

Habitat suitability correlates with mean population fitness of a threatened marsupial predator

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ABSTRACT

Context. Measuring the quality of habitats necessary for the survival of threatened species is a priority for conservation management, but traditional metrics are often too costly to implement. As a result, many practitioners rely on proxies such as habitat suitability, which are measured by relating environmental variables to species occurrence data using habitat suitability models. However, little research has examined how these proxies relate to actual measures of habitat quality, such as body condition. **Aim.** By testing the relationship between habitat suitability and habitat quality – as characterised by mean population fitness – the aim of this study was to improve our understanding of ways in which we can reliably map habitat of high importance for a particular species, as well as habitats where populations are most susceptible to local extinction. **Methods.** We used data from a large-scale monitoring program on the northern quoll (*Dasyurus hallucatus*), a threatened marsupial predator, which collected data on three measures of population mean fitness (measured as body mass accounting for size, tail circumference, and body mass). We correlated these measures with habitat suitability derived from a habitat suitability model. **Key results.** We found quoll mean population fitness increased with increasing habitat suitability. In addition, we found mean population fitness increased with increasing topographic ruggedness, annual rainfall, rainfall variability, and decreasing distance to water, consistent with previous studies that suggest quolls are able to persist better in habitat where resource availability (shelter, food) is higher. **Conclusions.** Our findings demonstrate the usefulness of habitat suitability models for predicting habitat quality for a threatened predator at a large scale, and that predictions of habitat suitability can correspond with measures of fitness. In addition, they support previous studies in highlighting the importance of topographically complex habitat for this species. **Implications.** These findings have important implications for identifying both source populations, where species recruitment is likely to exceed mortality, and more vulnerable populations that may require targeted conservation interventions to ensure their long-term persistence and stability.

Keywords: body condition, conservation management, fitness, habitat quality, habitat suitability, northern quoll, Pilbara, threatened species.

Introduction

Spatial variation in environmental conditions influences the distribution of resources, and, in doing so, shapes habitat quality for species (Pulliam 2000). Habitat quality can be defined as the extent to which an environment provides the conditions necessary for individual and population persistence (Hall et al. 1997). Indicators of habitat quality include population-based metrics such as abundance or population growth, as well as individual based fitness metrics such as body condition, survival, or reproduction (Johnson 2007). Identifying high quality habitat for target species has long been a priority for conservation managers (Van Horne 1983), but the process of mapping its occurrence at scale poses substantial logistical challenges. Directly measuring indicators of high quality habitat (i.e. population growth, individual fitness) requires extensive field work that is prohibitively costly for many conservation organisations, particularly if the target species

is not charismatic (Fleming and Bateman 2016; Bellon 2019) or funding is scarce (Wintle *et al.* 2019).

In lieu of directly measuring indicators of habitat quality, conservationists are increasingly relying on proxies (Stephens *et al.* 2015) such as habitat suitability (Bean *et al.* 2014). Habitat suitability models combine species presence (and sometimes absence) records with environmental data to produce a gridded surface, where each cell is ranked on a scale of 0–1 in an attempt to estimate the probability or relative likelihood that a species is present given the environment (Elith *et al.* 2011; Guillera-Arroita *et al.* 2015). Although ready access to data and software required to run habitat suitability models has made them a popular tool, it remains unclear as to what extent habitat suitability correlates with indicators of habitat quality (Falcucci *et al.* 2009; Bean *et al.* 2014).

Previous research has shown habitat suitability can be an important predictor of species abundance metrics (VanDerWal *et al.* 2009; Fancourt *et al.* 2015); however, less attention has been directed toward the impact of habitat suitability on measures of individual fitness, defined as attributes that increase the likelihood of an individual to pass on its genes (Ellis *et al.* 2012; Lee-Yaw *et al.* 2022). Mean population fitness refers to measures of individual fitness averaged across all individuals in a population (Lee-Yaw *et al.* 2022). Although population growth is the most rigorous measure of population fitness, a host of fitness components have been used to measure mean population fitness when such data are not available, including body size (Bean *et al.* 2014; Mammola *et al.* 2019), growth rate (Wittmann *et al.* 2016), and body condition (Lunghi *et al.* 2018). Measures of body condition are often associated with individual persistence (i.e. survival) (Romero and Wikelski 2001; Johnson *et al.* 2006) and population persistence (Suorsa *et al.* 2003; Hinam and Clair 2008; Dunlop and Morris 2018), and can be obtained when animals are captured to provide an indicator of fitness (Jakob *et al.* 1996; Stevenson and Woods 2006). Measures of body condition in animals often comprise a measure of fat content relative to body size, given fat reserves are critical for energetically demanding activities such as dispersal and reproduction, as well as survival, particularly in resource-limited environments (Stevenson and Woods 2006).

