The significance of topographic complexity in habitat selection and persistence of a declining marsupial in the Kimberley region of Western Australia

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Abstract.   Mammalian species in northern Australia are declining. The resources that many species from this region require to persist in the landscape remain poorly understood. We examined habitat selection and diet of the scaly-tailed possum (*Wyulda squamicaudata*, hereafter called Wyulda) in the north-west Kimberley, Western Australia, in relation to variation in complexity of rocky habitat, habitat heterogeneity, and recent fire history. We fitted GPS tags to 23 Wyulda between January 2013 and February 2014 and analysed step selection between GPS fixes to describe habitat choice. We assessed diet by microscopic analysis of plant fragments from 47 faecal samples. Individual Wyulda preferentially foraged in locations with high rock complexity and high habitat heterogeneity in a wide variety of habitats, but denned exclusively in complex rock piles. They used savannas of a range of post-fire ages, including recently burnt (1–2 months after fire) and long unburnt (>24 months after fire). They were highly frugivorous with, on average, 77% of plant fragments per scat sample identified as fruit epidermal layers. Overall, rock complexity appears to be an important landscape attribute for Wyulda, as it may provide den sites and protect fire-sensitive landscape features such as fruiting trees and habitat heterogeneity.

Introduction

Populations of many mammal species across northern Australia are currently declining (Corbett *et al*. 2003; Andersen *et al*. 2005; Woinarski *et al*. 2011, 2014). Several contributing threats have been identified, including the impacts of introduced herbivores (Legge *et al*. 2011*a*), feral cats (*Felis catus*) and contemporary fire patterns (Woinarski *et al*. 2011). Despite these declines, little is known regarding the resources many of these species require to persist in the landscape.

Loss of habitat heterogeneity and of fire-sensitive vegetation resources resulting from increased fire intensity and frequency has been proposed as an important driver of mammal decline (Firth *et al*. 2010; Hohnen *et al*. 2015; Leahy *et al*. 2016). In recent years dominant fire patterns in northern Australia have shifted from those prevalent during indigenous occupation (Vigilante 2001) to dominance by large, intense fires that burn primarily in the mid-to-late dry season and recur every 1–3 years (Andersen *et al*. 1998; Vigilante 2001; Fisher *et al*. 2003; Legge

et al. 2011*b*). Such patterns can change vegetation structure and composition, decreasing vegetation heterogeneity (Russell-Smith *et al*. 2012), causing mortality of fruiting and hollow-bearing trees (Russell-Smith *et al*. 1998; Williams *et al*. 1999; Vigilante and Bowman 2004*b*), and driving declines in fire-sensitive vegetation such as rainforest habitats (Russell-Smith and Bowman 1992). In the short term, intense fires can remove ground cover vegetation used as a shelter and food resource by small mammals.

The identification of areas or resources that provide refuge in fire-prone landscapes can inform conservation management strategies that aim to conserve biodiversity (Banks *et al*. 2011; Pereoglou *et al*. 2011). In northern Australia there is evidence that topographically complex areas may be especially important. For example, several mammal species such as the monjon (*Petrogale burbidgei*), golden-backed tree-rat (*Mesembriomys macrurus*), brush-tailed rabbit-rat (*Conilurus penicillatus*), and Kimberley rock-rat (*Zyzomys woodwardi*) that have declined substantially

now persist only in the topographically complex north-west Kimberley, having retracted from previously wider distributions (Sawle 1988; Start *et al.* 2007, 2012; Woinarski *et al.* 2014). More broadly, across Australia, mammal species that use rock features and habitats as foraging or shelter resources have lower than expected rates of extinction (Burbidge and McKenzie 1989; Smith and Quin 1996). However, few studies have examined how such species use these complex landscapes in relation to adjacent open areas, particularly after they have been affected by fire (Driscoll *et al.* 2010).

Wyulda squamicaudata (hereafter called Wyulda) is a possum species endemic to the Kimberley region of Western Australia. The species is largely restricted to the rugged north-west Kimberley region and has disappeared from the central and east Kimberley, with the exception of Emma Gorge in the Cockburn Ranges, where it was recently rediscovered (Doody *et al.* 2012; Woinarski *et al.* 2014). Limited studies have identified that Wyulda den within rock piles during the day (Runcie 1999) and use rocky savanna and vine thicket habitats for foraging (Humphreys *et al.* 1984; Bradley *et al.* 1987; Burbidge and Webb 2008).

In this paper we examine how Wyulda use rocky and open habitats at sites partially burnt by a severe and extensive fire, typical of contemporary fire patterns. We aimed to (1) test for preferences between topographically complex and open savanna habitats, (2) examine the effect of fire history on the use of savanna habitats and (3) identify key foraging and denning resources. From this information we suggest habitat characteristics that will support the persistence of Wyulda in the landscape.

Methods

Study areas

This study was conducted between January 2013 and February 2014 in the Artesian Range Wildlife Sanctuary, ~180 km north-west of Derby, in the Kimberley region of Western Australia (Fig. 1). This 172 820-ha sanctuary is managed by the Australian Wildlife Conservancy. It is characterised by areas of open savanna, eucalypt/spinifex woodlands, plus topographically complex areas dissected by sandstone gorges that often support small rainforest pockets. Average annual rainfall is 1200 mm, 94% falling in the November–April wet season (Bureau of Meteorology 2015).

We worked at three sites (Fig. 2): Site 1 on the Charnley River gorge ~16 km upstream from its entrance to the Walcott Inlet; Site 2 on the Charnley River gorge, 6 km downstream from Site 1; and Site 3, 20 km south-west of Site 2 on the southern edge of the Artesian Range. All sites consisted of a narrow rainforest gully bordered by steep cliffs and surrounded by various types of savanna.

We identified eight habitat types, differing in floristics and recent fire history: boulder scree, rainforest, river edge, and five savanna types (described below, in Fig. 2, Fig. 3 and Appendix 1). Rainforest and river edge are all topographically protected from fire. Savannas were divided into long-unburnt (burnt >24 months previously), and burnt within the preceding 12 months. Long-unburnt savanna had a ground layer dominated by spinifex (*Triodia* spp.). Recently burnt savanna habitats were more floristically variable, and were classed into four types based on
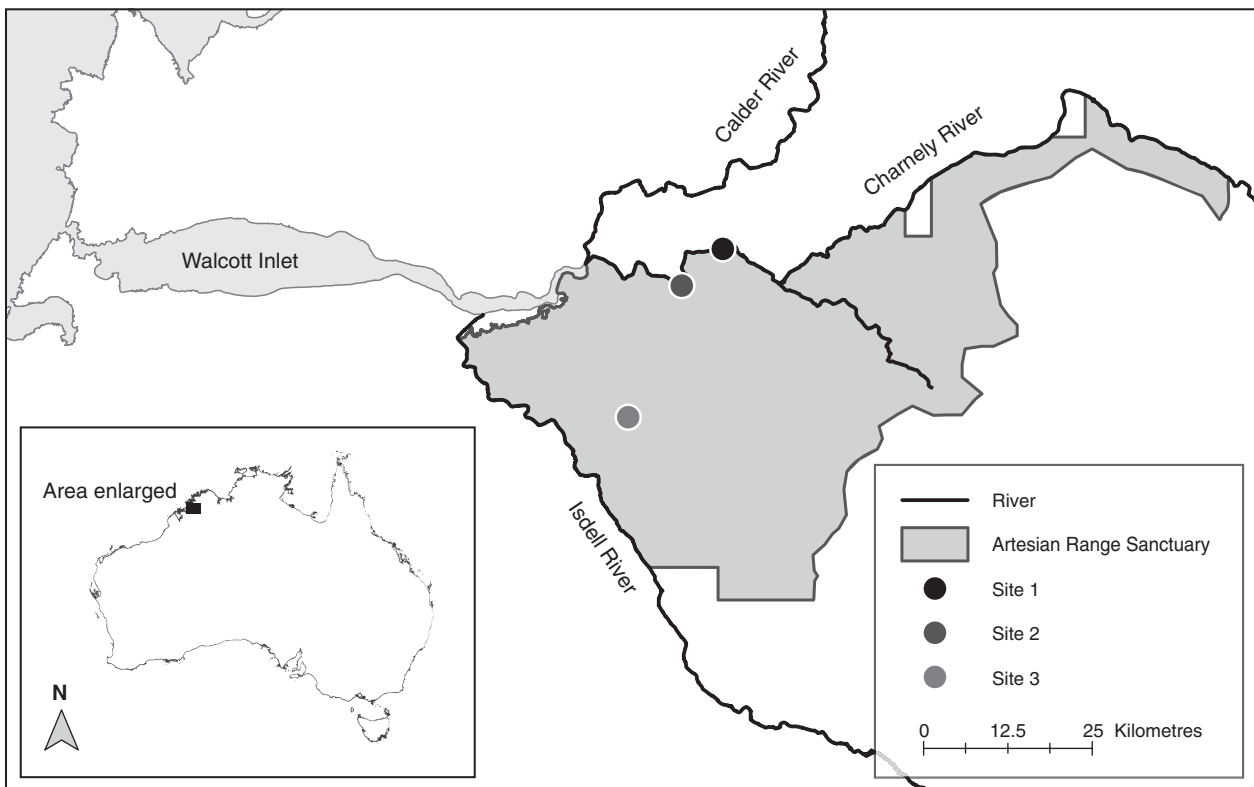

