 sites across 23 pre-defined site clusters (~75 hectares in size) across a 6000 km^2 study area in the Pilbara. Site clusters were chosen because they were comprised of rocky outcrops embedded within a matrix of spinifex grasslands, and thus constituted a likely naturally fragmented landscape for northern quolls. Within each cluster, we established ten sites: seven sites within rocky habitat and three sites within the spinifex grasslands surrounding the rocky outcrops (Fig. 1). Rocky sites were chosen to represent gradients of habitat quality (i.e., vegetation cover), outcrop size (area), shape (area-edge ratio), and geomorphology (see Table 1). Spinifex sites were positioned at either a small (~50 m), medium (~100 m), or large (~200 m) distance from rocky habitat, and were chosen to capture a gradient of vegetation ages, from recently burnt (<3 year), to mid-successional (4–10 years) and long unburnt (>10 years) vegetation using ArcMap 10.3 (ESRI 2011) and data from the Northern Australian Fire Information database (NAFI 2020). All sites were separated by at least 200 m.

In this study, a 'site' refers to a camera trapping station comprised of a Reconyx PC900 Hyperfire passive infrared triggered camera trap (Reconyx 2020). Cameras were oriented in one of two ways (vertical or horizontal) and within one of three arrays (combined, rocky, or spinifex grassland), and orientation was consistent within each array. Cameras were oriented in two ways for two reasons. First, to compare the capacity of vertical and horizontal cameras to detect quolls, as part of the broader monitoring program within which this study was embedded (Moore et al. 2020b). Second, to account for predicted differences

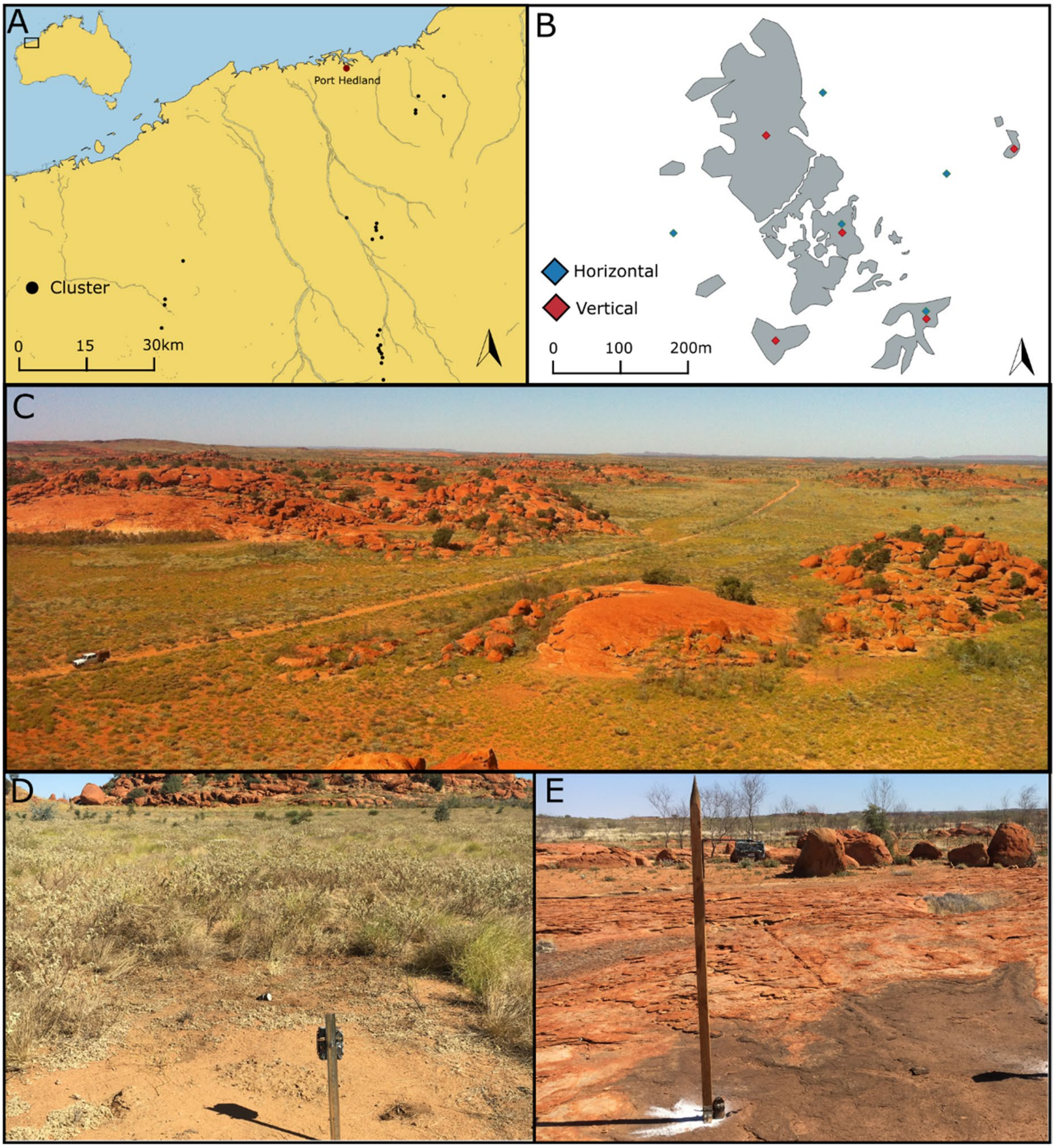

Fig. 1 **a** Site clusters located within the Pilbara bioregion in north-west Australia. **b** An aerial view of a typical site cluster, showing the position of vertical and horizontal facing camera traps deployed to detect northern quolls (*Dasyurus hallucatus*). **c** A typical 'site cluster' surveyed as part of the current study, comprised of granite outcrops surrounded by a matrix of spinifex (*Triodia* spp.) grasslands. **d** Horizontal camera trap set-up used at spinifex sites. **e** Vertical camera trap set-up used at rocky sites

in detectability within the two habitat types. Horizontally oriented cameras (i.e., facing outwards) have a larger detection zone, which can increase the number of detections (Meek et al. 2012), and are often more effective at detecting predators (Nichols et al. 2017; Moore et al. 2020b). Consequently, all cameras