Here, we make use of data from a large-scale monitoring program to examine the relationship between habitat suitability and mean population fitness using a threatened species of marsupial predator, the northern quoll (*Dasyurus hallucatus*). Once widespread across northern Australia (Braithwaite and Griffiths 1994), northern quolls have recently suffered large scale declines in both range and niche (Moore *et al.* 2019), and are now listed as endangered in Australia (DCCEEW 2022) and by the ICUN (Oakwood *et al.* 2016). Northern quolls are an ideal candidate species for testing the influence of habitat suitability on mean population fitness for several reasons. First, models mapping

northern quoll habitat suitability across their contemporary range exist and are easily accessible (Moore *et al.* 2019). Second, metrics of northern quoll body condition and their relationship to fitness have been studied for many years and are now relatively well understood (Heiniger *et al.* 2020; Rew-Duffy *et al.* 2020; Thomas *et al.* 2021). Finally, longitudinal monitoring data exists that captures northern quoll body condition across a suite of sites where habitat suitability estimates are available (Cramer *et al.* 2016; Dunlop 2016). By testing the relationship between habitat suitability and habitat quality as characterised by mean population fitness, we hope to improve our understanding of ways in which we can reliably map habitat of high importance for the species, as well as habitats where populations are most susceptible to local extinction.

Methods

The northern quoll

The northern quoll is a medium sized marsupial predator (300–1000 g) native to northern Australia. It is currently listed as endangered internationally (Oakwood *et al.* 2016), nationally (Department of the Environment 2016), and at the state level (Western Australian Government 2017). The Pilbara bioregion in Western Australia is regarded as a last remaining stronghold for the northern quoll, given it is the only major mainland population yet to be invaded by cane toads (Cramer *et al.* 2016; Indigo *et al.* 2023).

Study area

The Pilbara bioregion covers a 178 060-km² section of north-west Western Australia, bounded by the Indian Ocean in the west and sand deserts in the east and north (McKenzie *et al.* 2009) (Fig. 1). Climate in the region is characterised by hot summers and mild winters, especially in the northern section where average daily maximums exceed 35°C in summer (Sudmeyer 2016). Average annual rainfall is typically less than 350 mm and falls mostly between January and March when cyclone activity is at its peak (Sudmeyer 2016). Inter-annual rainfall variability is extremely high (BOM 2022). Surface geology is dominated by banded ironstone formations separated by rocky sand plains scattered with granite outcrops (McKenzie *et al.* 2009). Vegetation varies among subregions, but mostly comprises spinifex grasslands (*Tridodia* spp.) and open shrublands (*Acacia* spp.). Riparian zones support eucalypt (*Eucalyptus victrix*, *E. camaldulensis*) and paperbark (*Melaleuca argentea*) woodlands, and figs (*Ficus brachypoda*) and kurrajong (*Brachychiton acuminatus*) are common within and around breakaways and granite outcrops.