Fig. 1. The location of the three sites in the Artesian Range, north-west Kimberley, Western Australia.
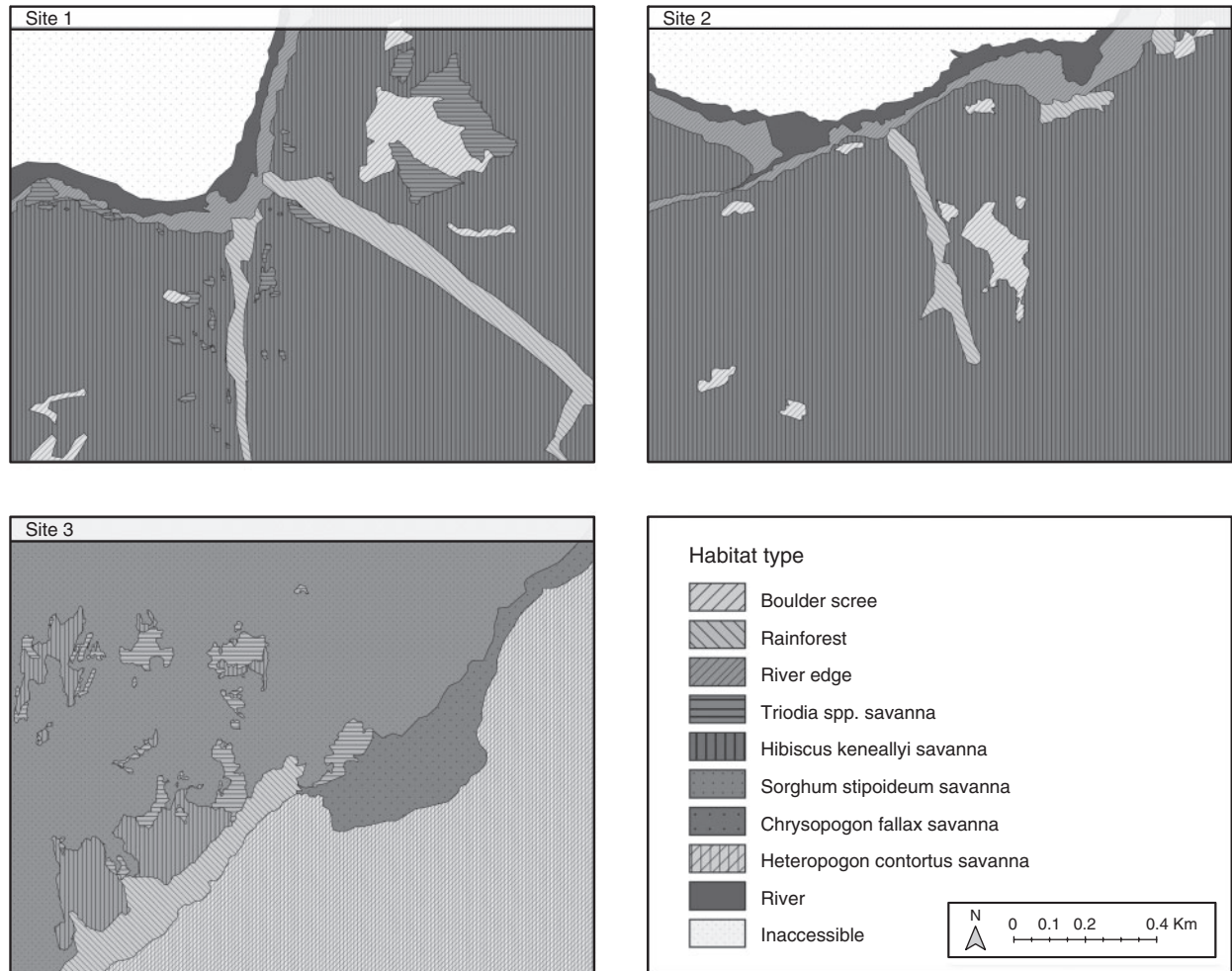
Fig. 2. Habitat composition of sites in the Artesian Range, north-west Kimberley, Western Australia.
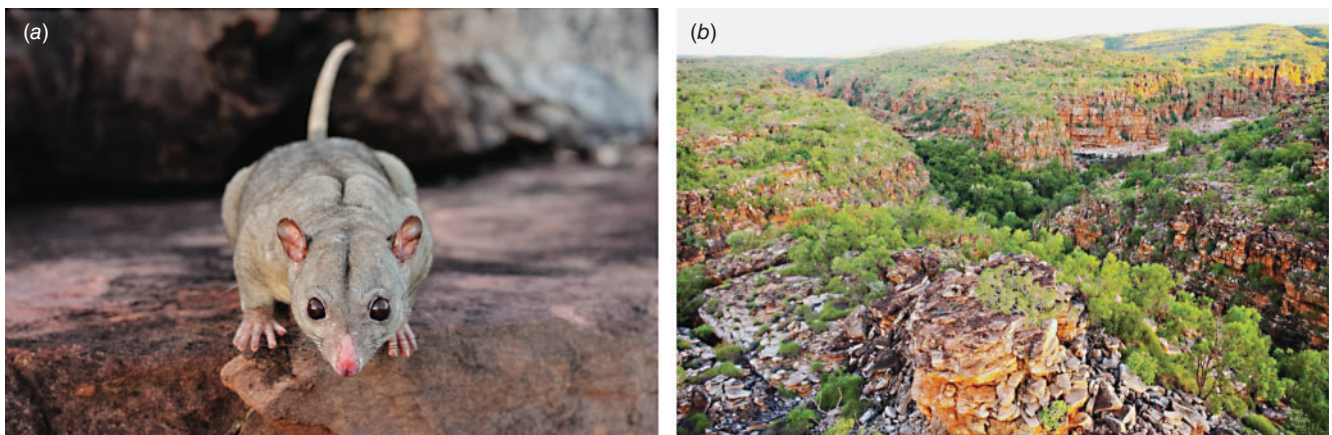
Fig. 3. Photos of (*a*) an individual male *Wyulda squamicaudata* and (*b*) typical rugged terrain in which this species is found.

understorey plants and substrate: (1) *Hibiscus keneallyi* savanna on skeletal sandy soils over a sandstone substrate; (2) *Sorghum stipoideum* savanna on shallow sandy soils over sandstone; (3) *Chrysopogon fallax* savanna on shallow sandy soils over sandstone substrate; and (4) *Heteropogon contortus* savanna on skeletal soils over basalt. We assessed floristic differences

between habitat types by analysing vegetation survey data by ordination as in Hohnen *et al.* (2015). The availability of these vegetation types varied between sites (Table 1).

Trapping

We captured Wyulda in treadle-operated wire cage traps (L × 30 cm H × 30 cm W × 70 cm; Sheffield Wire Products, Welshpool, Western Australia). At each site 30 traps were set 10–30 m apart and baited with a mixture of peanut butter, oats, honey and apple. Wyulda were monitored at Site 1 in four separate months, twice in the wet season (January 2013, December 2013) and twice in the dry season (April 2013, June 2013). Sites 2 and 3 were each visited once in the dry season (May and August 2013 respectively) and once in the wet season (February 2013 and January 2014 respectively), for a total of 4470 trap-nights.

On first capture each animal was weighed, sexed, and tagged with a nanotransponder microchip (Trovan, United Kingdom). Faecal pellets were collected from traps for diet analysis. Individuals were considered adult if they weighed >1000 g, or for females if their teats showed evidence of current or previous lactation. Trapped individuals >1065 g were fitted with GPS/ VHF composite collars (Telemetry Solutions, Concord, CA, USA). Collars weighed 32 g, constituting <3% of the animal's body weight. Each unit consisted of a GPS logger and a VHF transmitter attached to a strong lightweight material collar. During January and February 2013 the GPS collars were not yet available, so VHF collars were used. These collars weighed 30 g (Sirtrack, Havelock North, New Zealand), <3% of an individual's body weight, and were fastened around the neck with a leather strap.

The GPS collars logged foraging locations hourly between 1900 and 0500 hours for the maximum battery life of the collars (three weeks). Radio-collared Wyulda were located between one and four times each night by means of a radio receiver (Titley Scientific, Brisbane, Australia) and a Yagi antenna (Sirtrack, Havelock North, New Zealand) using the homing method outlined in White and Garrot (1990). Individuals were located a minimum of 1 h after a previous fix to minimise autocorrelation. As Wyulda were thought to den underground, where there is no GPS reception, den sites were located daily using the VHF signal for both collar types.