Table 1 Summary of variables used to describe habitat properties within rocky and spinifex patches

Habitat variables	Description	Justification	Array	Scale
Habitat type (rock/spinifex)	Habitat classed as rocky outcrop or spinifex	Rocky habitat is a preferred habitat of northern quolls (Hernandez-Santin et al. 2016), and we expected northern quolls within site clusters to mostly occur in rocky habitat. To test this prediction we included habitat type as a predictor variables in combined site models	C	L
Den availability	The availability of potential den sites was measured along a 50 m transect, centred at camera locations. A sampling point was marked at each end of the transect, and in the centre. From each sampling point, 4 quadrants delineated by north, south, east and west and extending up to 10 m away from the sample were marked out, and the presence or absence of a potential den was noted within each quadrant. Den availability was represented as the proportion of total quadrants for each transect (n = 12) within which potential dens were found	Den sites are critical to sheltering northern quolls from predation, extreme heat and fire (Oakwood 1997). Dens are also used by female northern quolls to store young in prior to their independence (Cowan et al. 2020)	R	WP
Vegetative cover (< 0.5 m)	Percent cover of vegetation less than 0.5 m in height. Vegetation cover was assessed visually within a 25 m radius of camera sites	Small to medium sized vertebrates often associate with habitats possessing high vegetation cover because it can be more difficult for predators to detect them (Kotler 1984; Doherty et al. 2015a; Loggins et al. 2019). For the northern quoll, vegetation low to the ground such as spinifex is likely to provide the most effective cover from predators	R,S	WP/M
Patch geomorphology	Granite outcrops were classed into major granite landform groups as described by Withers (2000). Major granite landforms were nubbins, ridge line, and inselbergs	Northern quolls may prefer some geomorphologies to others, based on physical characteristics that influence prey and den availability, as well as vulnerability to predation	R	P
Patch area	Total surface area of rocky outcrop on which camera site was established	Patch area has been recognised as an important factor in driving species occurrence across a range a taxa (Thornton et al. 2011)	R	P
Patch shape	Total surface area/perimeter length of rocky outcrops on which camera sites was established	Decreasing patch area to edge ratio can have detrimental consequences for prey species due to increased vulnerability to predation (Andrén 1995)	R	P
Landscape extent	Total surface area of rocky habitat (ha) within a 150 m radius of camera sites, corresponding to the radius of median female northern quolls home estimates collected using GPS collars within the study area (Moore, unpublished)	A decreasing amount of suitable habitat in the area surrounding a patch may influence patch suitability by limiting the availability of nearby resources such as food and shelter (Bennett et al. 2006)	R	L
Distance to rocky outcrop	Distance in metres between sites and the closest rocky outcrop over 50m^2 in area	Rocky habitat is a preferred habitat of northern quolls, and northern quolls are likely less exposed to predation in these areas because they provide high densities of structural refuges (Hernandez-Santin et al. 2016). Northern quolls moving further away from rocky habitat into spinifex habitat where less structural refuges are available are likely exposed to increasing levels of predation risk	S	M
Years since burnt	Time in years between the time the site was last burnt and the beginning of the sampling period	Vegetation structure in northern Australia is strongly influenced by fire (Miller and Murphy 2017). Prey species such as the northern quoll are likely to be more exposed to predation risk in habitat that have been recently burnt, because the structural complexity of vegetation is reduced (Nimmo et al. 2019)	S	M

R rocky array, *S* spinifex array, *C* combined array, *WP* within-patch, *P* patch, *L* landscape, *M* matrix deployed in the spinifex matrix (n = 3 per cluster, n = 69 overall) and a subset of cameras deployed on rocky outcrops (n = 2 per cluster, n = 46 overall) were positioned horizontally to improve detection rates, particularly in the spinifex matrix where we assumed quolls would be scarcer and less detectable.

Horizontal cameras were attached to a tree stake 50 cm above the ground, with the camera lens and PIR sensors focused at a 10° angle toward the ground surface, facing south, and were baited using PVC canisters containing pilchards (fish). All other cameras on rocky outcrops (n = 5 per cluster, n = 115 overall) were positioned vertically. Vertically orientated cameras were attached to a right-angle bracket on a wooden tree stake 1.5 m above the ground, with the camera lens and PIR sensors focused directly at the ground surface. Horizontal cameras deployed on rocky outcrops were positioned with vertical cameras (Fig. 1), however because data from vertical and horizontal cameras are never combined, we refer to these as separate sites. All cameras were set to high sensitivity, and five images were taken at one second intervals per trigger. Sites were sampled for 100 days in the Pilbara dry season (August – November) and 100 days in the wet season (total nights = 200) (December – March) (Figure S1). We used a period of 100 days because it was sufficient to be 95% confident of northern quoll absence at a site within the site cluster using either a vertically or horizontally orientated camera (Moore et al. 2020b). Twelve site clusters were sampled over the 2017–2018 period, and the remaining eleven site clusters were sampled over the 2018–2019 period. Although subsequent analysis showed no difference in either nightly detection or the number of detections of northern quolls between vertical and horizontal cameras (Moore et al. 2020b), we do not combine cameras with different orientations into a single analysis at any point.