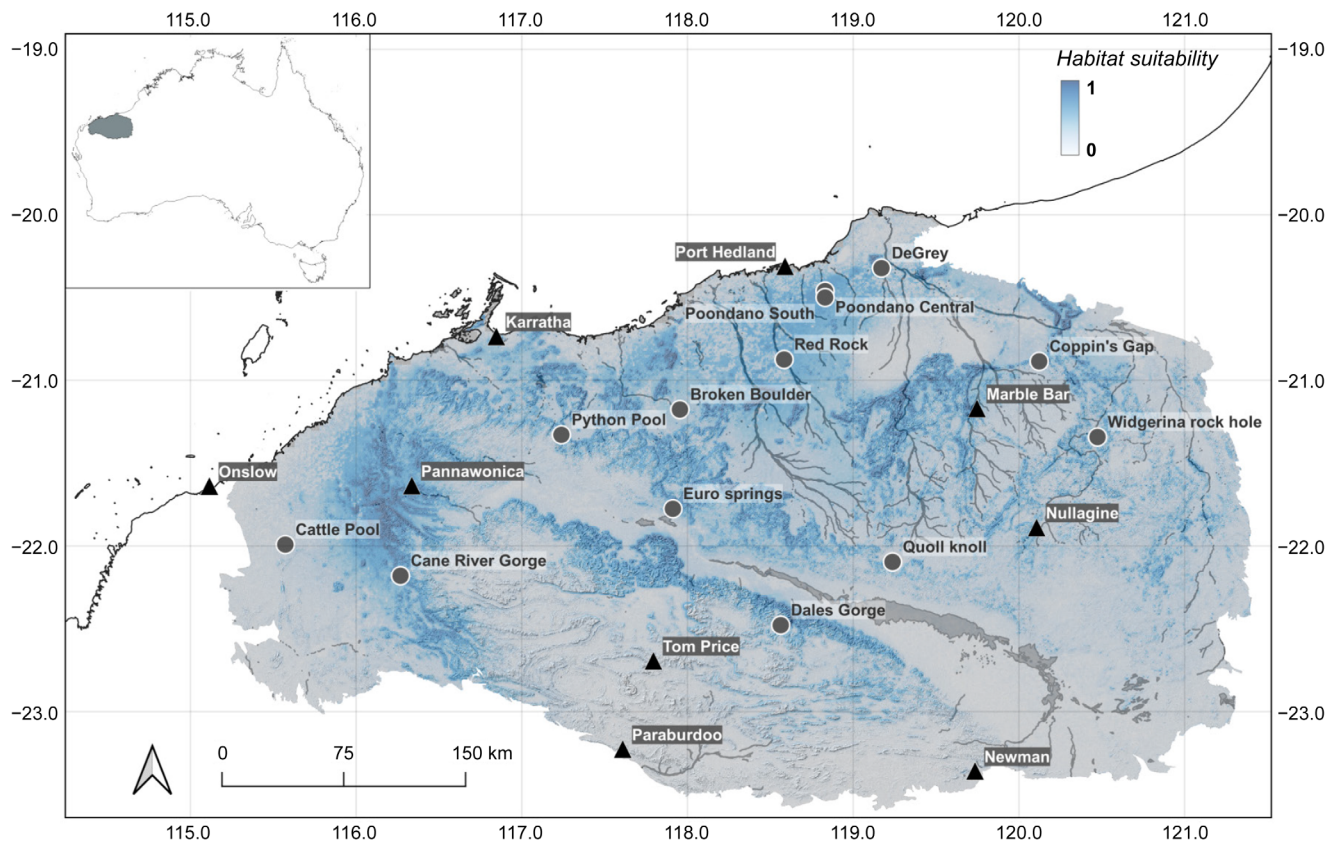


Fig. 1. Northern quoll (*Dasyurus hallucatus*) trapping sites (dark circles) used as part of the Pilbara northern quoll monitoring program, superimposed over northern quoll habitat suitability, as derived from Moore *et al.* (2019). Dark triangles are towns.

Trapping data

Live trapping data was collected as part of the Pilbara Northern Quoll Monitoring (PNQM) program – a program designed to track the status of northern quoll populations across the Pilbara bioregion (Cramer *et al.* 2016; Dunlop 2016). Here, we use data collected from 11 monitoring sites that were trapped at least once between 2014 and 2019. Either the entire set of 11 sites, or a subset thereof, were sampled annually using a trapping protocol developed specifically for northern quolls (Dunlop *et al.* 2014) (Supplementary Table S1). A larger number of sites were surveyed between 2014 and 2019, but some were excluded from this analysis due to low sample size. The protocol consisted of two transects of 25 traps, with each trap separated by 50 m and each transect separated by 200 m (Dunlop 2016). Traps were opened for four consecutive nights, and baited with a mixture of peanut butter, oats, and sardines. Northern quolls are regarded as semelparous, with males typically living for less than 1 year (Oakwood *et al.* 2001). To avoid times when males are either dead or in a deteriorated state, live trap surveys were conducted between March and September.

Data collected from trapped individuals included mass (g), head length (mm), pes (foot) length (mm), tail circumference

(mm) and sex (Dunlop 2016). In addition, all individuals captured were implanted with subcutaneous Passive Integrated Transponders (PIT) for individual identification. Data were first filtered by removing capture records that were missing information related to site, year, sex, mass, tail circumference, or head length. We also removed individuals that were not sexually mature (estimated using teeth condition and reproductive status). Age was not included as a predictor, given very few individuals were recorded living more than a year. Further, the age of adult individuals (1 year, 2 years etc.) could not always be assigned with a high level of confidence. Next, average body condition, tail circumference, and mass (Table 1) were calculated for each site within each year, for both males and females.

Habitat suitability and predictor variables

A measure of habitat suitability for all study sites was derived from a habitat suitability model developed as part of a previous study (Moore *et al.* 2019). The model was fit using the MaxEnt algorithm (Phillips *et al.* 2006), and covered the entire extent of the current study area (Fig. 1). The model output consisted of a spatial grid, with each cell measuring 1 km by 1 km. The value of each cell ranged from 0 to 1 and denoted the relative suitability of that location as a

Table 1. Measures of mean population fitness modelled in relation to habitat suitability for northern quolls (*Dasyurus hallucatus*).

