

Post-fire habitat use of the golden-backed tree-rat (*Mesembriomys macrurus*) in the northwest Kimberley, Western Australia

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Abstract Fire regimes are changing throughout the world. Changed fire patterns across northern Australian savannas have been proposed as a factor contributing to recent declines of small- and medium-sized mammals. Despite this, few studies have examined the mechanisms that underpin how species use habitat in fire-affected landscapes. We determined the habitats and resources important to the declining golden-backed tree-rat (*Mesembriomys macrurus*) in landscapes partially burnt by recent intense fire. We aimed to (i) compare the relative use of rainforest and savanna habitats; (ii) examine the effect of fire history on use of savanna habitats; and (iii) identify key foraging and denning resources. Habitat selection was examined by comparing the availability of eight habitat types around real (used) and generated (available) location points. Individuals used a range of habitats, but consistently selected long unburnt rainforest in preference to recently burnt savanna (1–12 months post-fire); however, recently burnt savanna was used in preference to long unburnt savanna. Tree-rats foraged in *Terminalia hadleyana*, *Planchonia rupestris*, *Celtis philippensis* and *Owenia vernicosa*, tree species that are found in a variety of habitat types. Individuals used a range of den sites, including cliffs, trees, logs, scree and stags found throughout the study area. Although multiple factors may have led to the decline of *Mes. macrurus* across its range, these results are consistent with the idea that changes in the savanna structure as a consequence of contemporary fire patterns could also have a role. The continued persistence of *Mes. macrurus* in the northwest Kimberley may be supported by land management strategies that conserve fruiting and hollow-bearing trees, and maintain the availability of fire-sensitive vegetation types.

Key words: Bayesian hierarchical mixed-effect model, fire regime, habitat use, northern mammal decline, rainforest, small mammal.

INTRODUCTION

Fire has transformative effects on ecosystems throughout Australia and the world (Bowman *et al.* 2009). Alteration of fire regimes by people can cause extensive changes in habitat structure (Bowman & Haberle 2010) and contribute to declines in diversity of a range of fauna, including mammals (Woinarski *et al.* 2011; Andersen *et al.* 2012), birds (Franklin 1999; Pons & Clavero 2010; Woinarski & Legge 2013), reptiles (Smith *et al.* 2013; King & Schlossberg 2014) and invertebrates (Andersen *et al.* 2014). Faunal responses to fire are complex and variable (Pastro *et al.* 2014), and knowledge of the mechanisms that mediate these responses is often limited (Keith *et al.* 2002). Conservation and management practices mostly aim to manage fire to encourage species diversity and abundance. Yet without an understanding of the

mechanisms that govern fauna responses to fire, management practices can be costly and ultimately ineffective (Driscoll *et al.* 2010).

In northern Australia's tropical savannas, the abundance and diversity of small mammals is declining dramatically (Corbett *et al.* 2003; Andersen *et al.* 2005; Woinarski *et al.* 2011, 2014). Several threats have been implicated, including the impacts of introduced herbivores, feral cats and contemporary fire patterns (Woinarski *et al.* 2011). Fire regimes in this region are currently dominated 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.* 2011b). This regime differs from the pre-European pattern maintained by indigenous fire management (Vigilante 2001).

Frequent and intense fires can affect small mammals by changing vegetation structure and composition and by altering resource availability (Fisher *et al.* 2003). Such features include heterogeneity in vegetation age (Russell-Smith *et al.* 2012); abundance of perennial

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Accepted for publication May 2015.

grasses (Russell-Smith *et al.* 2003); presence of flowering, fruiting and hollow-bearing trees (Russell-Smith *et al.* 1998; Williams *et al.* 1999; Vigilante & Bowman 2004b); and presence of fire-sensitive vegetation such as rainforest habitats (Russell-Smith & Bowman 1992). Contemporary fire patterns may also work in synergy with other threats, such as predation by feral cats. A number of studies have detected declines in mammal abundance after high-intensity fire (Kerle & Burgman 1984; Pardon *et al.* 2003; Legge *et al.* 2008), and in the central Kimberly predation was identified as the primary cause of post-fire mortality (Leahy *et al.* unpubl. data). Intense fires tend to remove vegetation more completely from within the fire scar (Russell-Smith *et al.* 2002), and feral cats favour hunting in areas recently burned by these types of fires (McGregor *et al.* 2014). Determining how small mammals use habitats after an intense fire is therefore important in understanding the potential impacts of fire patterns, including changes to vegetation structure and susceptibility to predation.

The golden-backed tree-rat (*Mesembriomys macrurus*) is an arboreal rodent native to northern Australia. It was formerly widespread from the Pilbara to the Northern Territory but is now restricted to the rugged northwest Kimberley and some offshore islands (Woinarski 2000; Woinarski *et al.* 2014). Previous studies suggest that *Mes. macrurus* uses a wide range of habitats such as rainforest, rugged sandstone scree, riparian areas, mangroves and open savanna (Bradley *et al.* 1987; Kerle 1987; Friend *et al.* 1991).

In this paper, we examine how *Mes. macrurus* uses habitat in landscapes partially burnt by an intense and extensive fire, typical of contemporary fire patterns. We used radio tracking to record resource use by *Mes. macrurus* at sites containing a mix of rainforest patches and savanna habitats ranging from recently burnt to long unburnt. We aimed to (i) compare the relative use of rainforest and savanna habitats; (ii) examine the effect of fire history on the use of savanna habitats; and (iii) identify key foraging and denning resources. We use our results to evaluate how current fire regimes may affect *Mes. macrurus*, and to suggest how fire could be managed to maintain habitat for the species.