The three camera arrays allow us to ask different questions about quoll occurrence in both the rocky patches and the spinifex matrix. The first array, which we refer to as the *combined array*, grouped the horizontally orientated cameras at rocky sites with horizontally orientated cameras in the spinifex matrix (Fig. 1). This array allows a comparison of northern quoll occurrence and activity between rocky and spinifex habitat (i.e., to confirm that occurrence and abundance are higher in rocky habitats than spinifex grassland), to test whether these landscapes are naturally fragmented for quolls. The second array, which we refer to as the *rocky array*, included only the vertically orientated cameras on rocky outcrops. Vertical cameras were ideal for capturing unique spot patterns located on the dorsal surface of northern quolls, which we used to identify individual animals (see 'detection data' section below). The rocky array allowed us to ask questions regarding the extent to which within-patch, patch, and landscape variables affect quoll occurrence and abundance in rocky outcrops. Here, we employed a 'focal patch' design (sensu Kaplan and White 2002), where detections collected by each camera within the rocky array were used to measure northern quoll responses to habitat at all three levels (within-patch, patch and landscape) (Fig. 2).

The final array, which we refer to as the *spinifex array*, was comprised of all horizontally orientated cameras deployed in the spinifex matrix. The spinifex array allowed us to ask questions regarding how matrix conditions affect quoll occurrence in the spinifex matrix.

Detection data

When northern quolls were detected on vertical cameras, we used unique spot patterning as well as scarring located on the dorsal surface of animals to identify individuals from camera trap imagery, following a similar process outlined in Moore et al. (2020a) (also see; Hohnen et al. 2013; Diete et al. 2016). Images from each detection event were catalogued into separate folders, and then within folders, we screened images in order to select those that represented individual spot patterns, preferably from multiple angles. Images that contained less than roughly 30% of the northern quoll's dorsal surface were immediately excluded from further image analysis unless they contained other distinctive features that could be used to identify individuals (e.g. unusual scarring patterns, missing ears etc.). Most detection events had at least one image suitable for individual identification. At least one screened image from each detection event was then entered into I3S Spot (Den Hartog and Reijns 2016), a freely available software package that can be used to identify individual animals based on spot patterns. Recent studies have used I3S to assist users in identifying individual whale sharks (Araujo et al. 2019), killer whales (Denkinger et al. 2020), and lizards (Moore et al. 2020a). The package uses a two-dimensional linear algorithm to rank the likelihood of two images containing the same animal, based on the coordinates, shape, and size of an animal's spots (Cerutti-Pereyra et al. 2018). Once images had been ranked in I3S, at least two observers confirmed if suggested matches were the same animal. If no match could be found, the image was marked as a new animal. If a consensus could not be reached between the observers, the individual was marked as 'unidentifiable'. To assess the rate at which horizontal camera traps were visited by northern quolls, we defined independent detection events as detections separated by 15 min. This was because Diete et al. (2016) found consecutive northern quoll detections separated by between 10 and 15 min were as likely to be a different individual as they were the previous individual.

It is important to note that although we were able to individually identify animals in this study, our data was not suitable for mark-recapture analysis. The main reason for this was the sparseness of the data; sampling at patches was limited to a single camera, and thus the number of captures and recaptures at the majority of sites was insufficient to estimate abundance reliably in this way. Instead, we calculated the minimum number of animals known to be alive (MNA) (Krebs 1989) at each site; an abundance metric commonly used in ecology when more sophisticated measures are not available (Wauters et al. 2000; Baker et al. 2017; Onodera et al. 2017). MNA was calculated by summing the number of animals detected at each site in both seasons (dry, wet).

Statistical analysis

All data was modelled using generalized linear mixed effects models (GLMMs) in R version 3.6.2 (R Core Team 2019). These models allowed for the inclusion of 'site cluster' as random effect to account for spatial autocorrelation as a result of our nested

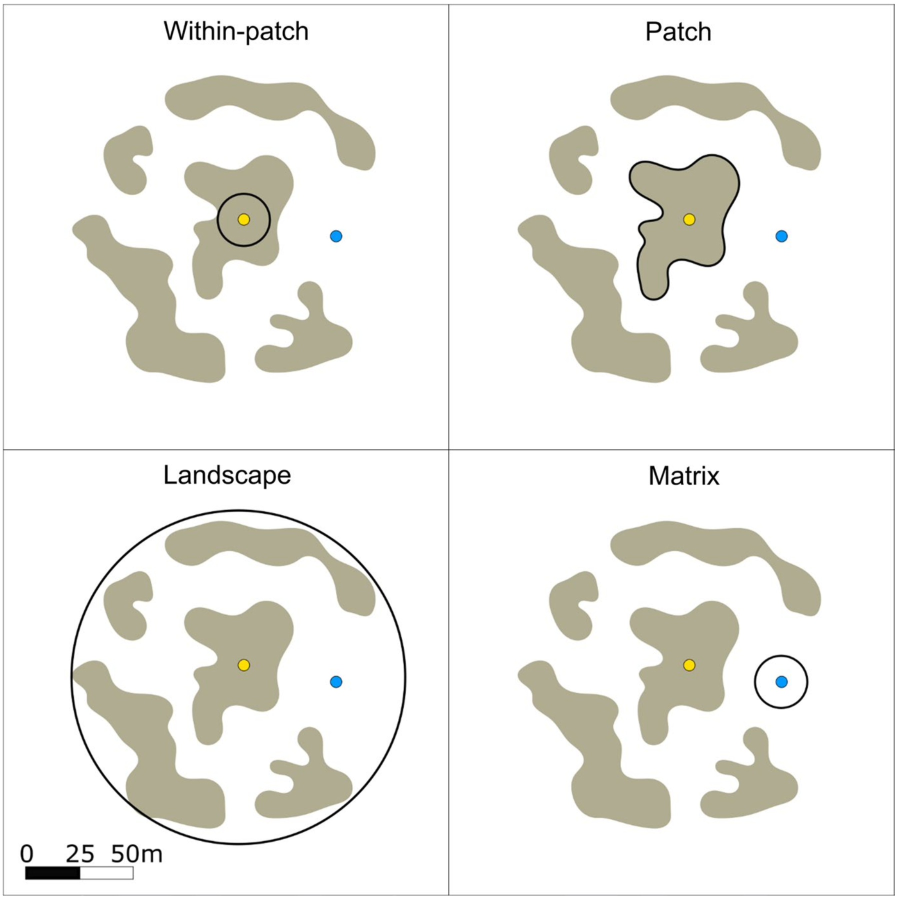

Fig. 2 An aerial view of the four scales (within-patch, patch, landscape, and matrix) at which northern quoll responses to habitat within fragmented landscapes were measured. Brown shading represents rocky habitat. The yellow dot represents a vertical camera site, and the blue dot represents a horizontal camera site. Bold outlines represent the scale in focus