Measure	Justification
Body condition	Measures of an animal's mass while accounting for size. Such measures are commonly used as proxies for habitat quality (Johnson 2007). A body condition index was calculated for the northern quoll by dividing body mass (g) by head length, following Jones (1996) who found head length was a more accurate gauge of quoll body size. Strong links between body condition and survival have previously been demonstrated in <i>Dasyurids</i> (Wolfe et al. 2004; Rew-Duffy et al. 2020). Northern quolls that occupy high quality rocky habitat exhibit higher body condition, as well as greater reproductive capacity and survival (Braithwaite and Griffiths 1994).
Tail circumference	Quolls store fat reserves in their tails (Thomson et al. 1985), and thus tail circumference has commonly been used as a metric for measuring northern quoll body condition (Schmitt et al. 1989; Oakwood 1994; Rankmore et al. 2008; Hernandez-Santin et al. 2019; Heiniger et al. 2020), as well as for other quoll species (Serena and Soderquist 1988). Female northern quolls are more likely to survive to at least 21 months of age with increased tail circumference (relative to body mass) (Rew-Duffy et al. 2020).
Mass	Body mass can be a useful indicator of habitat quality given it can be indicative of individual fat reserves (Wells et al. 2019), breeding activity (Rieger 1996), adult and juvenile survival (Sæther 1989; Plard et al. 2015), including for northern quolls (Griffiths et al. 2017). Variation in individual body mass has also been linked to resource availability (McNab 2010). In addition, body mass of northern quolls tends to peak during breeding season, indicating that it likely plays an important role in their reproductive success (Braithwaite and Griffiths 1994; Heiniger et al. 2020).

habitat for northern quolls. Model predictor variables included topographic ruggedness, distance to permanent water, elevation, precipitation seasonality, and annual precipitation. Model discrimination performance was high ($AUC > 0.9$), and the most important predictors of habitat suitability in the Pilbara were topographic ruggedness and precipitation seasonality (Moore et al. 2019). Values for predictor variables included in the habitat suitability model (ruggedness, annual rainfall etc.) were also recorded for each site used in this study. The data utilised for the creation of this model, as well as the raw model outputs, can be found in an online repository, which is referenced in Moore et al. (2019).

In order to account for inter-annual variation in resource availability, we measured the rainfall recorded at each site during the wet season (January to March) that preceded the trapping period. High rainfall during this period potentially affects quoll body condition by triggering a surge in resources, thereby increasing the abundance of key prey species such as insects and small vertebrates in the subsequent dry season. Although we explored the influence of dry season rainfall (April–December) in our preliminary analysis, the results indicated it was not as influential as the rainfall during the wet season, probably because inter-annual variation in rainfall is greater in the wet season.

Data analysis

All analysis was carried out using R ver. 4.1.2 (R Core Team 2021). The association between habitat suitability and mean population fitness (measured as body condition, tail circumference and body mass) was examined using Generalised Linear Mixed-Effects Models fit using the statistical package 'lme4' (Bates et al. 2015).

Two sets of models were used in this analysis. The first set was designed to examine the effect of habitat suitability derived from the habitat suitability model (Moore et al. 2019) on northern quoll mean population fitness. As such,

this set comprised global models that included average body condition, average tail circumference, and average mass as response variables. Habitat suitability (derived from the habitat suitability model; Moore et al. 2019), wet season rainfall, sex, and capture month (accounting for annual cycles in growth and resource availability) were set as fixed effects. Capture year was included as a random effect to account for any correlations in the data relating to inter-annual variations in climate that were not directly explained by the fixed effect of wet season rainfall.

The second set of models was designed to examine the effect of environmental factors on northern mean population fitness. This set of models again fit average body condition, average tail circumference (mm), and average mass as response variables, but fixed effects included elevation, topographic ruggedness, annual rainfall, rainfall seasonality, and distance to nearest permanent water source (Table S2) – all of which were used by Moore et al. (2019) to derive the habitat suitability layer used above. Sex and capture month were also included as fixed effects, and year was again included as random effect. Interactive effects between sex and other predictor variables were explored as part of preliminary analyses but received limited support and were therefore not included within final models.

Top models were ranked by AIC scores, corrected for small sample size (AICc), using the 'dredge' function in R package 'MuMIn'. Predictor variables were regarded as being strongly influential if the estimated 95% confidence intervals did not overlap zero (Nakagawa and Cuthill 2007). Model estimates were generated using the 'fixef' function from the package 'lme4' (Bates et al. 2015). Confidence intervals were generated using the 'confint' function in the R stats package (R Core Team 2021), and the 'ggpredict' function in the 'ggeffects' package (Lüdtke 2018). Model performance was assessed using marginal and conditional pseudo-R-squared values, calculated using the R package 'MuMIn' (Barton 2022). Marginal R^2 values represent the variance

explained by the fixed effects, and conditional R^2 values represent the variance explained by the fixed and random effects.

Results

The final trapping data set comprised 185 northern quoll individuals ($n = 95$ females, 90 males) captured over 6 years. A further 29 individuals were excluded because they were missing data or were not sexually mature. For female northern quolls, average body mass across all trapping sessions was 387.0 g (s.e. = 10.3 g), and average tail circumference was 49.8 mm (s.e. = 1.3 mm). Average male mass was 640.0 g (s.e. = 21.4 g), and average male tail circumference was 57.6 mm (s.e. = 1.3 mm).