METHODS

Study areas

The study was conducted between June 2012 and February 2014 at the Artesian Range Wildlife Sanctuary, a 172 820 ha area in the northwest Kimberley region of Western Australia managed by the Australian Wildlife Conservancy (Fig. 1). The area is characterized by its high topographic complexity, with open eucalypt savanna interspersed with pockets of closed canopy rainforest and dissecting sandstone gorges. Annual rainfall averages over 1200 mm, 94% of which falls between November and April (Bureau of Meteorology 2013).

We worked at three sites (Fig. 1). Site 1 was on the Charnley River gorge about 16 km upstream of its outlet to the Walcott Inlet; Site 2 was 6 km downstream from Site 1 on

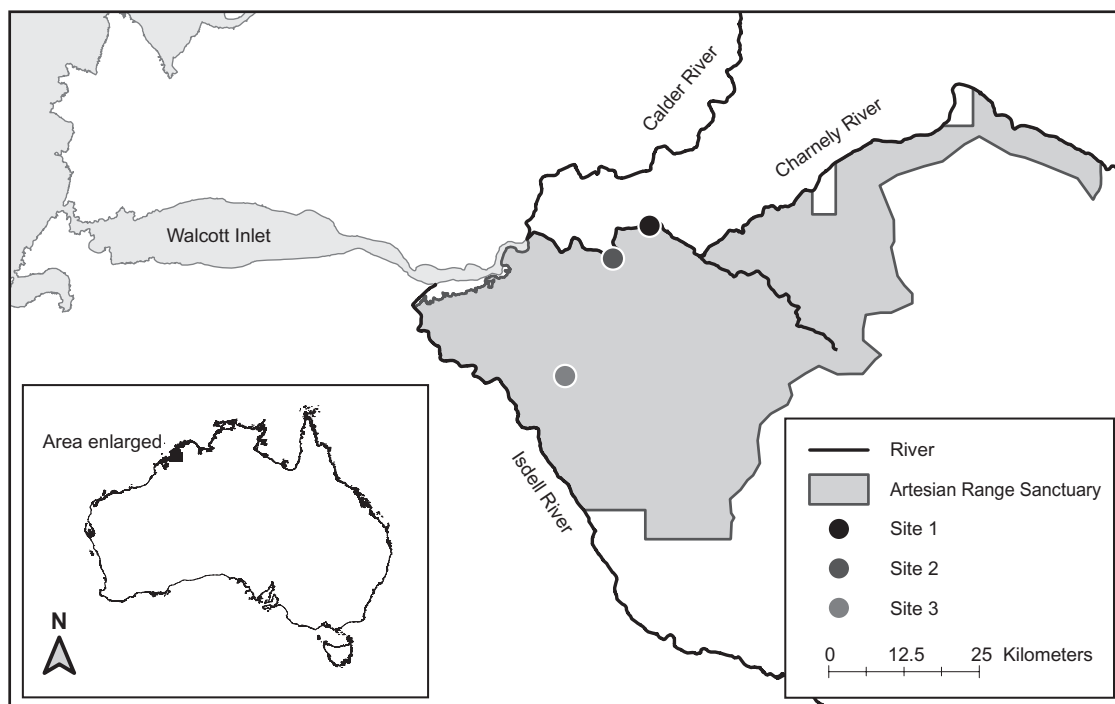


Fig. 1. Location of sites in the Artesian Range, northwest Kimberley, Western Australia.

the same gorge. Both sites were at junctions of narrow rainforest gullies bordered by steep cliffs and the main river gorge. Site 3 was 20 km southwest of Site 2 on the southern edge of the Artesian Range. It was bisected by a narrow rainforest gorge and surrounded by various types of savanna (see below). Sites were selected based on the detection of *Mes. macrurus* in Australian Wildlife Conservancy fauna surveys (Tuft and Legge unpubl. data).

We identified eight habitat types, differing in floristics and fire history: rainforest, boulder scree, river edge and five savanna types (described below and in Fig. 2). Rainforest, boulder scree and river edge are all habitats topographically protected from fire. Savanna habitats were divided between those that were long unburnt (burnt >24 months previously), and those burnt by an extensive, high-intensity fire within the 12 months preceding the study. Long unburnt savanna had a ground layer dominated by spinifex (*Triodia* spp.). Recently, burned savanna habitats were early successional stages of spinifex savannas, and more floristically variable. They were divided into four types according to differences in understorey plants and substrate type as follows: (i) *Hibiscus keneallyi* savanna was found on skeletal soils over a sandstone substrate; (ii) *Sorghum stipoideum* savanna was found on

sandy soils over a sandstone substrate; (iii) *Chrysopogon fallax* savanna was also found on sandy soils over a sandstone substrate; and (iv) *Heteropogon contortus* savanna was found on skeletal soils over a basalt substrate. We assessed floristic differences between habitat types by ordination of vegetation survey data (Appendix S1–S3). Therefore, although habitat types such as *Hi. keneallyi* and *So. stipoideum* are both post-fire successional stages moving towards *Triodia* spp. savanna, they were treated here as discrete habitats on the basis of plant species composition. Common plant species in each habitat type are listed in Appendix S4. The availability of these vegetation types varied among sites (Table 1).

Trapping and radio tracking

We captured *Mes. macrurus* in treadle-operated wire cage traps (30 cm H × 30 cm W × 70 cm L; Sheffield Wire Products, Welshpool, Western Australia). At each site, 30 traps were set 30 m apart and baited at dusk with a mixture of peanut butter, oats, honey and apple and checked the following morning before dawn. The total number of trap nights was 4470.