experimental design. Preliminary analysis indicated that there were many sites across all arrays with no northern quoll detections, leading to zero inflation. Models that ignore zero inflation can produce biased parameter estimates (Potts and Elith 2006). To model zero-inflated data in this study, we used hurdle models fit using the package *glmmTMB*. Hurdle models are commonly used to model zero-inflated ecological data (Balderama et al. 2016; Brown et al. 2016; Cunningham et al. 2018) and consist of two components. The first component is the zero-inflated model, which describes the probability of species absence at a site (Potts and Elith 2006). To simplify the interpretation, we plotted model predictions as the probability of presence throughout (i.e., 1—probability of absence). The second component is the conditional model, which uses a zero-truncated error distribution to describe the relationship between model predictors and non-zero count data. Given hurdle models operate using a two-step process, fixed effects can vary between binary and count models (Potts and Elith 2006). To account for over-dispersion, we fit hurdle models with a zero-truncated negative binomial distribution (Lindén and Mäntyniemi 2011). To account for uneven sampling effort as a result of camera failures, all models included the number of nights cameras were operational as an offset term. All model fixed effects were scaled prior to analysis to improve model stability and allow direct comparisons between model coefficients (Harrison et al. 2018). We regarded fixed effects as being influential if the 95% confidence intervals of variable coefficients did not intercept zero (Nakagawa and Cuthill 2007).

We modelled data from the three camera arrays separately. Data from different seasons (dry, wet) was also modelled separately, to account for differences in habitat use and resultant varying levels of productivity between seasons. We found northern quoll detection data from the spinifex array were too sparse for hurdle models to be used effectively. To overcome this issue, we pooled data from the spinifex array across seasons (dry, wet), and converted count data to a binary format (presence/absence). We then modelled pooled spinifex array data using a GLMM fit with a binomial distribution in package lme4 (Bates et al. 2007).

To confirm that quolls were more common on rocky outcrops compared to spinifex grasslands, we used data from the combined array to build a univariate model of quoll presence/absence (zero-inflated response variable) and total number of independent northern quoll detections (conditional response variable) in relation to habitat type; a categorical predictor variable with two levels indicating whether the site was located on a rocky outcrop or within spinifex grasslands. To examine the importance of within-patch, patch, and landscape variables for northern quolls, we used data from the rocky array to model quoll presence/absence (zero-inflated response variable) and total number of northern quoll individuals (conditional response variable) in relation to the six rocky array predictor variables (Table 1). Within-patch variables were den availability and vegetative cover, patch variables were patch size, shape and geomorphology, and the landscape variable was habitat extent (amount of rocky habitat within a 150 m buffer of sites) (Table 1). Finally, using data from the spinifex array, we modelled the total number of independent northern quoll detections in relation to two variables describing matrix condition (vegetative cover less than 0.5 m in height and years since fire) in addition to distance to nearest rocky patch (Table 1). No variables included together in any model shared pairwise correlations > 0.50 (Table S2, S3).

To select the most parsimonious model for the rocky and spinifex array models, we built models with all possible subsets of habitat variables in both binary and count model components. We then used Akaike's Information Criteria adjusted for small sample size (AICc) to rank zero-inflated and conditional models separately. All model selection was conducted using the dredge function in R package MuMIn (Barton 2020). A total of 64 rocky site models and 8 spinifex array models were compared. Parameter estimates were assessed from the most parsimonious model. To examine if our best models were biased by residual spatial autocorrelation, we calculated the correlogram of the model residuals based on Moran's I, using the *Pgirmess* package (Giraudoux 2018). We found no evidence of spatial autocorrelation in the residuals of any of the models described in the Results section (Figure S3).

Results

Across all cameras and seasons, we recorded a total of 1814 independent northern quoll detections. The majority of detections were recorded within the rocky array (n = 1768, ~ 97.5%), and fewer detections were recorded in the spinifex array (n = 46, ~ 2.5%). A total of 837 (~ 46%) northern quoll detections were recorded during the dry season, and 977 (~ 54%) during the wet season. Using image data from vertical cameras, we were able to identify individual northern quolls in 70.2% of detection events, from which a total of 153 northern quolls were identified. We found there was a strong positive correlation between the number of northern quoll individuals detected at a site and the total number of independent detection events (Figure S2, Table S1). Three cameras failed in the dry season sampling period (spinifex array = 2, rocky array = 1) and three cameras failed in wet season (spinifex array = 3).

Combined array

The probability of northern quolls being detected within the rocky array (47.8%, CI 33.4% – 62.3%) was three times higher than within the spinifex array (15.9%, CI 7.3% – 24.6%) in the dry season, and also three times higher in the wet season (rocky array = 21.7%, CI 9.8% – 3.7%, spinifex array = 7.2%, CI 1.1% – 13.4%), although lower overall (Table 2, Fig. 3). The total number of predicted quoll detections was eight times higher within the rocky array (n = 8, CI 3 – 9) when compared to the spinifex array (n = 1, CI 0.2 – 4) in the dry season, and 20 times higher within the rocky array (n = 10, CI 3–33.3) when compared to the spinifex array (n = 0.5, CI 0.1 – 2.6) in the wet season (Fig. 3).