Data analysis

Diet analysis

A reference collection of the epidermal layers of 161 plant species (including 161 leaf, 6 flower, and 18 fruit slides) were made from plant specimens collected at the three sites. Reference slides were made by soaking fragments of plant specimen in 42 g L^{-1} sodium hypochlorite for 24 h or until 90% of the material was visibly bleached, following the methods outlined in Tuft *et al.* (2011). The material was then rinsed, stained with 0.2 g L^{-1} gentian violet and mounted onto a slide using corn syrup. Of the 108 scat samples collected, 47 were selected for analysis to maximise the representation of the sexes (20 male, 28 female), sites (25 Site 1, 11 Site 2, 12 Site 3) and seasons (24 wet season, 24 dry season). To prepare scat samples for analysis, samples were broken up loosely and also soaked in 42 g L^{-1} sodium hypochlorite for 24 h or until 90% of the material was visibly bleached. The material was rinsed in water through a 250-μm sieve, whole seeds were removed, identified and counted. Remaining leaf material was stained using 0.2 g L^{-1} gentian violet and mounted on a slide using corn syrup. For each scat specimen, 100 identifiable fragments of plant material were counted in transects across the slides. Unidentifiable fragments (where the epidermal layer was not visible) were uncommon and were not included in counts.

Movement analysis

GPS points were first screened to remove erroneous fixes caused by GPS error. These included location points found on the opposite side of the impassable Charnley River (at Sites 1 and 2: see Fig. 2), or that displayed all of the following characteristics: distance from the last fix >300 m, and turning angle (in relation to the previous and the following fix) >180° (Bjørneraas *et al.* 2010). The combination of these characteristics indicated implausible spikes in which an individual appeared to deviate at high speed from his or her trajectory to a distant location, and then return to the original trajectory. Horizontal dilution of precision (HDOP) values were not used to filter fixes as data from two stationary test GPS collars indicated that there was no relationship between distance to known location and HDOP value.

Home ranges were estimated by minimum convex polygons (MCP) and fixed kernel density estimation methods in the program Geospatial Modelling Environment (Beyer 2012) and

Table 1. Proportions of habitat types available at three sites in the Artesian Range, north-west Kimberley, Western Australia
An asterisk indicates that last fire is unknown but >24 months preceding commencement of study period

Habitat type	Last fire	Age (months)	Site 1 Area (ha)	Site 1 Proportion (%)	Site 2 Area (ha)	Site 2 Proportion (%)	Site 3 Area (ha)	Site 3 Proportion (%)
Boulder scree	*	60+	6.69	3.83	3.59	2.03	0.00	0.00
Rainforest	*	60+	9.60	5.49	3.61	2.04	9.38	5.05
River edge	*	60+	6.67	3.82	5.58	3.15	0.00	0.00
Triodia spp. savanna	*	24+	6.17	3.53	0.00	0.00	6.15	3.31
Hibiscus keneallyi savanna	Nov 2012	1–12	145.55	83.33	164.48	90.78	10.81	5.82
Sorghum stipoideum savanna	Oct 2013	3	0.00	0.00	0.00	0.00	89.23	48.04
Chrysopogon fallax savanna	Oct 2013	3	0.00	0.00	0.00	0.00	11.37	6.12
Heteropogon contortus savanna	Oct 2013	3	0.00	0.00	0.00	0.00	58.82	31.66

interpreted in ArcMap 10.1 (ESRI). Kernel density estimates were calculated with a plug-in bandwidth. The 95% kernel (K95) utilisation contour estimated total home range and the 50% (K50) kernel utilisation contour estimated the core home range. All points (both foraging and denning) were included in the MCP and kernel estimates, and all areas that the animals could not use (including the river and land on the opposite side of the river), were removed from further consideration. Home-range estimates were tested for normality using the Shapiro–Wilk W test, and normalised by log-transformation. Differences in home-range size between sex and season were examined using generalised linear models, with a model-averaging approach using the package lme4 and MuMIn in the statistical program R ver. 3.0.3 (R Development Core Team 2005; Bartoń 2013; Bates *et al.* 2014).

We calculated the total percentage home-range overlap of K95 and core K50 home-range estimates for all neighbouring individuals. Home-range overlap was also compared using PHR (Percentile home range) and UDOI (Utilisation distribution overlap index) indices, which consider heterogeneity of space use within home ranges (Fieberg and Kochanny 2005) (see Appendix 2 for more detail). Differences in overlap extent were compared between dyads using the asymptotic Kruskall–Wallis test, as datasets did not meet assumptions of normality.

We used a discrete choice modelling approach to describe step selection of Wyulda during foraging periods. Coefficients were estimated from case-control logistic regression models using the 'clogit' command, in the package survival (Therneau 2014) within the statistical program R ver. 3.0.3. This regression method accounts for differing availabilities of habitats between observations by matching every known animal location to a choice set of randomly generated locations. To generate random points we first calculated the average distance travelled between fixes taken at 1-h, 2-h or 3-h (and so on) intervals. Then, for example, if between fix A and B there was a gap of 2 h, five points were randomly generated within a circle (with A at its centroid) that had a radius consisting of the average distance travelled by Wyulda in 2 h, clipped by the individual's 95% kernel home-range estimate. Those five points represent locations where the animal could have gone, and were compared in the modelling process to point B, the location where the animal did go.

For all points where Wyulda were found we recorded habitat type and rock complexity (Appendix 3). The variable 'rock complexity' comprised four categories: cliffs, high complexity (boulder size >2 m), medium complexity (boulder size <2 m) and low complexity (no exposed rock). Habitat and rockiness maps for each site were created in ArcMap 10.1 using geo-referenced satellite images from Google Earth (Google Inc. 2009). Other variables investigated were: distance to permanent water (referred to as 'distance to water'); number of habitat types within a 20-m radius ('habitat heterogeneity'); distance to unburnt habitat ('distance to unburnt patch'); fire ('time since fire'); and the distance from the point to the centre of the home range ('distance to home range centroid'). We chose 20 m as the radius of the circle within which to calculate habitat heterogeneity, as we aimed to take into account GPS error as well as an individual's perception of where it is relative to the habitats around it. We tested for correlation and redundancy between explanatory variables by identifying correlation coefficients of >0.5

(Fox 2002). The variables 'fire', 'distance to water', and 'distance to unburnt patch' were strongly correlated with one another, so 'distance to water' and 'distance to unburnt patch' were omitted from further analysis. Numerical variables including habitat heterogeneity, time since fire, and distance to home range centroid were standardised (mean = 0, standard deviation = 1) before analysis.

We created 31 candidate models based on combinations of the variables 'habitat type', 'time since fire', 'habitat heterogeneity', 'rock complexity' and 'distance to home range centroid', with 'individual' considered as a random effect. Candidate models were ranked on the basis of the Akaike's information criterion adjusted for small sample sizes (AICc). The selection for landscape characteristics by Wyulda was measured by the coefficient estimates and the odds ratio, which represents the relative change in the odds of selection for each unit of the predictor variable. We used model averaging to estimate variable coefficients and their weights according to Anderson (2008).

Den site selection

To explore den site selection by Wyulda we used Bayesian hierarchical logistic regression models. For each individual we compared known den sites with an equal number of randomly generated den sites within that individual's home range. Models comprised a binomial response variable (that described if a point was real (1) or generated (0)), and all combinations of the aforementioned predictor variables including habitat type, rock complexity, time since fire, habitat heterogeneity and distance to home range centroid. To account for variation in individual use of habitats, 'individual' was included as a random effect in all models (See Appendix 4 for more details). A Markov Chain Monte Carlo (MCMC) procedure was used to estimate posterior distributions using the package MCMCglmm (Hadfield 2010) in R ver. 3.0.3. MCMC chains were run with randomised starting values, a burn-in of 50 000 iterations, a thinning interval of 50, and a total of 200 000 iterations. Convergence of MCMC chains was evaluated following Gelman and Hill (2006). The Deviance Information Criterion (DIC) was used to compare all possible models and calculate model weights. We compared all subsets of the most complex model. We used model averaging to estimate variable coefficients, posterior credible intervals and variable weights according to Anderson (2008).

Results

Between January 2013 and January 2014, collars were deployed for one month each on 34 occasions on 23 Wyulda (15 males and 19 females). Of those deployments, 29 were GPS collars and 5 were VHF, giving a total of 3314 location points. Nine individuals were tracked on more than one occasion, and their home ranges were calculated separately for each tracking period (Appendix 5). The number of individuals known to be alive at each site varied between 5 and 14 (Appendix 6).

Diet

From the scat samples, 4700 fragments of plant material were identified. Fragments of leaf came from 42 species, fruit from 14 species and flower from one species (Appendix 7). The most common items were *Ficus platypoda* fruit (on average 47% of

fragments per sample), *Owenia vernicosa* fruit (10%), *Vitex acuminata* fruit (10%), *Grewia breviflora* fruit (8%), *V. acuminata* leaf (3%), *Strychnos lucida* fruit (2%), *O. vernicosa* leaf (2%), *Cryptocarya cunninghamii* leaf (2%), and *Acacia dimorpha* leaf (1%). Whole seeds were also frequently found in scats, the most common being *F. platypoda* (on average 55% of seeds per sample), followed by *V. acuminata* (15%), Unknown Species 3 (6%), Unknown Species 2 (4%) and *G. breviflora* (4%). *F. brachypoda*, Unknown Species 1, *Trachymene dendrothrix*, and *Cryptocarya cunninghamii* seeds were also present in low numbers. Plant species that took up, on average, a larger percentage composition per sample were also likely to be found in a greater number of samples (Appendix 7).