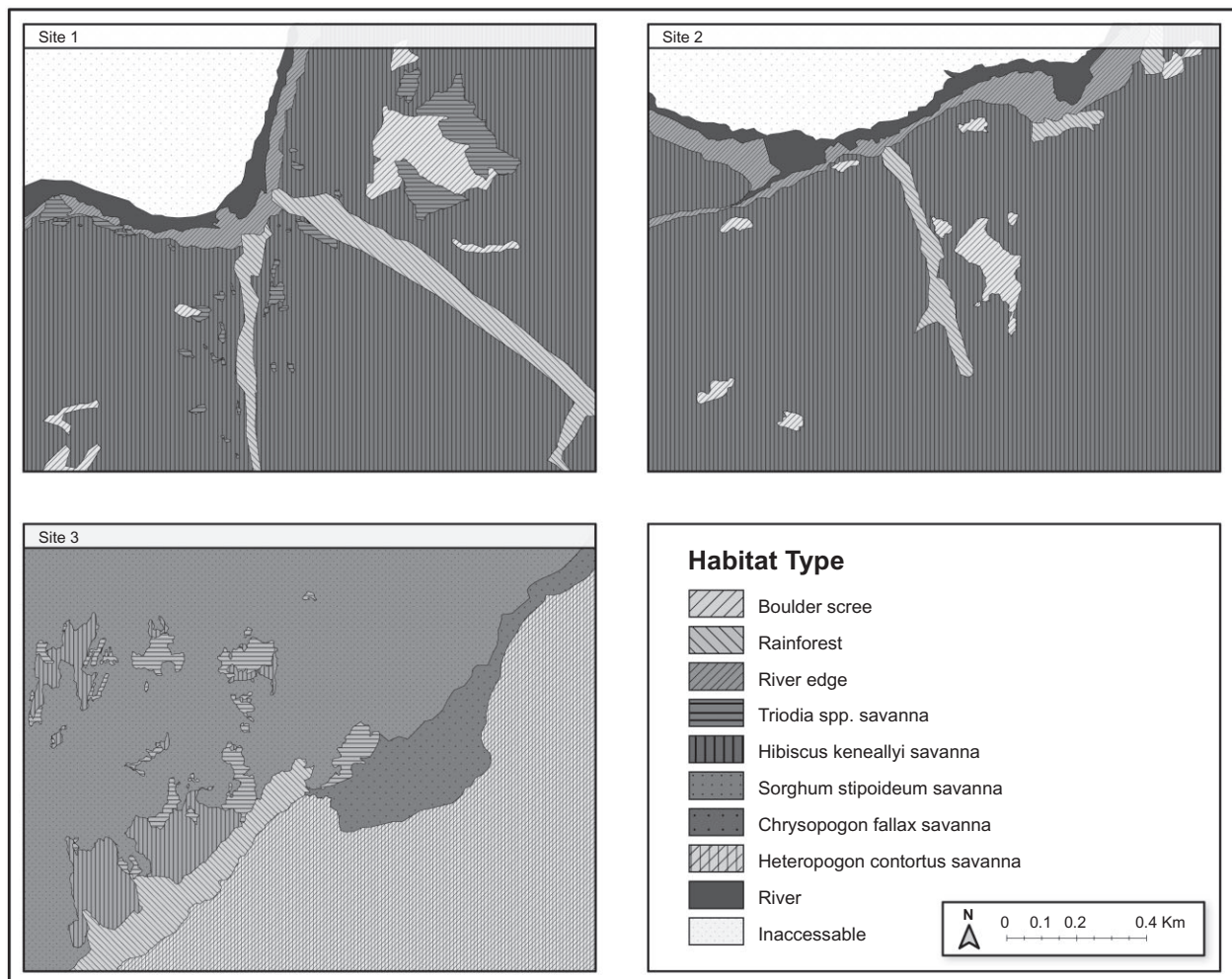


Fig. 2. Habitat composition of sites in the Artesian Range, northwest Kimberley, Western Australia.

Table 1. Proportions of habitat types available at three sites in the Artesian Range, north Kimberley, Western Australia

Habitat type	Last fire	Age (months)	Site 1		Site 2		Site 3	
			Area (ha)	Proportion (%)	Area (ha)	Proportion (%)	Area (ha)	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
Long unburnt savanna								
<i>Triodia</i> spp. savanna	†	24+	6.17	3.53	0.00	0.00	6.15	3.31
Recently burnt savanna								
<i>Hibiscus keneallyi</i> savanna	November 2012	1–12	145.55	83.33	164.48	90.78	10.81	5.82
<i>Sorghum stipoides</i> savanna	October 2013	3	0.00	0.00	0.00	0.00	89.23	48.04
<i>Chrysopogon fallax</i> savanna	October 2013	3	0.00	0.00	0.00	0.00	11.37	6.12
<i>Heteropogon contortus</i> savanna	October 2013	3	0.00	0.00	0.00	0.00	58.82	31.66

†Indicates last fire unknown but >24 months preceding commencement of study period.

On first capture, each animal was weighed and tagged with a nanotransponder microchip (Trovan, North Ferriby, United Kingdom). Animals were classed as adults if they weighed more than 220 g. Females lighter than this were still classified as adults if their teats showed evidence of current or previous lactation. Individuals greater than 170 g were fitted with VHF radio collars (Sirtrack, Havelock North, New Zealand) weighing 5 g (constituting <3% of the animal's body weight). *Mes. macrurus* were tracked at Site 1 in five separate months, twice in the wet season (January 2013 and December 2013) and three times in the dry season (June 2012, April 2013, June 2013). Animals were trapped and tracked at Sites 2 and 3 only in the wet season (February 2013 and January 2014). Each tracking period lasted 1 month and consisted of a week trapping individuals to deploy collars, 2 weeks tracking and a week re-trapping to retrieve collars.

Foraging locations were collected a maximum of four times each night for 14 nights. Individuals were located at least 1 h after a previous fix to minimize autocorrelation. Radio-collared individuals were located at night using the homing method outlined in White and Garrot (1990). For each location, we recorded GPS position, substrate (ground, tree, cliff face, vine, shrub or river edge), the plant species in which the animal was seen and activity (eating, moving or stationary). Den sites were located each day during daylight hours, and the GPS location and den type (tree, dead tree, scree, log, rock castle or cliff) recorded. Features of den trees were compared with an equal number of random trees, defined as the nearest tree within 30 m of the den tree that was greater than 5 m in height and 15 cm in diameter at breast height, and in the direction of one of eight compass bearings. Eighteen features of den and random trees were measured, based on Crane *et al.* (2008) (Appendix S5).