Rocky array

The most parsimonious model for the dry season rocky array included predictors measured at the within-patch scale (vegetative cover, den availability), the patch scale (patch shape) and the landscape scale (habitat extent) for the zero-inflated component, and the within-patch scale (vegetative cover) for the conditional component (Table 2). The probability of northern quoll occurrence increased significantly with increasing vegetation cover, den availability, and habitat extent, and decreased at sites with proportionally large amounts of edge habitat (patch shape) (Table 2, Fig. 4). The most parsimonious model for the wet season rocky array model also included predictors measured at the within-patch, patch and landscape scale; vegetative cover, patch shape, patch geomorphology and habitat extent as predictors for the zero-inflated component. The most parsimonious model for the conditional component was the null model (Table 2). The probability of northern quolls being active at sites increased significantly with increasing vegetative cover (0.5 m), and habitat extent and decreased at sites with proportionally large amounts of edge habitat (patch shape) (Table 2, Fig. 5).

Spinifex array

The most parsimonious model for the spinifex array included vegetative cover (0.5 m) and distance to rocky habitat (Table 2). The probability of northern quoll occurrence increased significantly with increasing vegetative cover, and decreased with increasing distance from rocky habitat (Table 2, Fig. 6).

Discussion

The distribution and abundance of species that occur in landscapes fragmented by humans is known to be driven by within-patch variables, patch variables, and landscape variables (Thornton et al. 2011), but far less is known about the responses of species to such factors in naturally fragmented habitats. We found northern quolls were significantly more likely to use rocky patches when compared to the spinifex matrix, irrespective of season, suggesting these landscapes are naturally fragmented to northern quolls. Habitat selection by northern quolls occurred at multiple scales: i) at the within-patch scale, quolls were more likely to use patches with more denning crevices and vegetation cover, (ii) at the patch scale, quolls were more likely to use patches with smaller amounts of edge habitat relative to patch area, and (iii) at the landscape scale, quolls were more likely to use areas with higher rocky habitat extent. Use of the matrix by quolls tended to occur in close proximity to rocky habitat, and was more common in areas with high vegetation cover. Together, these results indicate that critical habitat for northern quolls in the Pilbara is likely defined by large areas of condensed, complex rocky habitat, with intact vegetation occurring within and in the areas surrounding. More generally, our

Table 2 Response of northern quolls (*Dasyurus hallucatus*) to habitat variables at rocky, spinifex and combined (rocky and spinifex) sites in the Pilbara bioregion of Western Australia

Array	Season	Variable	Estimate	CI	Std. Error
Combined	Dry	*Conditional*			
		Intercept	− 2.01	− 12.50 to 8.49	5.35
		Habitat (rocky)	**2.60**	**1.04–4.16**	**0.79**
		Zero-inflated model			
		Intercept	1.66	1.01–2.31	0.33
		Habitat (rocky)	**− 1.57**	**− 2.44 to − 0.70**	**0.44**
	Wet	*Conditional*			
		Intercept	− 0.81	− 2.40 to 0.77	0.80
		Habitat (rocky)	**2.90**	**1.74–4.07**	**0.59**
		Zero-inflated model			
		Intercept	2.55	1.64–3.46	0.46
		Habitat (rocky)	**− 1.27**	**− 2.42 to − 0.12**	**0.59**
Rocky	Dry	*Conditional*			
		Intercept	0.52	0.04–0.99	0.24
		Vegetation cover (< 0.5 m)	**0.19**	**0.03–0.35**	**0.08**
		Patch area	0.23	− 0.03 to 0.48	0.13
		Zero-inflated model			
		Intercept	− 0.19	− 0.66 to 0.27	0.24
		Den availability	**− 0.63**	**− 1.15 to − 0.11**	**0.26**
		Vegetation cover (< 0.5 m)	**− 0.79**	**− 1.40 to − 0.17**	**0.31**
		Patch shape	**− 1.27**	**− 2.30 to − 0.24**	**0.53**
		Habitat extent	**− 0.72**	**− 1.38 to − 0.06**	**0.33**
	Wet	*Conditional*			
		Intercept	0.52	− 0.20 to 1.24	0.91
		Zero-inflated model			
		Intercept	− 0.82	− 2.61 to 0.96	0.91
		Geomorphology_Inselberg	1.33	− 0.62 to 3.30	1.00
		Geomorphology_Nubbin	1.90	− 0.01 to 3.82	0.98
		Geomorphology_Ridge	− 1.15	− 3.95 to 1.65	1.43
		Vegetation cover (< 0.5 m)	**− 0.94**	**− 1.58 to − 0.31**	**0.32**
		Patch shape	**− 0.67**	**− 1.23 to − 0.11**	**0.28**
		Habitat extent	**− 0.48**	**− 1.05 to − 0.07**	**0.28**
Spinifex	Dry + wet	Intercept	− 2.41	− 3.66 to − 1.52	0.53
		Vegetation cover (< 0.5 m)	**1.00**	**0.21 to 2.01**	**0.45**
		Distance to rocky patch	**− 1.24**	**− 2.49 to − 0.35**	**0.53**

Dry season models used data collected from August-November and wet season models used data collected from December to March. Significant results are shown in bold

results confirm the importance of understanding species' habitat requirements at multiple scales and the importance of matrix condition within naturally fragmented landscapes.