The most parsimonious models of those examining the effect of habitat suitability on quoll body condition, tail circumference, and mass all included habitat suitability and sex as predictors (Table S3). The models for body mass and tail circumference also included previous wet season rainfall and capture month. Variance explained by the most parsimonious model was high for all three measures: body condition (Marginal $R^2 = 69.8\%$); tail circumference ($R^2 = 49.9\%$); and body mass ($R^2 = 71.2\%$).

Predicted body condition, tail circumference, and body mass all increased with increasing habitat suitability (Table 2, Fig. 2). Female and male body condition was 27.4% and 18.9% higher respectively, at sites with maximum habitat suitability (0.89) compared to sites with minimum habitat suitability (0.14). Similarly, predicted quoll tail circumference increased by 10.63 mm between minimum and maximum habitat suitability values, translating to a 20.4% increase for females, and a 17.7% increase for males. Body mass increased by 170 g ($F = 39.2\%$, $M = 24.5\%$). Body mass also increased significantly within increasing previous wet-season rainfall.

The most parsimonious models from those examining the effect of environmental factors on quoll condition all included topographic ruggedness and sex (Table S4). Elevation, annual rainfall, and month were also included in the top model for predicting quoll tail circumference and body mass (Table 3). Variance explained was high for body condition (Marginal $R^2 = 63.6\%$), tail circumference ($R^2 = 50.3\%$), and body mass ($R^2 = 75.8\%$) (Fig. 3).

Both female and male predicted body condition increased by 17.8% and 12.4% respectively when topographic ruggedness increased from the minimum recorded value to the maximum. Similarly, predicted tail circumference increased by 10.9 mm ($F = 21.0\%$, $M = 18.4\%$), and predicted body mass increased by 241.18 g ($F = 47.7\%$, $M = 31.7\%$). Predicted quoll tail circumference was higher earlier in the year (May, June) when compared with later months (August, September), and increased with increasing average

Table 2. Outputs from generalised linear mixed-effects models testing the effect of habitat suitability and sex on metrics of northern quoll (*Dasyurus hallucatus*) population mean fitness. Statistically significant results are indicated in bold.

Variable	Estimate	Lower 85% CI	Upper 95% CI
Body condition			
(Intercept)	5.6	5.0	6.1
Habitat suitability	0.5	0.2	0.7
Sex (male)	2.8	2.3	3.4
Tail circumference			
(Intercept)	47.6	40.5	54.9
Month 5	6.6	−1.0	13.8
Month 6	5.6	−1.9	12.9
Month 7	4.7	−3.3	12.4
Month 8	−2.5	−10.5	5.1
Month 9	−5.6	−14.7	4.1
Month 10	−4.1	−17.5	8.6
Habitat suitability	2.8	1.2	4.5
Previous wet season rainfall	1.8	−0.4	4.2
Sex (male)	8.1	5.4	10.8
Mass			
(Intercept)	364.0	259.4	468.6
Month 5	17.1	−99.1	133.2
Month 6	50.1	−66.7	166.9
Month 7	35.3	−79.1	149.8
Month 8	−9.7	−122.0	102.7
Month 9	0.0	−132.7	132.6
Month 10	−42.4	−236.9	152.0
Habitat suitability	45.5	19.6	71.5
Previous wet season rainfall	40.2	13.5	67.0
Sex (male)	261.1	217.9	304.4

annual rainfall (Table 3, Fig. 4). Quoll body mass also increased in response to increasing annual rainfall – body mass was 201.8 g ($F = 42.3\%$, $M = 27.6\%$) higher at the wettest site (annual rainfall = 595 mm) when compared with the driest site (annual rainfall = 114 mm).

Discussion

Our results suggest habitat suitability models are useful for estimating quoll mean population fitness: all three measures of mean population fitness were positively related to habitat suitability predicted by a habitat suitability model. These results are partially supported by a recent review of how species population mean fitness responds to habitat