Data analysis

Home range

Home ranges were estimated by minimum convex polygons (MCPs) and fixed kernel density estimators using the

program Geospatial Modelling Environment (Beyer 2012) and interpreted in ArcMap 10.1 (ESRI 2011). Kernel density estimates were calculated using a bandwidth chosen by the least-squares cross-validation technique, which is considered robust for data sets with relatively few locations per individual (Harris *et al.* 1990). The 95% kernel (K95) utilization contour estimated the total home range and the 50% (K50) kernel utilization contour estimated the core home range. All areas included in the MCP and kernel estimates that the animals could not use (including the river and land on the opposite side of the river) were clipped. Overlaps in home ranges of neighbouring individuals tracked over the same period and site were calculated for both core (K50) and total (K95) home-range estimates in ArcMap 10.1. Home-range estimates were tested for normality using the Shapiro–Wilk *W* test, and normalized by log-transformation, before examining differences between sexes and seasons using two-way ANOVA.

Selection of den and foraging sites

We assessed preference for denning and foraging tree species by comparing the percentage of observations in a particular tree species with the relative availability of that species (from vegetation surveys described in Appendix S1) at that site using Ivlev's (1961) preference index. We used classification trees to identify the characteristics that best predicted the likelihood of a tree being used as a den site. A binary response variable was allocated for each tree to identify if it was used by a tree-rat (1) or was an unoccupied tree (0). All variables collected in den tree surveys were used to generate the classification tree.

Habitat selection

We compared the availability of habitat types around used locations and an equal number of randomly generated points, using Bayesian hierarchical mixed-effects models with a model-averaging approach. Habitat maps for each site were created in ArcMap 10.1 using geo-referenced satellite images

Table 2. The mean home-range size of *Mesembriomys macrurus* across sexes, sites and seasons for 18 individuals, with four tracked on multiple occasions

	MCP \pm SE (ha)	K95% \pm SE (ha)	K50% \pm SE (ha)
Female ($n = 11, m = 2$)	1.68 \pm 0.41	2.92 \pm 1.03	0.72 \pm 0.29
Male ($n = 12, m = 2$)	10.580 \pm 2.33	21.45 \pm 6.29	5.13 \pm 1.70
Site 1 ($n = 19, m = 4$)	4.67 \pm 1.16	7.66 \pm 1.98	1.72 \pm 0.45
Site 2 ($n = 2, m = 0$)	15.47 \pm 14.98	36.73 \pm 35.95	9.71 \pm 9.55
Site 3 ($n = 3, m = 0$)	10.14 \pm 3.42	26.04 \pm 15.14	6.32 \pm 4.18
Dry season ($n = 10, m = 3$)	4.69 \pm 1.76	6.70 \pm 2.70	1.43 \pm 0.54
Wet season ($n = 13, m = 0$)	7.58 \pm 1.77	17.12 \pm 4.68	4.24 \pm 1.25
All sites ($n = 23, m = 4$)	6.34 \pm 1.53	13.10 \pm 3.92	3.04 \pm 0.99

K50%, 50% kernel utilization; K95%, 95% kernel utilization; m, number of home ranges used to calculate the average that were from the same individual but from separate occasions; MCP, minimum convex polygon.

from Google earth (Google Inc 2009). Random points were generated within an area bounded by an individuals' MCP home-range estimate, plus a 92-m buffer, this being the average distance between consecutive foraging fixes and so representing the area that the individual had access to but did not use. The proportion of habitat types around these observed and generated locations was extracted from a habitat map within the circular buffers with a 20-m radius.

Data on habitat use were modelled for all sites pooled and also separately for Site 1. Too few individuals were tracked at Sites 2 and 3 for separate analysis. To reduce the number of predictor variables and summarize differences among habitats, we ordinated the habitat data using principal component analysis (PCA). Principal components (PCs) were considered to have high loadings for a habitat variable if the loading value was greater than 0.5. PCAs were run on the data from all sites (1, 2 and 3), and separately for Site 1. Bayesian hierarchical logistic regression models included a binomial response variable (that described if a point was real (1) or generated (0)), and PCs as fixed effects. To account for variation in the availability of habitat types between sites, and individual use of those habitats, site and individual were included as random effects in all models. No relevant biological interactions were expected between habitat variables and so none were included in the models. The use by *Mes. macrurus* of a location point 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 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 (PCs). The probability of a point being used was modelled as:

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

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 :

$$\alpha_j \sim \text{Normal}(\mu, \sigma^2), \text{ for } j = 1, \dots, k$$

For the variance parameters, σ^2 , we determined and utilized non-informative uniform prior hyperparameter distributions, specified as σ^2 -Uniform (0, 100), which was used across all models. Markov chain Monte Carlo (MCMC) procedure was used to estimate posterior distributions using the package MCMCglmm (Hadfield 2010) in the statistical program R (R Development Core Team 2005). MCMC chains were run with randomized starting values, a burn-in of 50 000 iterations, a thinning interval of 20 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. Variable weights were calculated by summing the weights of all models that contained the relevant variable and we used model averaging to estimate variable coefficients and posterior credible intervals according to Anderson (2008).

RESULTS

We tracked 18 individuals for 14–21 days each during one or more of seven separate tracking periods between June 2012 and January 2014, resulting in a total of 945 location points. Of the nine males and nine females tracked, four individuals were tracked during more than one period, and for those individuals we calculated home ranges separately for each period.