An extensive catalogue of literature predicts the occurrence of species metapopulations within landscapes fragmented by human activities, but our study adds to a smaller body of work focused on landscapes that are naturally fragmented. Here, we found multiscaled responses by northern quolls aligned closely with species responses in human fragmented landscapes (Thornton et al. 2011). In addition, we

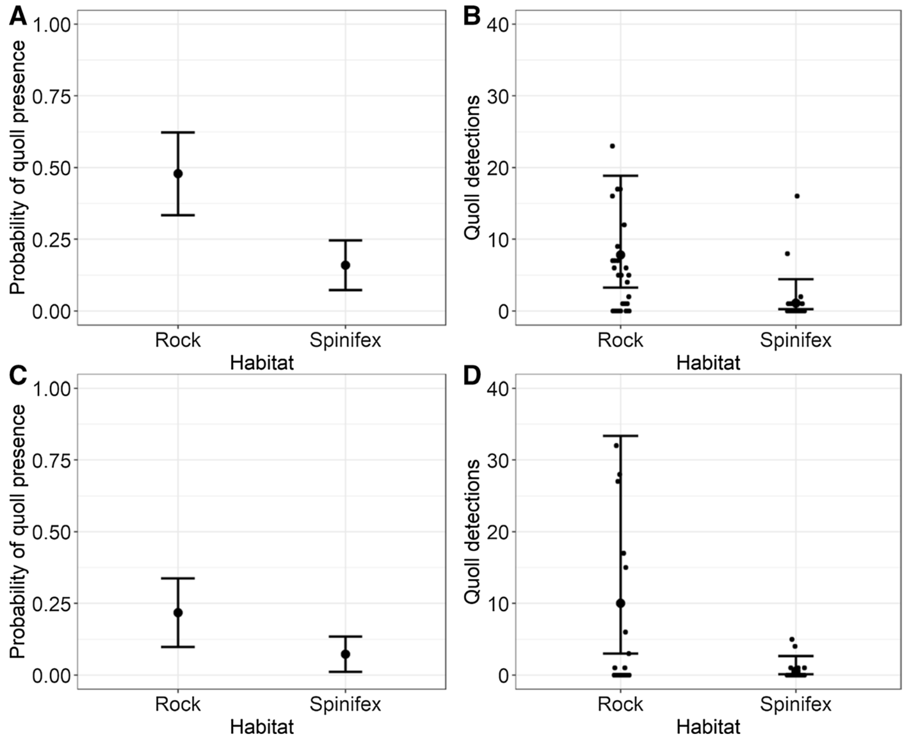

Fig. 3 Response of northern quoll (*Dasyurus hallucatus*) site use to habitat type in the Pilbara bioregion of northern Australia. Plots derived from hurdle models. **a** Changes in the probability of northern quoll presence at sites in response to habitat type in the dry season. **b** Changes in the total number of northern quoll detections at sites in response to habitat type in the dry season. **c** Changes in the probability of northern quoll presence at sites in response to habitat type in the wet season. **d** Changes in the total number of northern quoll detections at sites in response to habitat type in the wet season

found the response of northern quolls to naturally fragmented rocky habitat was similar to that of other species occurring in comparable naturally fragmented landscapes (Murray et al. 2008). For example, Central Australian rock-rats (*Zyzomys palatalis*) are more likely to occur at rocky patches with higher vegetation cover, and within landscapes that have greater habitat extent (Trainor et al. 2000). These commonalties in species responses to landscapes fragmented through both natural and human mediated processes suggest factors determining species habitat selection may be similar in both. However, in order to explore these comparisons further in more detail, future research focused on the occurrence of species within naturally fragmented landscapes is required.

While this study is the first to quantify the spatial influence of rocky habitats on northern quolls, previous studies have shown rocky patches to be important sources of refuge for persisting populations across their range, likely for a combination of factors, including providing shelter from fire (Oakwood 2000), predators (Hernandez-Santin et al. 2016), and climatic extremes (Cowan et al. 2020). Other species within the northern quolls range also rely on rocky patches (Trainor et al. 2000; Hohnen et al. 2016), and at a global scale, rocky structures provide critical habitat for taxa ranging from apex predators (Bleich et al. 1996; Harrison et al. 2019) to predators (Mares 1997) and prey species (Kotler et al. 1999; Metallinou et al. 2015). Nonetheless, rocky habitats are subject to a number of threats, including destruction for resource extraction and degradation by agriculture practises and recreation activities (Fitzsimons and Michael 2017). Further, species occurring in rocky habitats that are naturally fragmented, like northern quolls, have the potential to be impacted by additional threats that operate in the areas between rocky patch, such as fire and predation (Nimmo et al. 2019). This study adds to a growing body of research highlighting the importance of rocky patches as species habitat (Fitzsimons and Michael 2017; Michael and Lindenmayer 2018), and as such the need to protect them.

Within-patch variables

Within-patch variables determine patch quality, and therefore are often strong predictors of species occurrence and abundance (Thornton et al. 2011). We found this to be true for northern quolls, which were more likely to use patches comprised of increased