Home range

Estimated home-range size was not correlated with the number of fixes per individual (Appendix 8). Mean home-range size was 8.17 ± 1.34 ha (MCP) or 8.02 ± 1.29 ha (K95), and mean core home-range size (K50) was 2.14 ± 0.38 ha (Table 2). Mean home-range size for males was 9.32 ± 2.10 (MCP) or 9.81 ± 2.33 (K95) and for females was 7.25 ± 1.76 (MCP) or 6.61 ± 1.37 (K95). In the sets of models describing both variation in MCP and K95 home-range estimates with sex and season, multiple models were competitive with one another (Appendix 9). For the MCP models, the confidence intervals of the model-averaged coefficient estimates overlapped zero for the variable 'sex', but did not overlap zero for the variable 'season'. The coefficient estimate of the variable 'dry season' was positive. For the K95% models, both the variables 'sex' and 'season' had model-averaged coefficient estimates and confidence intervals that overlapped zero (Appendix 10).

Table 2.   The mean home-range size of *W. squamicaudata* across sexes, sites and seasons

	MCP ± s.e. (ha)	K95% ± s.e. (ha)	K50% ± s.e. (ha)
Female ($n=19$)	7.25 ± 1.76	6.61 ± 1.37	1.94 ± 0.46
Male ($n=15$)	9.32 ± 2.10	9.81 ± 2.33	2.39 ± 0.65
Dry season ($n=21$)	10.18 ± 1.99	9.55 ± 1.96	2.13 ± 0.50
Wet season ($n=13$)	4.92 ± 0.92	5.55 ± 0.90	2.14 ± 0.61
Site 1 ($n=13$)	7.25 ± 1.07	6.39 ± 0.59	1.25 ± 0.12
Site 2 ($n=8$)	14.33 ± 4.91	13.9 ± 4.83	4.61 ± 1.23
Site 3 ($n=13$)	5.28 ± 0.68	6.03 ± 0.94	1.50 ± 0.26
GPS ($n=29$)	8.74 ± 1.55	8.57 ± 1.48	1.91 ± 0.38
VHF ($n=5$)	4.86 ± 0.95	4.86 ± 1.00	3.47 ± 1.45
Total ($n=34$)	8.17 ± 1.34	8.02 ± 1.29	2.14 ± 0.38

Home-range overlap

Home-range overlap occurred frequently between neighbouring Wyulda (Table 3). Extent of total home-range overlap differed between dyad types for the static K95% contour, PHR and UDOI indices of total home-range overlap (Table 4). Total home-range overlap occurred most frequently between individuals of different sexes (Appendix 11), and least frequently between neighbouring males (Table 3). The extent of core home-range overlap also differed between sex dyads and was most common between males and females (Fig. 4, Appendix 11).

Foraging site selection

Two models (model weights of 30% and 16%) were within two ΔAIC of the top model (model weight of 41%: Table 5). The variables 'habitat type', 'rock complexity', 'habitat heterogeneity', and 'distance to home range centroid' all had high variable importance weights of >99%, and the variable time since fire had a low importance weight of 27%. Model-averaged coefficient estimates suggested that Wyulda selected against both low and medium levels of rocky complexity (Fig. 5, Table 6). Weak but positive selection was detected for locations at greater distances from the centre of an individual's home range. Wyulda selected areas of high habitat heterogeneity while foraging, and used long unburnt habitats such as rainforest, and savanna dominated by *Triodia* spp, as well as recently burnt savanna (1–12 months after fire) dominated by *Hibiscus kenealleyi* and *Sorghum stipodeum*, in preference to recently burnt *Heteropogon contortus*–dominated savanna. There was no selection for or against river-edge habitat types, or in relation to the variable 'time since fire'.

Den site selection

Individuals were tracked to a total of 736 den sites, all of which were in rock features: 548 in piles of rocky scree, 108 in cracks in cliffs, 57 in vertical clefts in large rocky slabs, and 23 in massive rocky outcrops. Of the models built on the den site data only, five were competitive (within 2 ΔDIC) with the top model (Table 7). Importance weights were highest for the variables 'habitat type', and 'rock complexity' (92% and 83% respectively), followed by 'distance to home range centroid' (68%), 'habitat heterogeneity' (59%) and 'time since fire' (36%). Model-averaged coefficient estimates suggest that Wyulda selected against denning in topographically simple habitats and at long distances from their home range centroids (Fig. 6). Wyulda selected to den in *Hibiscus kenealleyi* and *Sorghum stipodeum*–dominated savanna habitats, both 1–12 months after fire, and against denning in long-unburnt

Table 3.   Frequency and average home-range overlap between adjacent *W. squamicaudata* monitored concurrently, at three sites in the Artesian Range, north-west Kimberley, Western Australia (mean ± s.e.), using two-dimensional (K95% and K50%) and three-dimensional (PRH and UDOI) indices
Tnd = Total no. of neighbouring dyads; Tndo = Total no. of neighbouring dyads that overlapped; F, female; M, male

Sex dyad	Tnd	Tndo (K95)	Tndo (K50)	Mean total overlap			Mean core overlap		
				K95%	PRH	UDOI	K50%	PRH	UDOI
FF	24	22	6	20.19 ± 4.56	0.27 ± 0.06	0.11 ± 0.04	4.37 ± 2.39	0.06 ± 0.03	0.05 ± 0.02
FM	37	34	16	37.00 ± 6.04	0.48 ± 0.07	0.33 ± 0.07	20.68 ± 5.45	0.21 ± 0.05	0.13 ± 0.04
MF	37	34	16	24.24 ± 4.05	0.37 ± 0.06	0.33 ± 0.07	11.99 ± 3.19	0.11 ± 0.02	0.07 ± 0.02
MM	26	22	6	12.10 ± 3.02	0.20 ± 0.04	0.04 ± 0.01	0.71 ± 0.32	0.02 ± 0.01	0.01 ± 0.00

rainforest and river-edge habitats. Credible intervals of the variable '*Triodia* spp. savanna' included zero, suggesting neutral selection. Wyulda also appeared to select for older post-fire ages of all habitat types, but this variable had a low importance weight.

Discussion

This study sought to test utilisation of complex landscapes and surrounding areas by a declining mammal in the presence of intensified fire regimes. Rock complexity appears to be a key habitat feature selected for by Wyulda. Individuals avoided foraging in habitats with low rock complexity and consistently

denned within rock structures. Wyulda preferred to forage in areas of high habitat heterogeneity, using both habitats that were recently burnt (1–2 months after fire), habitats that were long unburnt (>24 months after fire), and habitats that very rarely burn (boulder scree, river edge and rainforest). Within these habitats Wyulda were highly frugivorous with, on average, 77% of plant material fragments per scat sample identified as fruit epidermal layers. Rock structure may contribute to protecting habitat heterogeneity and the availability of fruiting tree species from extensive hot fires that can homogenise habitats and kill trees (Williams *et al.* 1999; Vigilante and Bowman 2004*a*). Overall, our results demonstrate diverse uses of heterogeneous habitat by Wyulda and emphasise the critical importance of these habitats in the conservation of small mammals in northern Australia.

Previous research has suggested that rocky complexity is a key habitat feature for Wyulda as the species was detected at sites with rock and rainforest elements (Humphreys *et al.* 1984; Bradley *et al.* 1987; Doody *et al.* 2012), both for foraging and as den sites (Runcie 1999). Wyulda's preference for rocky habitats could be a by-product of their denning requirements; however, it is likely that other factors are involved. Rocky structure may provide cover from predators such as cats, which appear most adept at hunting in more open habitats (McGregor *et al.* 2015), particularly after
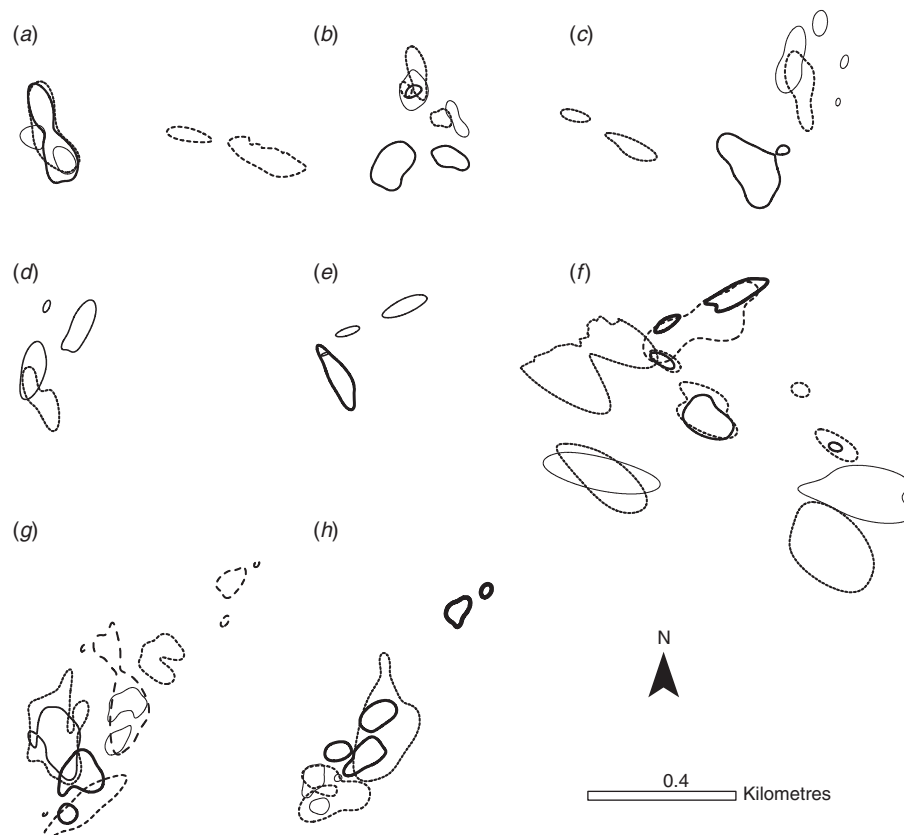
Table 4. Asymptotic Kruskal–Wallis tests of home-range overlap between sex dyads, using two-dimensional (K95% and K50%) and three-dimensional (PRH and UDOI) indices