Home range

Estimated home-range size was not correlated with the number of fixes taken per individual (MCP: $r = -0.240$, $P = 0.865$, $n = 23$; K95%: $r = -0.376$, $P = 0.962$, $n = 23$; K50%: $r = -0.432$, $P = 0.981$, $n = 23$, Appendix S6). Home-range size varied markedly between individuals, from 0.24 to 30.44 ha (MCP) and 0.55 to

Table 3. A two-way ANOVA examining the variance associated with sex and season for the three measures of home-range size ($n = 23$)

Source of variance	d.f.	MS	F	P
MCP				
Sex	1	20.284	31.387	<0.001
Season	1	0.077	0.119	0.734
Sex*Season	1	1.959	3.032	0.098
K95%				
Sex	1	21.503	26.392	<0.001
Season	1	1.028	1.261	0.275
Sex*Season	1	2.317	2.843	0.108
K50%				
Sex	1	19.994	21.475	<0.001
Season	1	1.247	1.339	0.262
Sex*Season	1	2.286	2.455	0.134

K50%, 50% kernel utilization; K95%, 95% kernel utilization; MCP, minimum convex polygon. Significant values ($P < 0.05$) are in bold.

72.67 ha (K95%) (Appendix S7). Males had significantly larger total home ranges (MCP and K95%) and core home ranges than females (Tables 2 and 3). There were no significant differences in home-range size between the wet and the dry season (Tables 2 and 3). Estimates of home range (K95) overlap for male–male and male–female dyads were similar, at 38.2 and 38.3%, respectively (Appendix S8); overlaps of core home range (K50) were also similar, at 18.7 and 18.4%. In contrast, female–female overlap in total home ranges (K95) and core home ranges (K50) was lower, at 12.9 and 7.4%, respectively.

Den site selection

A total of 363 den sites were documented. The majority were in cliffs (53%) and live tree hollows (33%), with the remaining in logs (5%), scree (4%), rock castles (4%) and dead-standing trees (0.3%). Males spent more time denning in cliffs than females, and females spent more time denning in trees than males (Fisher's test, $P < 0.01$, Appendix S9).

Tree-rats were tracked on 128 occasions to 31 different individual den trees. Of the 78 tree species available across the three sites, only 11 (14.1%) were used as den sites. The species used most frequently were *Syzygium angophoroides* (nine trees), *Xanthostemon paradoxus* (seven), *Eucalyptus rupestris* (four) and *Eu. miniata* (three). Other used species included *Erythrophleum chlorostachys*, *Eu. brachyandra*, *Melaleuca leucadendra*, *Pandanus spiralis*, *Stenocarpus cunninghamii* and *Vitex acuminata*. All species used by tree-rats as dens had positive selection indices ($E_i \geq 0$), indicating more frequent use than expected from availability. *Pa. spiralis* at Site 3 and *Eu. brachyandra* at

Site 1 were the only species used by *Mes. macrurus* with $E_i \leq 0.4$, suggesting weak positive selection. All of the 67 tree species that were not used as dens had $E_i = -1$ (Appendix S10).

Classification tree analysis identified tree species as the factor responsible for the first split between used and unused trees, accounting for 32% of variation and driven by use of *Sy. angophoroides*, *X. paradoxus* and *Eu. rupestris*. The next split was defined by number of hollows: 64% of used trees had more than three hollows and accounting for 21% of the variation. Of the 11 selected trees that had less than three hollows, seven were less than 28 cm from the nearest tree, accounting for 16% of the variation in the data set. The misclassification error rate of the tree was 3.2% (Appendix S11).

Foraging site selection

A total of 582 foraging observations were made, of which 382 (66%) were in trees, 81 (13.9%) on the ground, 62 (11%) on a cliff face, 48 (8.3%) in boulder scree along the river's edge, eight (1.4%) in vines and one (0.2%) in a shrub. Of the 382 observations in trees, the tree species could be identified in 334. These included 39 tree species from 25 families, representing 55.9% of tree species recorded in vegetation surveys (Appendix S12). At Site 1, there were 272 observations of 13 individuals using trees. The most frequently visited species were *Terminalia hadleyana* (23.6%), *Planchonia rupestris* (12.1%) and *Celtis philippensis* (8.5%). At Site 2, there were 28 observations of two individuals using trees, including *Ozwenia vermicosa* (20.6%), *Ad. gregorii* (17.7%) and *T. hadleyana* (8.8%). At Site 3, there were 34 observations of four individuals in trees, and those most frequently visited were *T. hadleyana* (33.3%), *O. vermicosa* (6.1%), *Brachychiton fitzgeraldianus* (6.1%), *Buchanania oblongifolia* (6.1%) and *Bu. obovata* (6.1%). Almost all tree species with visitation frequencies greater than 1% were visited more frequently than expected from local availability ($E_i \geq 0$). Only three tree species, *Pa. spiralis* at Site 1, *Polyalthia australis* at Site 2 and *Acacia delibrata* at Site 3, were avoided relative to their local availability ($E_i \leq 0$). Of the 582 foraging observations, on only 83 occasions were direct feeding observations made (Appendix S13). Animals were most often seen feeding on fruits of *T. hadleyana*, *Pl. rupestris*, *O. vermicosa*, *Ce. philippensis* and *Ad. gregorii*, and occasionally foraged under bark of *T. hadleyana* and *Eu. confertiflora*.