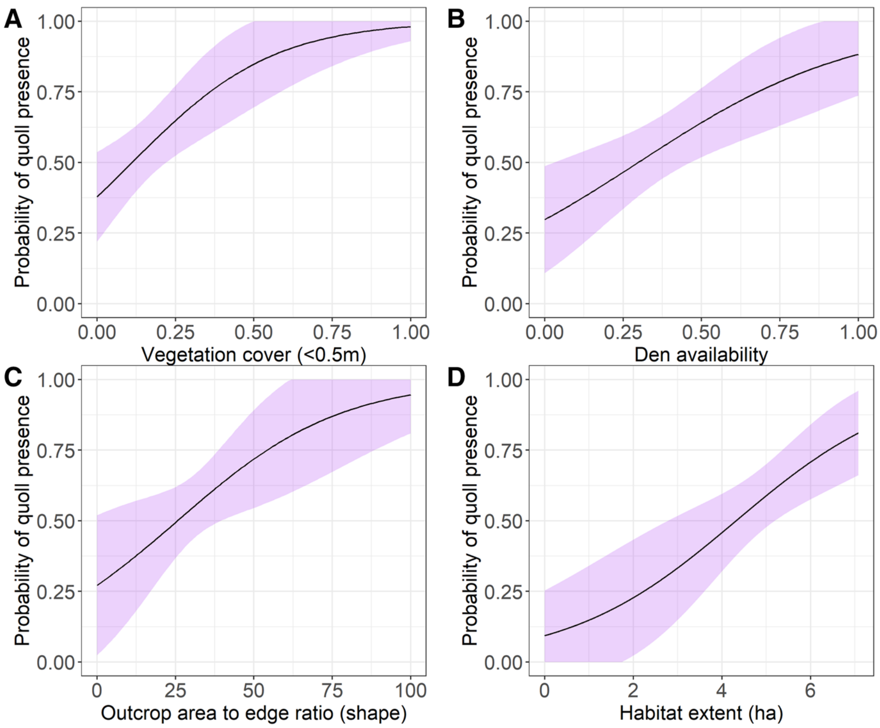

Fig. 4 Probability of northern quoll (*Dasyurus hallucatus*) site use within rocky patches during the dry season in the Pilbara bioregion of northern Australia. Plots derived from hurdle models. **a** Vegetation cover (<0.5 m) was measured as the proportion of ground covered with vegetation less than 50 cm in height within a 25 m radius of camera sites. **b** Den availability was measured as the availability of potential den sites at quadrats spread along a 50 m transect, centred at camera locations (Table 1). **c** Outcrop shape was measured as the area to edge ratio of rocky outcrops at which a camera site was positioned. Larger values describe sites with larger amount of basal habitat area when relative to edge habitat. **d** Habitat extent was measured as the amount of rocky habitat (ha) within a 150 m radius of camera sites. Dry season data was collected between August and November. Purple shading represents 95% confidence intervals

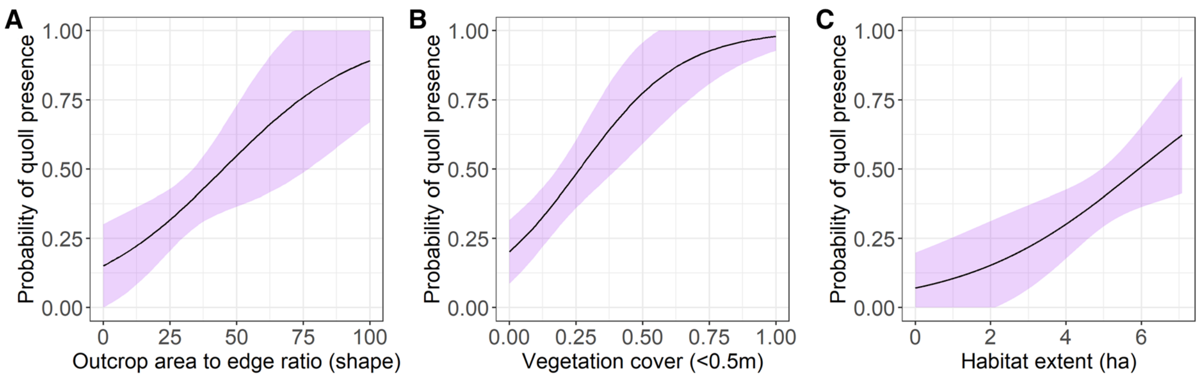

Fig. 5 Probability of northern quoll (*Dasyurus hallucatus*) site use within rocky patches during the wet season in the Pilbara bioregion of northern Australia. Plots derived from hurdle models. **a** Outcrop shape was measured as the area to edge ratio of rocky outcrops at which a camera site was positioned. Larger values describe sites with larger amount of basal habitat area when compared to edge habitat. **b** Vegetation cover (<0.5 m) was measured as the proportion of ground covered with vegetation less than 50 cm in height within a 25 m radius of camera sites. **c** Habitat extent was measured as the amount of rocky habitat (ha) within a 150 m radius of camera sites. Wet season data was collected between December and March. Purple shading represents 95% confidence intervals

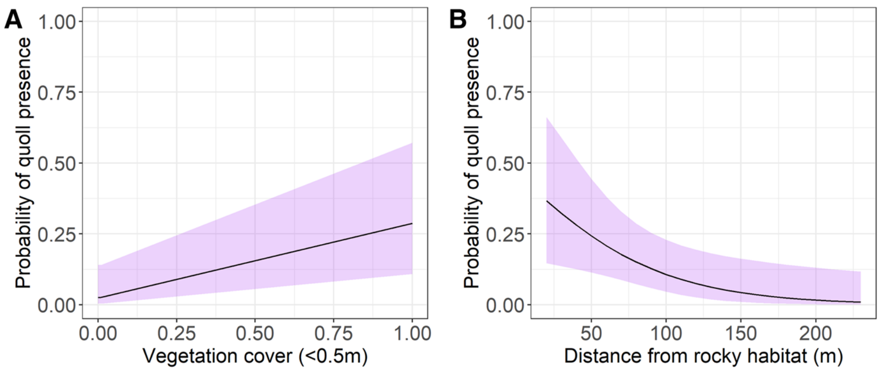

Fig. 6 Response curves, derived from generalised linear models, showing changes in the probability of northern quoll (*Dasyurus hallucatus*) occurrence at spinifex sites in response to habitat variables in the Pilbara bioregion in Western Australia. **a** Vegetation cover (<0.5 m) was measured as the proportion of ground covered with vegetation less than 50 cm in height within a 25 m radius of camera sites. **b** Distance from rocky patch was defined as the distance in metres between sites and the closest rocky patch over 50m^2 in area. Purple shading represents 95% confidence intervals

vegetation cover, regardless of season. Patches with increased vegetation cover probably provide increased food resources for northern quolls in the form of edible vegetation (seeds, flowers, fruits); an important component of the northern quolls diet in the Pilbara (Dunlop et al. 2017), while also supporting larger populations of prey species hunted by northern quolls, such as invertebrates, rodents, reptiles and smaller *Dasyurids,* given many of these species also rely on vegetation for both food and shelter (Menkhorst and Knight 2001; Wilson and Swan 2013). Increased vegetative cover may also provide northern quolls with increased cover from predators such as feral cats and dingoes, both of which are typically more common, and better hunters, in structurally simple habitats (McGregor et al. 2015; Geary et al. 2020; Stobo-Wilson et al. 2020). This was demonstrated during a recent reintroduction attempt, where northern quolls released into a recently burnt area within Kakadu national park were subject to extreme levels of dingo predation (Jolly et al. 2018). The association of northern quolls with potential den availability underscores the importance of shelter sites for quolls to escape fire, climatic extremes, and predators, as well as providing thermally stable nursery sites for offspring (Oakwood 2000). We recommend measures of den availability, such as the one used here, and elsewhere (Oakwood 1997; Hernandez Santin 2017), be incorporated as part of future northern quoll habitat suitability assessments, given they are time efficient and require little training to complete.