Values shown in bold are significant at $P < 0.05$

	Total overlap (95%)		Core overlap (50%)	
	χ^2	P	χ^2	P
K	8.272	**0.041**	7.863	**0.049**
PRH	9.099	**0.028**	6.921	0.074
UDOI	8.485	**0.037**	4.125	0.248

Fig. 4. Core home-range overlap (K50) between all male (dashed lines), and female (solid lines) *W. squamicaudata* tracked in the Artesian Range, north-west Kimberley, Western Australia. (*a*) Site 1, January 2013 wet season. (*b*) Site 1, April 2013 dry season. (*c*) Site 1, July 2013 dry season. (*d*) Site 1, December 2013 wet season. (*e*) Site 2, February 2013 wet season. (*f*) Site 2, August 2013 dry season. (*g*) Site 3, May 2013 dry season. (*h*) Site 3, January 2014 wet season. Note that different individuals during each month-long tracking period can be distinguished by differing line weight or dash interval.

understorey vegetation has been simplified by intense fire or grazing (McGregor *et al.* 2014). Reduced hunting success in rocky habitats may explain why cat density in this environment is very low (Hohnen *et al.* 2016). Also, at a slightly larger spatial scale, rocky landscapes tend to burn more patchily than open savannas, thus retaining more heterogeneity in vegetation age (Price *et al.* 2003). In this study, Wyulda selected for high levels of habitat heterogeneity at both den and foraging sites, and used all ages of post-fire savannas as long as rocky features were present. Habitat heterogeneity appears to be important for several vertebrate species in northern Australia (Bolton and Latz 1978; Ingleby and Westoby 1992; Pardon *et al.* 2003; Southgate *et al.* 2007) and elsewhere (Doumas and Koprowski 2013).

While Wyulda are capable of consuming a wide range of plant species, fruit is clearly a key component of their diet. This adds to information from a previous radio-tracking study that

Table 5.   Top five candidate discrete choice models derived from foraging data for *Wyulda squamicaudata*

n1, no. of real points included in the model; n0, no. of generated points included in the model. Abbreviations are as follows: hab_type, habitat type; het, habitat heterogeneity; rock, rock complexity; distc, distance to home range centroid; fire, time since fire

Model	K	AIC	ΔAIC	*w*
Foraging model (n1 = 2615, n0 = 13071)				
hab_type+ het+ rock	3	9141.89	0.00	0.41
hab_type+ het + rock + distc	4	9142.54	0.65	0.30
hab_type+ fire + het + rock	4	9143.73	1.84	0.16
hab_type+ fire + het + rock + distc	5	9144.25	2.36	0.13
hab_type+ het	2	9151.47	9.58	0.00

identified Wyulda foraging within *Xanthostemon paradoxus*, *Xanthostemon eucalyptoides*, and *Planchonia careya* (Runcie 1999), all fruit-bearing species. Fruit also makes an important contribution to the diet for other arboreal marsupials native to north-western Australia (Kerle 1985). Intense and frequent fires can kill or delay the fruiting of tree species (Williams *et al.* 1999; Vigilante and Bowman 2004*a*; Atchison *et al.* 2005; Atchison 2009). Rocky structures (such as gorges or rock outcrops) can provide conditions such as shade and water retention that favour some fruiting species (such as *Ficus platypoda*), and also protect them from fire. Thus rock structure may contribute to the protection of fire-sensitive foraging resources used by Wyulda.

While the results of this study suggest that Wyulda favour rocky landscapes, it is unclear whether the observed relationship reflects a true habitat preference, or is a result of recent reductions of habitat quality in the open savannas caused by current fire regimes, grazing by introduced herbivores, and the impacts of feral cats. Wyulda have been detected in fauna surveys on rocky escarpments of Charnley River Station, separated from sites used in this study by more than 15 km of open basalt plains (K. Tuft and S. Legge, unpubl. data). On a larger scale, Emma Gorge (where the species was recently rediscovered in the east Kimberley) is separated from other historical records in the north Kimberley (e.g.: Mitchell Plateau) by more than 200 km, and large stretches of open plains (Doody *et al.* 2012). The highly disjunct nature of this distribution suggests that there may have been a time when the species moved more freely over open landscapes. A recent phylogenetic study found that, unlike several saxicolous rock wallaby species in the region, Wyulda showed no deep structure between eastern and western populations, suggesting recent colonisation or connectivity across the Kimberley (Potter
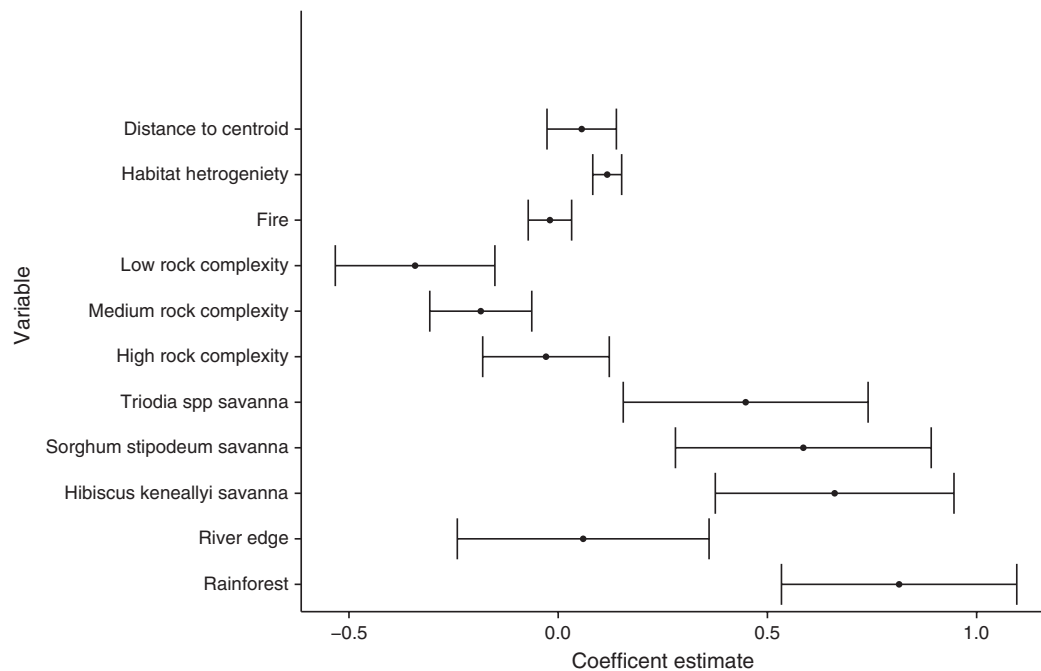

Fig. 5.   Model-averaged coefficient estimates with 95% credible intervals of discrete choice models describing foraging-site selection by *W. squamicaudata* in the Artesian Range, north-west Kimberley, Western Australia. The reference habitat type was *Heteropogon contortus* savanna, and level of rock cover was cliff.

et al. 2014). Historical records from the east Kimberley suggest that the species did once persist in much drier habitats (Alexander 1919).

Wyulda in this study continued to den and forage in habitats that had been recently burnt (1–12 months after fire), a pattern also observed in several other northern Australian mammal studies (Hohnen *et al.* 2015). For pale field rats (*Rattus tunneyi*) in the central Kimberley, Leahy *et al.* (2016) found that while population size decreased after an intense fire, individual rats

stayed within their original home ranges and did not move to adjacent unburnt areas. Low-intensity fire did not displace northern quolls (*Dasyurus hallucatus*) from their home ranges in the north Kimberley (Cook 2010), or significantly affect home-range size or location of northern bettongs (*Bettongia tropica*) in north-east Queensland (Vernes and Pope 2001). The continued use of savanna habitats after fire by Wyulda suggests that the costs of shifting home range are greater than any resource bottleneck caused by recent or frequent fires. The minimal home-range overlap between adjacent males and adjacent females in this study suggests a degree of territoriality that may also inhibit home-range movement.