Habitat selection

Ordination of habitat types around used and generated points at all sites produced eight PCs. Models were

Table 4. Loading values for PCs summarizing vegetation characteristics from Sites 1–3 and just Site 1

Site	Variable	PCA loading values				
		PC1	PC2	PC3	PC4	PC5
Sites 1–3	Proportion of variance	55.90	23.06	12.94	3.94	2.78
	Boulder scree	0.01	–0.01	0.01	0.09	–0.01
	Rainforest	–0.71	0.53	–0.08	–0.24	0.02
	River edge	0.01	–0.54	–0.64	–0.32	0.04
	Long unburnt savanna					
	<i>Triodia</i> spp. savanna	0.01	–0.03	0.05	0.59	0.68
	Recently burnt savanna					
	<i>Hibiscus keneallyi</i> savanna	0.70	0.54	–0.06	–0.26	0.00
	<i>Sorghum stipoides</i> savanna	–0.02	–0.36	0.76	–0.38	0.01
	<i>Chrysopogon fallax</i> savanna	–0.00	–0.05	0.03	0.52	–0.73
<i>Heteropogon contortus</i> savanna	0.00	0.00	0.00	0.00	–0.00	
Site 1	Proportion of variance	67.67	27.46	3.35	1.21	
	Boulder scree	0.00	–0.01	0.14	0.84	
	Rainforest	–0.72	0.42	–0.31	–0.19	
	River edge	0.02	–0.78	–0.37	–0.23	
	Long unburnt savanna					
	<i>Triodia</i> spp. savanna	0.02	0.00	0.80	–0.41	
	Recently burnt savanna					
	<i>Hibiscus keneallyi</i> savanna	0.69	0.46	–0.34	–0.19	

Values in bold indicate values of variables that load most strongly (loading >0.5) on the respective PC. The proportion of variance is shown on the top row followed by the loading values of each variable on each PC. PC, principal component; PCA, principal component analysis.

run on the top five PCs, which described more than 98% of the variation in the data (Table 4). The PCA for Site 1 alone produced five PCs and models were run on the first four, which describe more than 99% of the variance in the data (Table 4).

In the models run on all data, all five PCs had variable importance weights that were greater than 50% indicating that they were all important in describing variance in the data (Table 5). Of all possible combinations of variables, the one that included all five PCs had the lowest DIC and the highest model weight of 35%. The next closest model had a weight of 25% and included PC1, PC2, PC4 and PC5. When the models were averaged, PC1, PC2, PC3 and PC4 had 95% posterior credible intervals that excluded zero, suggesting these PCs and the habitat variables they described differed between the used and generated points (Fig. 3). Although PC5 had 95% posterior credible intervals that included zero, it still had a high variable importance weight as the highest ranking model included in all PCs.

The model-averaged parameter coefficient of PC1 was negative, suggesting that at Site 1, rainforest was more common around used points than expected, and *Hi. keneallyi* savanna (between 1 and 12 months post-fire) less. PC2 also had a negative model-averaged parameter coefficient, implying selection for river edge habitat over surrounding *Hi. keneallyi* savanna, and rainforest habitats. The model-averaged coefficient for PC3 was also negative, suggesting selec-

Table 5. The variable importance weights of principal components (Table 4) influencing habitat use by *Mesembriomys macrurus* in the Artesian Range, north Kimberley, Western Australia

Model	Parameter	Variance = 100	
		Mean	SD
Sites 1–3	PC 1	0.967	0.110
	PC 2	0.966	0.110
	PC 3	0.746	0.100
	PC 4	0.786	0.104
	PC 5	0.841	0.109
Site 1	PC 1	0.972	0.219
	PC 2	0.868	0.222
	PC 3	0.904	0.223
	PC 4	0.824	0.224

Estimation used included a burn-in = 50 000, thinning interval = 20, total iterations = 250 000 and prior variance coefficients = 100.

tion for *So. stipoides* savanna (3 months post-fire) and against river edge habitat. This could reflect variation in availability of these habitats, as at sites where *So. stipoides* savanna was available, river edge habitats were not. The negative model-averaged coefficient of PC4 suggests *Ch. fallax* savanna (3 months post-fire), and long unburnt *Triodia* spp. savanna were selected against. The credible intervals of the