Patch variables

Northern quolls also responded to patch shape, a patch-level variable; quolls were more likely to occur at patches that had less edge relative to patch size. This is a likely 'edge effect' (Andrén 1995) whereby animals that occur in patches with lower area to edge ratios are more exposed to biological processes that are amplified around habitat transition zones, such as predation (Marini et al. 1995; Michel et al. 2016). For example, replica lizards positioned within edge habitats were significantly more likely to be attacked by predators when compared to replica lizards positioned in patches of remanent vegetation (Hansen et al. 2019). In Australia, feral cats and dingoes are thought to use habitat edges to improve hunting success (Doherty et al. 2015b; McGregor et al. 2017), and thus the risk of northern quolls being predated upon is likely higher in habitat comprised of greater amounts of edge habitat. Further, the severity and type of edge effects can determine the effective habitat area or 'core habitat' remaining within a patch, which can be an important determinant of patch quality for species (Laurance and Yensen 1991).

Landscape variables

Habitat extent has previously been identified as a major driver of species occurrence in patchy landscapes (Thornton et al. 2011), and we found this to be true within the current study; northern quolls were more likely to use patches that were surrounded by greater extents of rocky habitat. A likely explanation for this result is that northern quolls are engaging in landscape supplementation (Dunning et al. 1992), where individuals increase their access to resources by visiting patches outside of their 'home patch'. For example, Mexican mantled howler monkeys (*Alouatta palliata Mexicana*) living in fragmented forest landscapes are able to increase access to foods like fruits and flowers by visiting multiple patches (Asensio et al. 2009). This explanation may be particularly likely in the case of northern quolls given that they are predators, and as such may require access to areas of habitat larger than a single patch in order to meet their dietary requirements.

Matrix type can also influence species use and persistence within landscapes (Ricketts 2001; Eycott et al. 2012). Understanding factors that determine matrix permeability may be particularly important for northern quolls, because sub populations are prone to local extinction (Moro et al. 2019), and thus are dependent on dispersal for recolonization. Matrix type also plays a crucial role in maintaining functional connectivity between sub populations. For example, landscape heterogeneity is important for maintaining functional connectivity in the Allegheny woodrat (*Neotoma magister*), a small rodent that specialises on rocky outcrops (Kanine et al. 2018). We found that northern quolls tended to remain close to rocky habitats when entering the matrix, likely due to the quolls 'boundary response'; the tendency of species to either advance or retreat upon encountering a patch boundary (Fahrig 2007; Nimmo et al. 2019). Species that occupy patches surrounded by high-risk matrix types should most often exhibit strong boundary responses that lead them back to habitat patches where risk is reduced (Fahrig 2007). For northern quolls, crossing the boundary from rocky patches into spinifex matrix is likely to substantially increase predation risk (Hernandez Santin 2017), and so remaining close to rocky refuges could allow a rapid retreat to escape a predator. Similar behaviour has been observed in caribou, which typically remain less than 500 m from unburnt habitats (safer habitat) when moving within recently burnt habitat (riskier habitat) (Joly et al. 2003).

Differences in vegetation structure across the matrix can correspond to differences in predation risk, which can influence a species capacity to disperse through the matrix to other habitats (Nimmo et al. 2019). For example, white-shouldered fire-eye *(Pyriglena leucoptera*) survival was significantly lower when traversing through matrix with lower vegetation cover when compared to sites with high vegetation cover, likely due to higher predation risk (Biz et al. 2017). Hohnen et al. (2016) found northern quoll populations separated by less topographically rugged areas were typically more closely related, suggesting that such habitats are easier for quolls to disperse through. Although the results of the current study were unable to demonstrate how differences in vegetation structure specifically impacted quoll dispersal, they do demonstrate northern quolls were generally less likely to use matrix sites with lower vegetation cover, potentially as a response to increased levels of perceived predation risk. This result suggests landscapes where matrix vegetation is structurally simple may be less favourable for quoll persistence, due to lower probabilities of colonization. Given vegetation structure within the northern quolls range is typically determined by fire (Miller and Murphy 2017) and grazing pressure (Liedloff et al. 2001), this result has important management implications for northern quoll populations in fragmented landscapes. For example, managing landscapes to create 'corridors' of intact vegetation running between rocky habitat patches could facilitate increased inter-patch movement, potentially benefiting northern quolls by (i) reducing the vulnerability of isolated populations to local extinction, and (ii) increasing the likelihood of recolonization should local extinctions occur (Bennett 1990).

It's important to consider that factors such as sex may also influence the likelihood of quolls using matrix habitat. For example, a recent study focused on another short-lived marsupial, the southern brown bandicoot (*Isoodon obesulus obesulus*), found adults males were significantly more likely to use matrix habitat when compared to females, or juveniles of either sex (Maclagan et al. 2019). While we were unable to examine the influence of sex on matrix use as part of the current study, it's possible sex may have a similar effect in northern quolls given males are known to move considerably larger distances than females, particularly during the mating season (Hernandez-Santin et al. 2020).

Conclusion

The results of our study indicate that granite outcrops nested within spinifex grasslands act as naturally fragmented landscapes for northern quolls in the Pilbara, and add to a growing body of literature in highlighting the importance of rocky habitat to a range of taxa (Hohnen et al. 2016; Fitzsimons and Michael 2017). Further, we found northern quolls respond to habitat variables measured at the within-patch, patch and landscape scales, indicating species responses in naturally fragmented landscapes can mirror those and potentially aid predictions about the effects of fragmentation on species in more heavily-modified and human-dominated landscapes.

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