The average home-range size estimated in this study (8.17 ± 1.34 ha (MCP) or 8.02 ± 1.29 ha (K95)) was larger than previous estimates of 1.0 ha (Runcie 1999) and a maximum of

Table 6. Odds ratios derived from the model-averaged coefficient estimates, from discrete choice models of foraging data for *Wyulda squamicaudata*

Variable	Foraging data	
	Odds ratio	Robust s.e.
Recently burnt habitats		
Hibiscus keneallyii savanna	1.94	0.29
Sarga stipodeum savanna	1.80	0.31
Long-unburnt habitats		
Rainforest	2.26	0.28
River edge	1.06	0.30
Long-unburnt savanna	1.57	0.29
Rock complexity		
Rock complex	0.97	0.15
Rock medium	0.83	0.12
Rock simple	0.71	0.19
Other variables		
Fire	0.98	0.05
Habitat heterogeneity	1.12	0.03
Home-range distance	1.06	0.08

Table 7.   Top five candidate models derived from den data for *Wyulda squamicaudata* using Bayesian hierarchical logistic regression models
n1, number of real points included in the model; n0, number of generated points included in the model. Abbreviations are as follows: hab_type, habitat type; het, habitat heterogeneity; rock, rock complexity; distc, distance to home range centroid; fire, time since fire

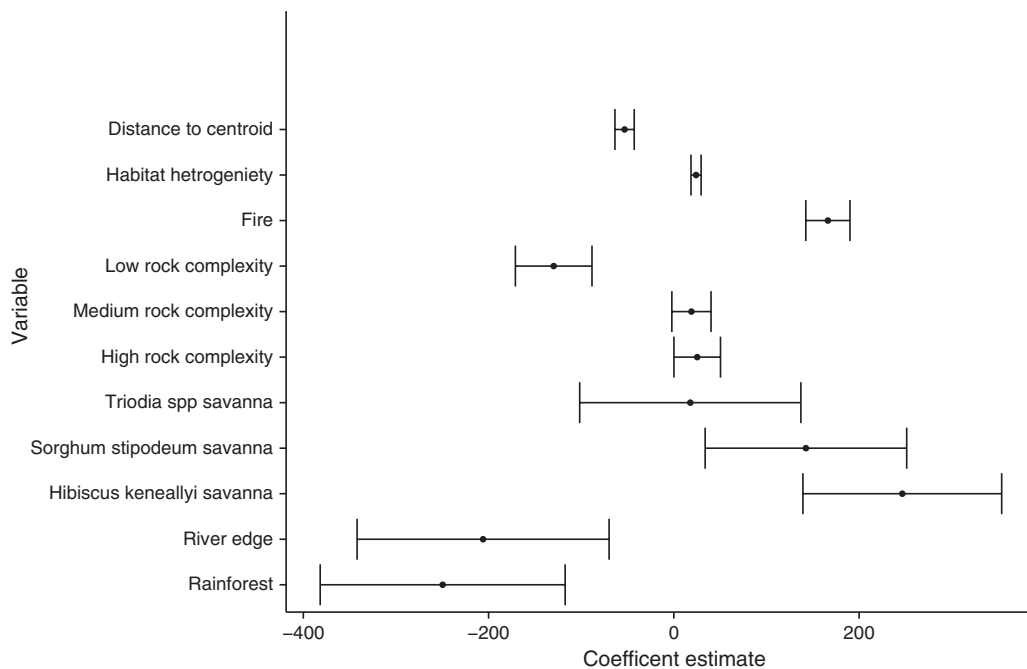| Model	K	DIC	ΔDIC	w
Den model (n1 = 736, n0 = 736)				
hab_type + rock + het + distc	4	30.08	0.00	0.17
hab_type + rock + distc	3	30.58	0.50	0.14
hab_type + rock + het	3	30.66	0.58	0.13
hab_type + rock + het + fire + distc	5	31.23	1.15	0.10
hab_type + rock + fire + distc	4	31.47	1.39	0.09
hab_type + het	2	31.78	1.70	0.07

Fig. 6.   Model-averaged coefficient estimates with 95% credible intervals of Bayesian hierarchical logistic regression models describing den site selection by *W. squamicaudata* in the Artesian Range, north-west Kimberley, Western Australia. The reference habitat type was *Heteropogon contortus* savanna, and level of rock cover was cliff.

272 m long (Humphreys *et al*. 1984). Potentially, this reflects differences between the two studies in habitat quality, and/or the number of location points recorded per individual. Home-range estimates from this study were larger than those of other north Kimberley arboreal marsupials including the northern brushtail possum (*Trichosurus vulpecula arhnemensis*) (0.87–1.12 ha: Kerle 1998) and the cohabiting saxicolous rock ringtail possum (*Petropseudes dahli*) (0.5–1.2 ha: Runcie 2000). While home-range size did not vary between sexes, overlap occurred much more frequently and extensively between males and females than between individuals of the same sex. Several other possum species native to northern Australia move and den in family groups (Kerle 1998; Runcie 2000). Potentially, Wyulda also practice some degree of sociality and pair bonding.

Currently the distribution of Wyulda is restricted to the topographically complex north Kimberley, with a small isolated population persisting in the east Kimberley. While this species may have once been more widely distributed in the central and east Kimberley, including in a wider range of habitats, habitat heterogeneity, the availability of fruiting tree species and particularly the availability of topographic and rock complexity were key habitat features selected for by Wyulda. Rock complexity may provide some buffer to Wyulda from threats such as intense fires and feral cats, offer shelter from predation during the post-fire period, with cliffs and rock outcrops forming natural barriers to such fires, protecting sensitive vegetation and promoting habitat heterogeneity. Mammal declines have occurred in topographically complex areas of the Arnhem Land plateau (Woinarski 2000; Ziembicki *et al*. 2015), Kakadu National Park (Woinarski *et al*. 2001), and the south-west Kimberley (McKenzie 1981; Sawle 1988). Thus substrate complexity alone does not guarantee mammal species security. Management strategies that aim to maintain availability of habitat heterogeneity and fruiting trees may support the persistence of Wyulda in rocky habitats. Such strategies could include lighting small-scale, low-intensity fires early in the dry season to prevent the incidence and extent of large-scale fires that occur late in the dry season.

Acknowledgements

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Appendix 1.　Dominant plant species available in eight habitat types at three sites in the Artesian Range, northwest Kimberley, Western Australia

Habitat type	Overstorey	Understorey
Boulder scree	*Gyrocarpus americanus*	*Santalum album*
	Celtus philippinensis	*Cucurbitacea* sp.
	Ficus platypoda	*Triodia bitextura*
	Acacia debrilla	*Bridelia tomentosa*
	Eucalyptus brachyandra	*Dodonaea lanceolata*
Rainforest	*Syzigium angopheroides*	*Hypoestes floribunda*
	Cryptocarya cunninghamii	*Strychnos lucida*
	Xanthostemon paradoxus	*Ampelocissus acetosa*
	Terminalia hadleyana	*Atalaya hemiglauca*
	Celtus philippinensis	*Wrightia pubescens*
River edge	*Melaleuca leucadendra*	n.a.
	Melaleuca argentea	
	Pandanus aquaticus	
	Syzigium eucalyptoides	
	Celtus philippinensis	
Triodia spp. savanna	*Owenia vernicosa*	*Triodia bitextura*
	Corymbia dendromerinx	*Grevillea wickhamii*
	Terminalia canescens	*Calytrix exstipulata*
	Adansonia gregorii	*Stemodia lythrifolia*
	Brachychiton fitzgeraldianus	*Acacia debrilla*
Hibiscus keneallyi savanna	*Owenia vernicosa*	*Triodia bitextura*
	Corymbia dendromerinx	*Trachymene dendrothrix*
	Terminalia canesens	*Hibiscus keneallyi*
	Adansonia gregorii	*Grevillea wickhamii*
	Brachychiton fitzgeraldianus	*Triumfetta triandra*
Sorghum stipoideum savanna	*Owenia vernicosa*	*Sorghum stipoideum*
	Terminalia hadleyana	*Triodia* sp. 2
	Buchanania obovata	*Heteropogon contortus*
	Acacia debrilla	*Chrysopogon fallax*
	Brachychiton viscidulus	*Phyllanthus aridus*
Chrysopogon fallax savanna	*Eucalyptus miniata*	*Chrysopogon fallax*
	Eucalyptus polycarpa	*Cymbopogon procerus*
	Planchonia careya	*Sorghum stipoideum*
	Pandanus spiralus	*Stemodia lythrifolia*
	Buchanania obovata	*Triodia bitextura*
Heteropogon contortus savanna	*Adansonia gregorii*	*Sorghum stipoideum*
	Hakea arborescens	*Heteropogon contortus*
	Eucalyptus tectifica	*Chrysopogon fallax*
	Bauhinia cunninghamii	*Triodia* sp. 2
	Terminalia canescens	*Cajanus hirtopilosus*

Appendix 2.　Home range overlap values

PHR calculates the probability that an animal's location j will be found within the utilisation distribution of animal i (Fieberg and Kochanny 2005). PRH values differ between individuals of a dyad as they represent the proportion of home range overlapped by another individual, relative to an individual's own utilisation distribution.

$$PHR_{i,j} = \iint\limits_{A_i} \widehat{UD_j}(x, y)dxdy$$

where A_i is the home-range area of animal i and $\widehat{UD_j}$ is the estimated UD of animal j. UDOI measures the amount of overlap relative to two individuals using the same space uniformly (Fieberg and Kochanny 2005). This index does not differ between individuals of a dyad, and values range from 0 (no overlap) to 1 (uniform use and complete overlap).

$$UDOI = A_{i,j} \int\limits_{-\infty}^{\infty} \int\limits_{-\infty}^{\infty} \widehat{UD_i}(x, y) \times \widehat{UD_j}(x, y)dxdy$$

where $A_{i,j}$ is the overlapping area of the two UDs.