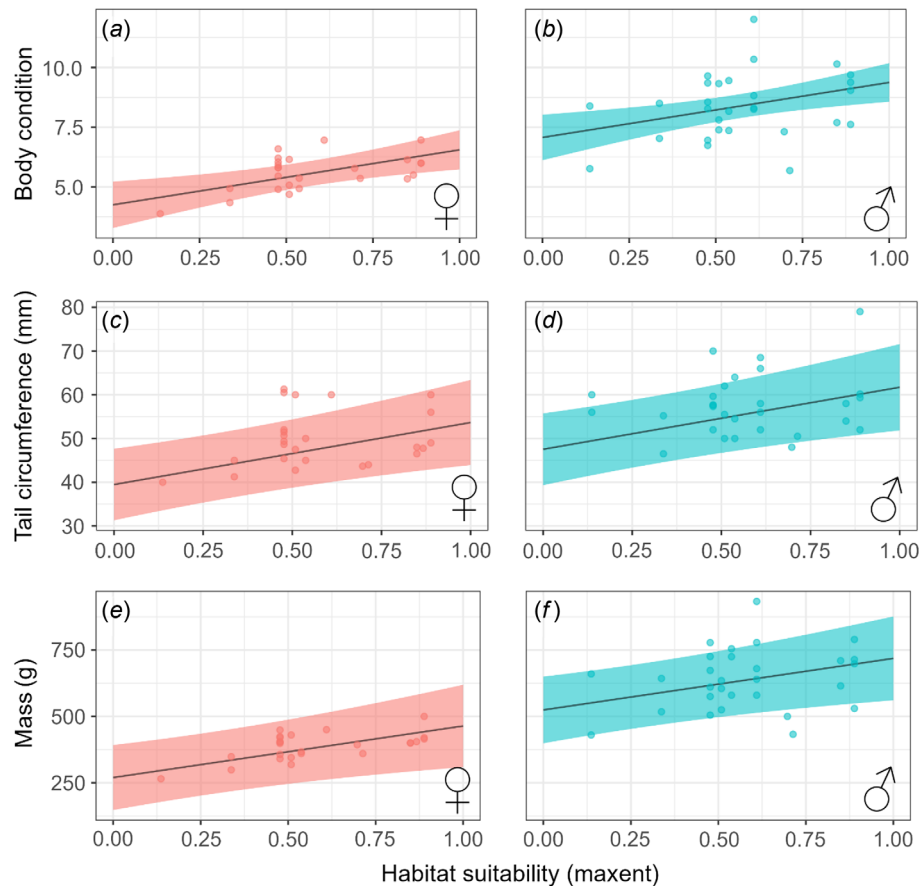


Fig. 2. The effect of habitat suitability and sex on metrics of northern quoll (*Dasyurus hallucatus*) population mean fitness, including body condition (a, b), tail circumference (c, d) and mass (e, f). Shading represents 95% confidence intervals.

suitability. Lee-Yaw *et al.* (2022) systematically reviewed 42 studies that compared habitat suitability predicted by habitat suitability models with measures of mean population fitness and found that only 15 studies supported the hypothesis that more suitable sites would have higher measures of mean population fitness, and 12 studies offered mixed support. However, they note that studies like ours that use measures of fitness components other than population growth rate tended to find more consistent relationships, as did studies focusing on individual species. For instance, Brambilla and Ficetola (2012) found that territories of red-backed shrikes (*Lanius collurio*) were smaller (indicative of higher quality habitat), Wittmann *et al.* (2016) found growth rates of grass carp (*Ctenopharyngodon idella*) were higher, and Lunghi *et al.* (2018) found that a salamander species (*Hydromantes flavus*) had better body condition in areas with high habitat suitability predicted from habitat suitability models. Studies that offered mixed support often found that a relationship existed for one measure of fitness but not for others, with Lee-Yaw *et al.* (2022) suggesting that such variability may arise due to variable relationships between fitness measures and environmental gradients, and

the negative relationships between demographic measures (i.e. demographic compensation). Our three measures are all conceptually related and would not be expected to negatively co-vary, potentially explaining the consistency of our results. Overall, this study is another example of habitat suitability models correctly identifying areas with high mean population fitness for an individual species.

Topographic ruggedness has been demonstrated to be an important predictor of species habitat quality globally (Esquerré *et al.* 2019; Dilts *et al.* 2023), largely due to the role of rugged habitats in mitigating predator-prey interactions (Fox *et al.* 1992; Forshee *et al.* 2022), providing protection from extreme temperatures (Chytrý *et al.* 2022) and fire (Krawchuk *et al.* 2016), and fostering a diversity of microclimates (Dobrowski 2011). Our study further confirms the importance of topographically rugged areas for northern quolls. Braithwaite and Griffiths (1994) found that northern quolls in topographically complex rocky habitat in the Northern Territory and Kimberley were in better condition than quolls in topographically simple savanna habitat, and survived longer. In this study, we showed that northern quoll body condition, tail circumference, and body mass

Table 3. Outputs from generalised linear mixed-effects models testing the effect of environmental factors and sex on metrics of northern quoll (*Dasyurus hallucatus*) population mean fitness including body condition (a, b), tail circumference (c, d) and mass (e, f).

Variable	Estimate	Lower 95% CI	Upper 95% CI
Body condition			
(Intercept)	5.6	5.1	6.1
Ruggedness	0.4	0.1	0.6
Sex (male)	2.7	2.1	3.3
Tail circumference			
(Intercept)	45.3	38.6	52.1
Month 5	9.6	2.8	16.1
Month 6	9.6	2.5	16.4
Month 7	6.9	−0.5	14.1
Month 8	0.3	−6.8	7.3
Month 9	−4.2	−12.6	4.2
Month 10	1.3	−10.6	13.1
Annual rainfall	1.8	0.0	3.6
Elevation	−1.3	−3.1	0.4
Ruggedness	3.5	2.0	5.0
Sex (male)	7.5	5.0	10.0
Mass			
(Intercept)	361.5	271.6	454.1
Month 5	12.7	−98.7	112.4
Month 6	93.6	−19.7	197.3
Month 7	32.5	−67.4	130.6
Month 8	−15.5	−115.0	82.5
Month 9	−9.0	−131.2	133.4
Month 10	−41.7	−227.3	139.0
Annual rainfall	50.7	25.1	77.4
Elevation	−29.7	−57.1	−3.2
Distance to water	1.9	−30.1	31.0
Rainfall variability	40.5	8.5	74.6
Ruggedness	78.0	45.0	113.0
Sex (male)	254.6	216.0	292.6