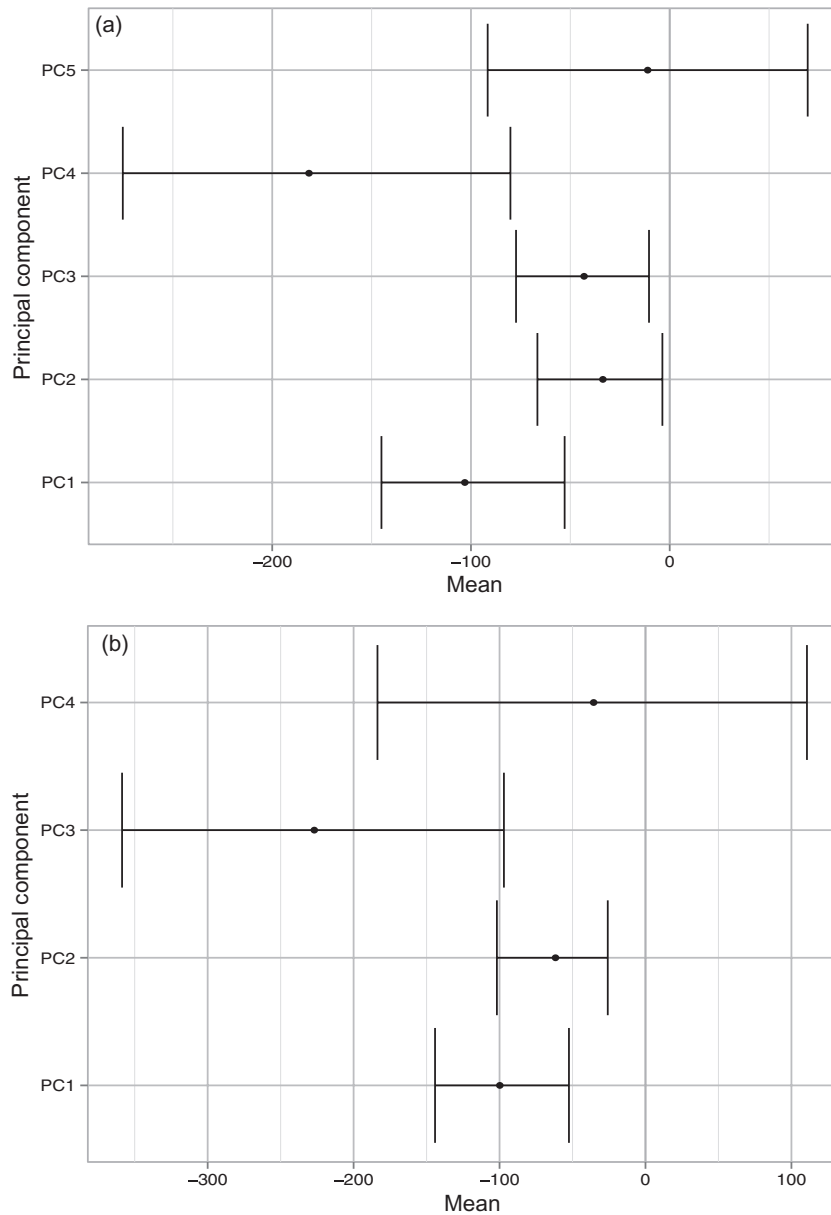


Fig. 3. Model-averaged coefficient estimates with 95% credible intervals for habitat variables from models describing habitat selection by *Mesembriomys macrurus* in the Artesian Range, northwest Kimberley, Western Australia, fitted to the data from Sites 1–3 (a) and Site 1 (b).

model-averaged parameter coefficient of PC5 included zero, suggesting no strong selection of *Triodia* spp. savanna over *Ch. fallax* savanna.

In models run for Site 1 alone, all four PCs had importance weights greater than 50% (Table 5). The model with the smallest DIC value included all PCs and had a model weight of 64%. The next closest model included PC1, PC3 and PC4 and had a weight of 11%. When the models were averaged, PC1, PC2 and PC3 had posterior credible intervals that did not include zero (Fig. 3). The parameter coefficient of PC1 was negative, suggesting that at Site 1, high propor-

tions of long unburnt rainforest and low proportions of *Hi. keneallyi* savanna (between 1 and 12 months post-fire) were found around used points. The model-averaged coefficient of PC2 was also negative, suggesting that used points were also more likely to be in river edge habitat. The negative coefficient of PC3 suggests that used points were less likely to be found in patches of long unburnt *Triodia* spp. savanna. The final PC in the model, PC4, had posterior credible intervals that included zero, suggesting that both used and generated points did not vary in their occurrence in boulder scree habitat.

DISCUSSION

Our results suggest that fire could plausibly threaten the persistence of *Mes. macrurus* in northern Australia, because the denning and fruiting trees preferred by *Mes. macrurus* are known to be vulnerable to fires, with effects ranging from delayed fruiting through to the death of the tree (Williams *et al.* 1999; Vigilante & Bowman 2004b). Preferred tree species were found in a broad range of habitat types, including savanna and riparian areas. However, although *Mes. macrurus* was likewise active in a broad range of habitats, individuals consistently selected for rainforest in preference to recently burnt savanna. *Mes. macrurus* is thus capable of using and persisting in a wide range of vegetation types given sufficient resources, but rainforest patches may be important refuges in post-fire periods when surrounding savanna habitats have been burnt.

The quality and quantity of shelter sites is likely to influence reproductive success and survival (Rendell & Robertson 1989; Sedgeley 2001). *Mes. macrurus* used a variety of den types including trees and rock features (which this species has not previously been recorded using). The high availability of rock features in the dissected sandstone habitats of the study region may contribute to the persistence of *Mes. macrurus* in the area. Several studies have found that Australian mammal species that shelter in rock features have lower rates of extinction than other species (Burbidge & McKenzie 1989; Smith & Quin 1996). The features that most strongly defined trees used by *Mes. macrurus* were species identity and the availability of hollows. These two factors may be connected as certain tree species are more likely to form hollows (Braithwaite *et al.* 1985). Only three of the 11 species used as den trees were found primarily in rainforest (*Sy. angophoroides*) or riparian habitats (*Mel. leucadendra* and *Pa. spiralis*), and the remaining eight species were found in a variety of habitats.

The tree species most frequently visited by foraging *Mes. macrurus* were fruit bearing and occurred in a range of habitats. *Mes. macrurus* were also observed foraging beneath peeled bark, presumably for arthropods, and opportunistically in debris washed up after a late wet season flood (resulting in high observed use of river edge habitat). This adds to information from a dietary study of *Mes. macrurus* in the Mitchell Plateau, north Kimberley, which recorded animals feeding on leaves of *Eu. tetradonta*, flowers of *Persoonia falcata* and *Hypoestes floribunda*, fruit of *Canarium australianum* and termites (Morton 1992). Presumably, *Mes. macrurus* will exploit a wide range of resources according to availability.

In the habitat selection models, all PCs and the habitats they represented were important in describing the distribution of *Mes. macrurus* locations. In both

models, *Mes. macrurus* selected for rainforest over recently burnt savanna. Although tree species used by *Mes. macrurus* for foraging and denning were for the most part not rainforest specialists, rainforest habitats may offer higher densities of these species. Fires of high intensity can also cause mortality of large- and medium-sized tree stems (Williams *et al.* 1999; Vigilante & Bowman 2004a), especially older hollow-bearing trees (Isaac *et al.* 2008). Reproductive cycles of trees are altered by fire, and Aboriginal people used fire to control the fruiting and flowering cycles of particular species (Haynes 1985; Vigilante & Bowman 2004b). In the north Kimberley, *Bu. obovata*, *Pe. falcata* and *Planchonia careya* flowered significantly less in areas burnt by mid dry season fires and were found in greater densities in areas with lower fire frequencies (Vigilante & Bowman 2004a; Atchison 2009). It is therefore possible that the selection of rainforest by *Mes. macrurus* also reflects the use of trees that were not burnt and whose reproductive cycles were unaffected by fire.