Appendix 3.   Rock complexity composition of sites in the Artesian Range, north-west Kimberley, Western Australia
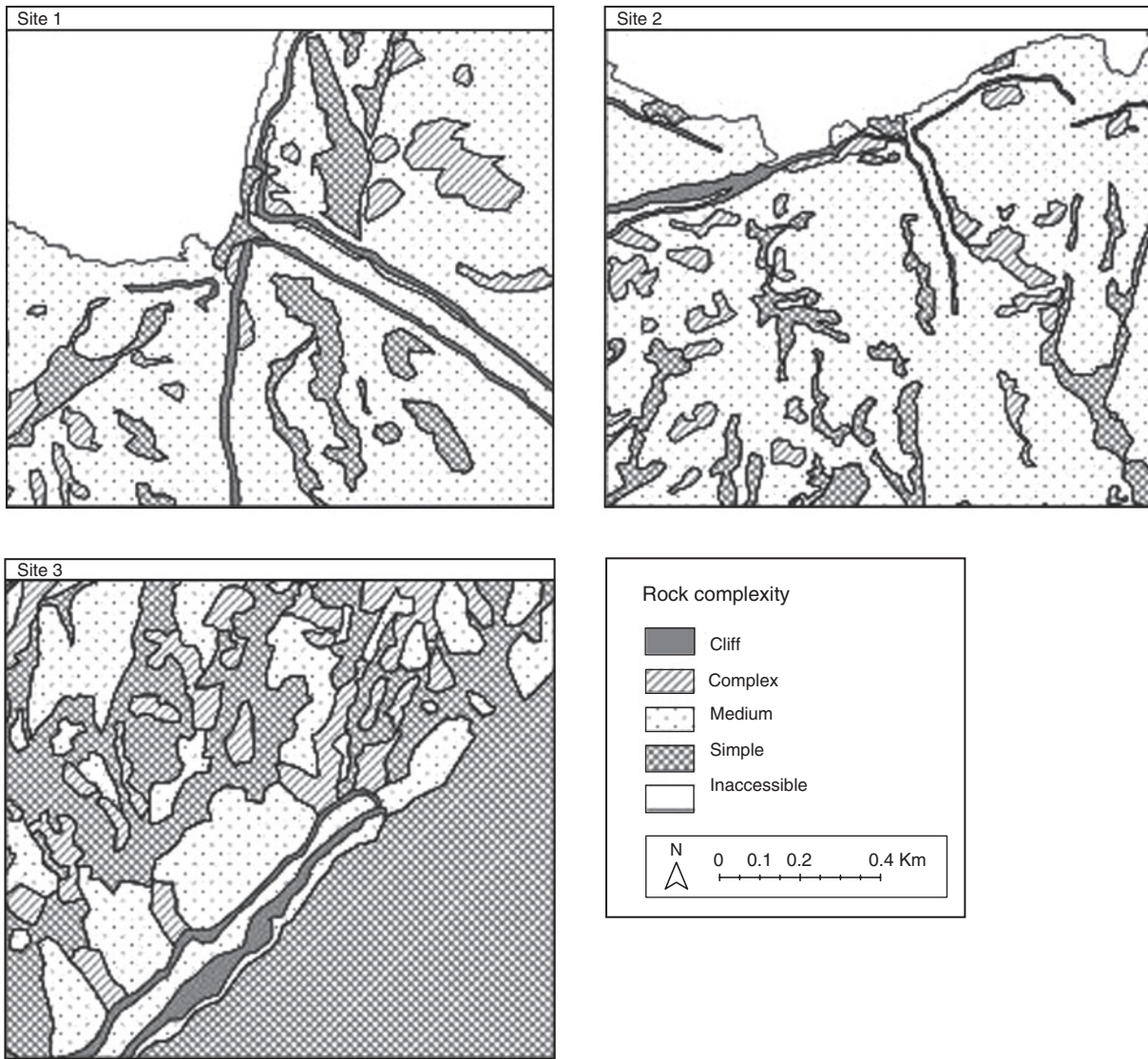
Appendix 4.   Detail on den use models

The use by Wyulda of a den site was assumed to have a Bernoulli distribution with parameter π_{ij}:

$$Y_{ij}|\pi_{ij} \sim \text{Bernoulli}(\pi_{ij})$$

where π_{ij} is the probability that observation (i) of an individual at a site (j) being at a used point. We modelled the probability that an observation was a used point, π_{ij}, based on predictor variables. The probability of a point being used was modelled as:

$$\text{logit}(\pi_{ij}) = \alpha_{ji} + \beta_i x_i$$

where α and β are the model intercept and slope, for observation i varying by individual at site j, and x was the predictor variable for individual i. Prior distributions for all model parameters in the hierarchy were given with the goal of providing conjugate priors that contain little to no influence on the posterior distributions of all the model parameters. We assumed normal prior distributions on slopes, α, and intercept β, with mean μ and variance σ^2:

$$\alpha_j \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2), \text{ for } j = 1, \ldots, k$$

For the variance parameters, σ^2, we determined and utilised non-informative uniform prior hyperparameter distributions, specified as $\sigma^2 \sim \text{Uniform}(0, 100)$, which was used across all models.

Appendix 5.   Home range estimates and tracking effort for *Wyulda squamicaudata* at three sites in the Artesian Range, north-west Kimberley, Western Australia

Symbols indicate the same individual tracked on separate month-long occasions

| Number	Sex	Site	Season	Month tracked	Recorder	No. of fixes	MCP	K95%	K50%
1	F	1	Wet	Jan 13	VHF	47	4.59	6.50	1.63
2✤	F	1	Wet	Jan 13	VHF	43	7.99	2.67	0.67
3◯	M	1	Wet	Jan 13	VHF	49	5.80	7.90	1.78
4	F	2	Wet	Feb 13	VHF	48	2.31	3.14	0.51
5	F	2	Wet	Feb 13	VHF	47	3.13	3.77	5.55
6⊙	F	1	Dry	Apr 13	GPS	210	12.88	9.85	1.60
7✤	F	1	Dry	Apr 13	GPS	132	7.72	5.36	0.89
8★	M	1	Dry	Apr 13	GPS	101	7.97	5.78	1.46
9◯	M	1	Dry	Apr 13	VHF	130	4.99	4.66	0.85
10	F	3	Dry	May 13	GPS	144	6.12	7.11	1.65
11	M	3	Dry	May 13	GPS	68	2.88	2.51	0.47
12·	F	3	Dry	May 13	GPS	78	4.14	5.00	1.20
13❖	F	3	Dry	May 13	GPS	131	3.43	3.57	0.93
14	M	3	Dry	May 13	GPS	138	6.64	4.59	1.01
15◆	M	3	Dry	May 13	GPS	133	7.35	6.10	1.41
16✚	M	3	Dry	May 13	GPS	95	7.09	9.20	2.21
17	M	3	Dry	May 13	GPS	106	7.89	10.10	3.00
18⊙	F	1	Dry	Jan 13	GPS	124	14.47	9.79	2.02
19★	M	1	Dry	Jul 13	GPS	75	4.43	4.25	0.67
20✤	F	1	Dry	Jul 13	GPS	118	5.55	6.70	1.26
21✪	M	1	Dry	Jul 13	GPS	68	3.79	5.15	1.07
22	F	2	Dry	Aug 13	GPS	114	34.41	28.95	5.48
23	F	2	Dry	Aug 13	GPS	149	14.02	8.56	1.31
24	F	2	Dry	Aug 13	GPS	53	2.81	3.46	7.72
25	M	2	Dry	Aug 13	GPS	97	11.64	9.94	2.40
26	M	2	Dry	Aug 13	GPS	96	36.99	40.52	10.79
27	M	2	Dry	Aug 13	GPS	69	9.34	12.90	3.13
28✤	F	1	Wet	Dec 13	GPS	75	1.80	8.33	1.52
29✪	M	1	Wet	Dec 13	GPS	108	12.28	6.16	0.83
30·	F	3	Wet	Jan 14	GPS	146	2.54	2.70	0.62
31	F	3	Wet	Jan 14	GPS	92	2.48	2.27	0.40
32❖	F	3	Wet	Jan 14	GPS	88	4.58	5.33	1.47
33◆	M	3	Wet	Jan 14	GPS	40	3.32	6.02	1.76
34✚	M	3	Wet	Jan 14	GPS	102	10.28	13.89	3.42

Appendix 6.   The minimum number of *Wyulda squamicaudata* known to be alive at each site during each trapping period

Month	Site	Season	Males	Females	Total
January 2013	1	Wet	3	3	6
February 2013	2	Wet	2	3	5
April 2013	1	Dry	3	2	5
May 2013	3	Dry	8	6	14
July 2013	1	Dry	3	3	6
August 2013	2	Dry	5	4	9
December 2013	1	Wet	4	5	9
January 2013	3	Wet	3	4	7