Statistically significant results are indicated in bold.

were positively associated with topographic ruggedness. Given that our measures of mean population fitness all relate to fat reserves, an obvious explanation of our findings would be that rugged areas have a greater abundance of food for northern quolls; however, a recent study suggests this may not be the case: [Hernandez-Santin et al. \(2022\)](#) did not find any difference in prey availability when comparing rugged rocky habitats with simple sandplain areas. However, they did find that rocky areas had a greater abundance of both dens and temporary shelters that are used to evade predation. This increased density of resources in rugged rocky habitat has been demonstrated to allow northern quolls

occurring here to use smaller home ranges when compared with open sand plain country ([Cowan et al. 2022](#)), likely reducing overall energy costs. Predators are also less common in rocky areas when compared with adjacent sandplains ([Hernandez-Santin et al. 2016](#)). Given that predation risk can compromise the ability of animals to acquire and maintain energy reserves by increasing stress and interrupting foraging activity ([Pérez-Tris et al. 2004](#); [Sabino-Marques and Mira 2011](#); [DeWitt et al. 2019](#)), it would be expected that quolls forage more efficiently in rocky habitat than in open sand plain country. This has been demonstrated in the Pilbara – [Murphy et al. \(2021\)](#) found northern quolls were more likely to visit a foraging site, and visit a foraging site more often, when the site was in structurally complex habitat compared with habitat that was less structurally complex. Our results build on the findings of these studies by providing evidence that rocky habitats increase body condition, supporting the idea that increased foraging opportunities and reduced predation risk can improve northern quoll mean population fitness in the Pilbara.

In addition to habitat suitability and topographic ruggedness, we found mean individual northern quoll mass and tail circumference increased with increasing average annual rainfall, and mass and tail circumference increased with increasing previous wet season rainfall. These trends are consistent with previous studies that have found habitats that receive higher rainfall are preferable for northern quolls ([Hohnen et al. 2016](#); [Moore et al. 2019](#); [von Takach et al. 2020](#)). Northern quolls are likely able to accrue greater body mass in areas where water availability is higher due to increased primary productivity, resulting in increased availability of prey such as insects, small rodents and reptiles ([Braithwaite and Muller 1997](#); [Letnic and Dickman 2005, 2010](#)). This theory is supported by previous studies that have demonstrated that northern quoll body mass declines following years of unseasonably low rainfall ([Heiniger et al. 2020](#)), and northern quoll declines and local extinctions have been most prevalent within the arid parts of their range ([Braithwaite and Griffiths 1994](#); [Ziembicki et al. 2013](#); [Moore et al. 2019](#)). Similarly, quoll body mass may be lower at higher elevations given availability of potential prey such as insects may be lower here, due to cooler and drier conditions ([Hodkinson 2005](#)).

Northern quoll condition is known to fluctuate with season ([Oakwood 1994](#); [Hernandez-Santin et al. 2019](#)), and we found evidence of this in our study; tail circumference measurements were significantly higher in May and June, before declining to their lowest point in September. Although month did not have a significant effect on other indices of population mean fitness, boxplots of the raw data suggested similar trends may exist for mass and body condition but were too weak to be detected in our analysis. Observed declines in tail circumference are likely attributable to two primary factors. Firstly, the semelparous reproductive strategy of male quolls, in which they invest