Although *Mes. macrurus* displayed preferences for long unburnt rainforest pockets, there was no clear selection for long unburnt savanna habitats. Savannas at earlier post-fire successional stages (2–12 months old), with understoreys characterized by *Hi. keneallyi* and *So. stipoides*, were used in preference to long unburnt savanna. *Hi. keneallyi* dominated early post-fire successional stages have high plant diversity of the understorey, are more open, and perhaps easier for *Mes. macrurus* to move through, than long unburnt savanna with *Triodia* spp. in the understorey. Savanna with a *Sorghum* sp. understorey is common in the Kimberley in areas with relatively high fire frequencies (Scott *et al.* 2009). Although such habitats were used by tree-rats in this study, monitoring surveys in the King Leopold Ranges in the central Kimberley have not detected *Mes. macrurus* in recently burnt *Sorghum* sp. habitats in recent years (Radford unpubl. data; Legge and Tuft unpubl. data).

In the north Kimberley, relatively recent surveys have reported *Mes. macrurus* at sites with dense vegetation including rainforest (McKenzie *et al.* 1975; Bradley *et al.* 1987; Friend *et al.* 1991; Start *et al.* 2007), *Livistona* sp. palm or mangrove elements (Kitchener *et al.* 1981). However, previous studies have detected the species in a wider variety of habitats. There are early records of the species using eucalypt woodland in open red sand plains in the central (McKenzie 1981) and southwest Kimberley (Dahl 1897). In addition, recent surveys both on the Kimberley mainland (Start *et al.* 2012) and offshore islands (Gibson & McKenzie 2012) have found *Mes. macrurus* in open savanna habitats. These records indicate that given sufficient resources the species can utilize a number of habitats, despite preferences for rainforest displayed in our study.

In northern Australia, frequent high-intensity fires cause the retreat of rainforest edges (Russell-Smith 1991; Russell-Smith *et al.* 1993; Prior *et al.* 2007), decline of obligate-seeding species (Russell-Smith *et al.* 1998) and reduction of tree species diversity in the savanna (Williams *et al.* 1999). Although studies in the Northern Territory have detected both damage to rainforest patches (Russell-Smith & Bowman 1992) as well as regional increases in patch size (Banfai & Bowman 2006), the most recent analysis suggests that fire-sensitive elements of the savanna mosaic are in decline (Russell-Smith *et al.* 2012). In the north Kimberley, fire damage was recorded in over 40% of surveyed rainforest pockets (McKenzie & Belbin 1991), and studies indicate that a regime of frequent, extensive and intense fires are likely to cause displacement of fire-sensitive vegetation types, as well as long lived, and obligate-seeding species (Fisher *et al.* 2003; Vigilante & Bowman 2004a).

The topographic complexity of our study area may contribute to the retention of resources important to *Mes. macrurus*, and provide a degree of direct protection from potential threats such as fire, predation by feral cats and grazing by feral herbivores. In the Kimberley, rainforest pockets characteristically persist in areas that are topographically protected from intense fires (McKenzie *et al.* 1991; Russell-Smith & Bowman 1992; Bowman 1994). Fire patchiness at a very fine scale is promoted by dissected rocky complexity and can allow the retention of fruit and hollow-bearing trees. Predation by feral cats is also thought to be a key driver of mammal declines in northern Australia (Fisher *et al.* 2014; Frank *et al.* 2014) and in the central Kimberly cats were found to target habitats recently burnt by intense fire (McGregor *et al.* 2014). Rocky substrates may provide protective cover from feral cats as well as other predators, particularly in recently burnt areas. Further, rocky country is a natural barrier to introduced herbivores and therefore mitigates their impacts upon habitat structure, productivity and ultimately native fauna (Legge *et al.* 2011a).

Although declines of small mammals in northern Australia may be driven by multiple threats, our results suggest that for *Mes. macrurus* the impact of contemporary fire regimes on vegetation structure (and the various indirect consequences of those changes) could be an important driver. Although *Mes. macrurus* is evidently capable of surviving in a broad range of open savanna habitats, individuals in a relictual population select for fire-sensitive landscape elements. To retain resources used by *Mes. macrurus* including hollow-bearing and fruiting tree species and fire-sensitive vegetation, landscape management strategies should aim to implement low-intensity burns during the late wet and early dry seasons to reduce the incidence of intense and extensive fires in the mid-to-late dry season.

ACKNOWLEDGEMENTS

This study was funded by the Australian Wildlife Conservancy, Australian Research Council Linkage Grant (LP100100033) and the Department of Parks and Wildlife (Western Australia). The study methods were approved by the University of Tasmania Animal Ethics Committee (permit number A12516). Fieldwork would not have been possible without the hard work of numerous volunteers, and the support of staff at Australian Wildlife Conservancy's Mornington Wildlife Sanctuary.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Vegetation survey methods.

Appendix S2. PERMANOVA analysis examining differences in vegetation types at the three sites.

Appendix S3. Comparisons of habitat types at the three sites.

Appendix S4. Dominant plant species available in eight habitat types at the three sites.

Appendix S5. Variables recorded for den trees.

Appendix S6. Correlations between number of fixes and estimates of home range area.

Appendix S7. Home range estimates and tracking effort for each individual.

Appendix S8. Proportion of home range overlap between adjacent individuals.

Appendix S9. Den types used by males and females.

Appendix S10. Selectivity indices of tree species available for use as dens.

Appendix S11. Classification tree using the causal variables that predict if an individual tree was used or unused as a den site.

Appendix S12. Tree species *M. macrurus* were sighted in.

Appendix S13. Feeding observations of *M. macrurus*.