Appendix 7.   Dietary items identified in faecal samples of *Wyulda squamicaudata* at three sites in the Artesian Range, north-west Kimberley
%c, average percentage composition per sample; %s, percentage of samples within which that plant was found

Dietary item	Total	%c	%s	Dietary item	Total	%c	%s
Seed cuticle (fragment)				Leaf (fragment) continued			
Ficus platypoda	2205	46.91	87.23	*Grevillea velutinella*	15	0.32	4.26
Owenia vernicosa	491	10.45	31.91	*Syzygium eucalyptoides*	15	0.32	6.38
Vitex acuminata	477	10.15	40.43	*Trachymene dendrothrix*	15	0.32	4.26
Grewia breviflora	377	8.02	29.79	*Acacia dunnii*	14	0.30	4.26
Strychnos lucida	113	2.40	19.15	*Distichostemon hispidulus*	12	0.26	2.13
Ficus brachypoda	25	0.53	6.38	*Eucalyptus tectifica*	9	0.19	2.13
Myristica insipida	19	0.40	2.13	*Ampelocissus acetosa*	8	0.17	2.13
Syzygium eucalyptoides	18	0.38	2.13	*Ingofera* sp. A kimberleyflora	5	0.11	2.13
Planchonella pohlmaniana	14	0.30	2.13	*Ficus brachypoda*	4	0.09	2.13
Xanthostemon paradoxus	14	0.30	2.13	*Fimbristylis* sp.	4	0.09	2.13
Unidentified 1	6	0.13		*Smilax australis*	4	0.09	2.13
Terminalia hadleyana	5	0.11	2.13	*Eucalyptus grandifolia*	3	0.06	2.13
Cryptocarya cunninghamii	4	0.09	2.13	*Timonius timon*	3	0.06	2.13
Trachymene dendrothrix	3	0.06	2.13	*Cajanus hirtopilosus*	2	0.04	2.13
Flower (fragment)				*Eucalyptus polycarpa*	2	0.04	2.13
Vitex acuminata	86	1.83	12.77	*Gonocarpus leptothecus*	2	0.04	2.13
Leaf (fragment)				*Grewia breviflora*	2	0.04	2.13
Vitex acuminata	133	2.83	19.15	*Hibiscus kenneallyi*	2	0.04	2.13
Owenia vernicosa	81	1.72	8.51	*Melaleuca minutifolia*	2	0.04	2.13
Cryptocarya cunninghamii	74	1.57	4.26	*Melaleuca nervosa*	2	0.04	2.13
Acacia dimorpha	49	1.04	4.26	*Terminalia canescens*	2	0.04	2.13
Chrysopogon fallax	46	0.98	8.51	*Acacia delibrata*	1	0.02	2.13
Alphitonia excelsa	39	0.83	4.26	*Grevillea refracta*	1	0.02	2.13
Melaleuca argentea	39	0.83	4.26	*Gyrocarpus americanus*	1	0.02	2.13
Strychnos lucida	32	0.68	12.77	Seed (whole)			
Ichnocarpus frutescens	30	0.64	2.13	*Ficus platypoda*	2808	55.09	68.09
Wrightia pubescens	30	0.64	2.13	*Vitex acuminata*	102	14.66	25.53
Eucalyptus rupestris	28	0.60	6.38	Seed 3	15	5.92	8.51
Canarium australianum	23	0.49	4.26	Seed 2	512	4.17	8.51
Syzygium angophoroides	21	0.45	2.13	*Grewia breviflora*	20	4.13	10.64
Eucalyptus camaldulensis	20	0.43	2.13	*Ficus bracypoda*	37	1.23	2.13
Planchonia rupestris	18	0.38	2.13	Seed 1	14	1.17	4.26
Homalanthus novo-guineensis	17	0.36	4.26	*Trachmene dendrothrix*	4	0.48	4.26
Triodia bitextura	17	0.36	4.26	*Cryptocraya cunninghamii*	1	0.03	2.13
Macarthuria vertex	16	0.34	4.26				

Appendix 8.   Correlations between (*a*) the no. of fixes and K95 home range estimates and (*b*) the no. of fixes and MCP home range estimates for *Wyulda squamicaudata* in the Artesian Range, north-west Kimberley, Western Australia
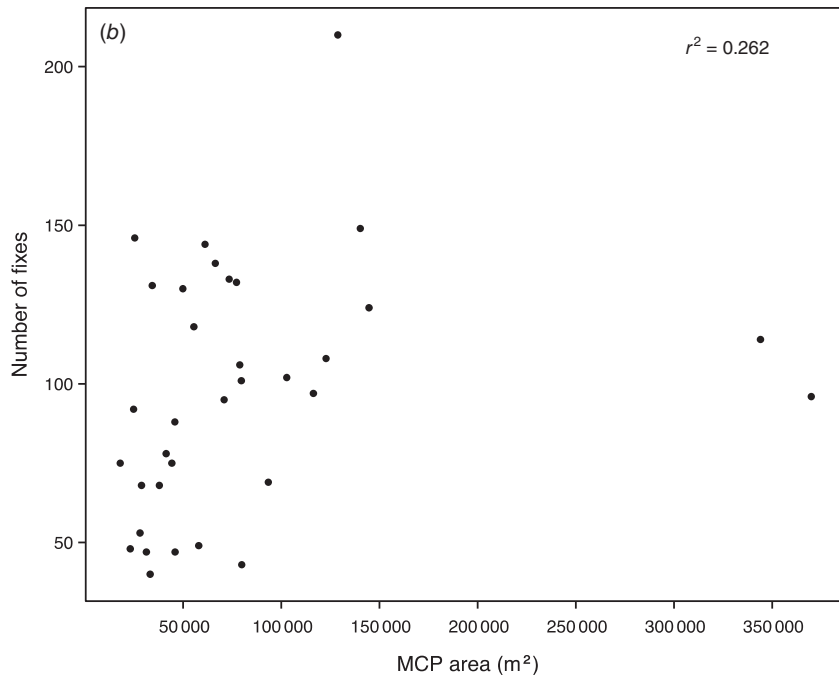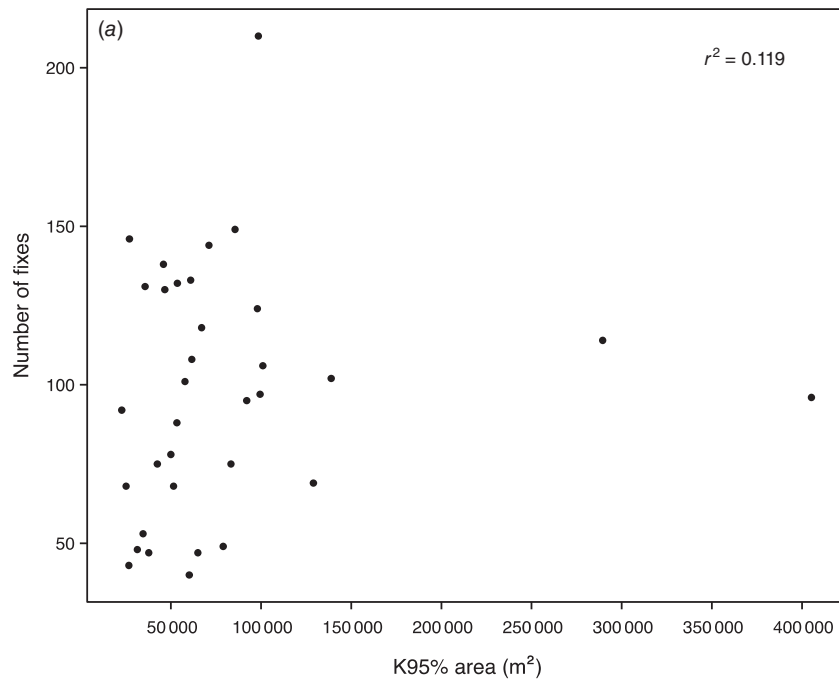
Appendix 9.   Generalised linear models describing variation in minimum convex polygon (MCP) and kernel 95% contour (K95) home range estimates for *Wyulda squamicaudata* between sexes and seasons

Home-range estimate	Variables	AIC	ΔAIC	*w*
MCP	Season	71.90	0.00	0.58
	Sex + Season	73.00	1.12	0.33
	Sex	77.00	5.06	0.05
	Null	77.20	5.30	0.04
K95	Sex + Season	67.50	0.00	0.32
	Season	67.60	0.10	0.30
	Sex	67.90	0.40	0.26
	Null	69.30	1.78	0.13

Appendix 10.   Model-averaged coefficient estimates of explanatory variables describing variation in home range size for *Wyulda squamicaudata* between sexes and seasons
**, $P < 0.01$

Home-range estimate	Variables	Coefficient	s.e.
MCP	Wet season	−0.63	0.23**
	Male	0.28	0.23
K95	Wet season	−0.40	0.22
	Male	0.37	0.21

Appendix 11.   Core (dark grey) and total (light grey) home-range overlap of *Wyulda squamicaudata* dyads for (*a*) percentage kernel overlap, (*b*) PHR score and (*c*) UDOI score