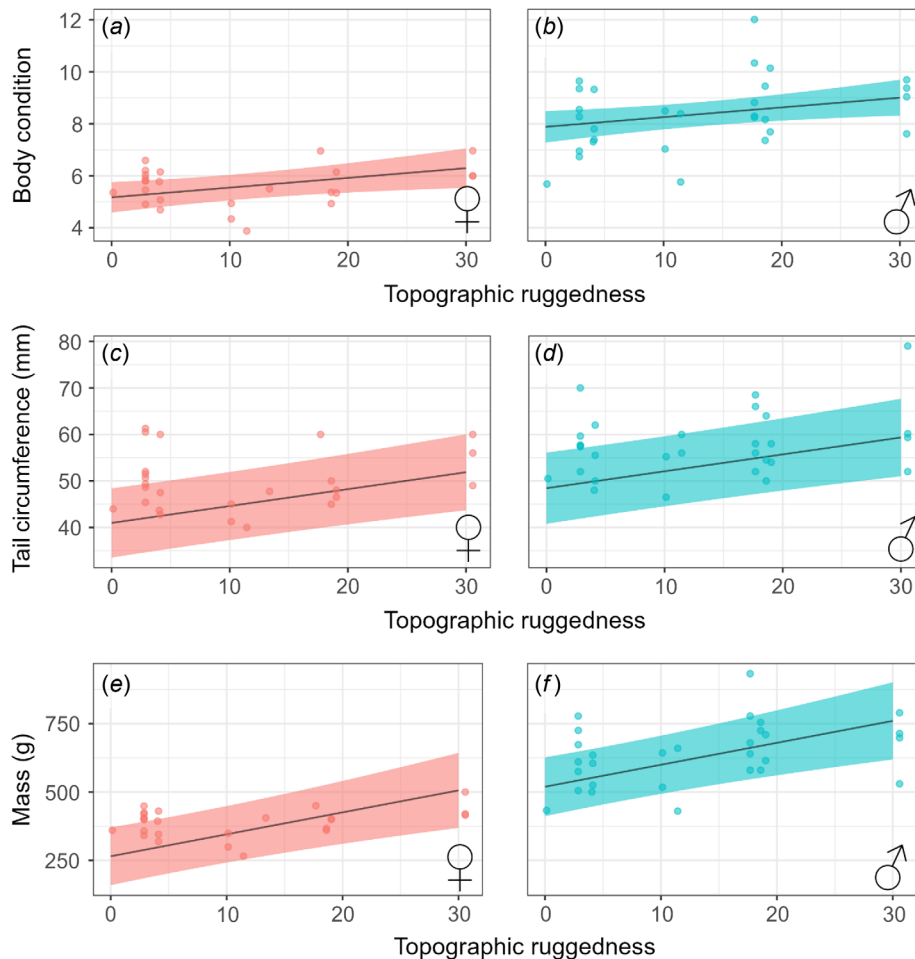


Fig. 3. The effect of topographic ruggedness and sex on metrics of northern quoll (*Dasyurus hallucatus*) population mean fitness, including body condition (a, b), tail circumference (c, d) and mass (e, f). Statistically significant results are indicated in bold. Shading represents 95% confidence intervals.

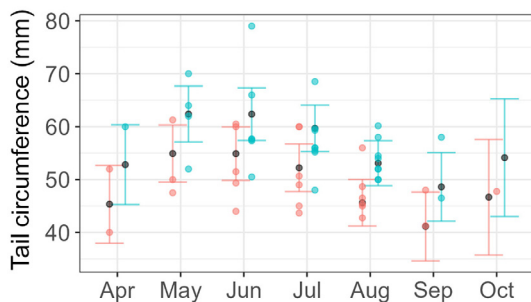


Fig. 4. The effect of month and sex on northern quoll (*Dasyurus hallucatus*) tail circumference.

heavily in a single breeding season, causes a considerable physical toll on the animals (Oakwood 2004). As the males engage in exhaustive mating behaviour and competition for limited opportunities, their energy reserves and overall body condition tend to deteriorate over time, potentially

contributing to the decline in tail circumference (Gaschk et al. 2023). Secondly, the decline in tail circumference might also be linked to the seasonal changes in resource availability, particularly during the dry season in northern Australia (Oakwood 1994). As food resources become scarcer, the northern quolls face increased challenges in maintaining their energy balance and overall body condition. This could result in decreased tail circumference as the animals utilize their fat reserves for survival during this resource-scarce period.

In addition to highlighting the utility of habitat suitability models in predicting habitat quality for northern quolls, these results have important implications for the management of this species, specifically in the identification of critical habitat where 'source' populations may occur. Source populations are defined as habitats where species recruitment outweighs mortality, and are generally considered important from a conservation perspective given they play a critical role in supplying excess individuals to 'sink' populations, where

mortality outweighs recruitment (Furrer and Pasinelli 2016). Identifying and protecting source populations is of particular importance for northern quolls, given their semelparous life history (males live for only 1 year) predisposes them to naturally high rates of local extinction (Oakwood 2000), even from small (5% per annum) declines in recruitment (Moro *et al.* 2019). Building on these results, we suggest future research should examine the influence of northern quoll body condition on other population attributes, such as growth patterns, spatial use, population density, and reproductive timing, similar to previous work on other threatened fauna (Heithaus *et al.* 2007; Williams *et al.* 2013; Dunlop and Morris 2018). Better understanding these interactions will likely improve our ability to predict population consequences of subtle decreases in available resources that are effected through anthropogenic disturbances such as mining. Overall, our results support previous studies that suggest habitat suitability model outputs can indeed be useful in predicting mean population fitness, as well as those that suggest conservation efforts aimed at protecting northern quolls should focus on preserving and restoring habitats that are topographically rugged, lower in elevation, receive higher rainfall, and are closer to permanent water.

Supplementary material

Supplementary material is available [online](#).

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Data availability. Data will be made available on Figshare upon publication.

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