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Niche partitioning explains the difference between widespread and restricted distributions, and detection rarity of arboreal mammals from north Kimberley savannas

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ABSTRACT

Context. Conservation managers often have little information on distribution ranges and ecological characteristics of rare species, thereby hindering effective decision-making. This challenge is evident for arboreal mammals of northern Australia where species vary widely in abundance, are nocturnal and cryptic, and exhibit regionally divergent patterns of rarity and decline. **Aims.** We compare (1) trapping niche, (2) denning and foraging niche and (3) vegetation habitat preferences to test for links between niche and rarity among arboreal species. **Methods.** Survey data obtained using a variety of terrestrial and arboreal methods are used to define trapping niche, vegetation habitat preferences and abundance/distribution of arboreal mammal species in Western Australia's northern Kimberley. Denning and foraging niche is defined based on available literature. **Key results.** Based on combined niche observations, we suggest that arboreal denning species with a preference for open forest vegetation are the most prone to rarity, restricted distributions and decline in the Kimberley. Very restricted extent of suitable open forest vegetation in the Kimberley may locally exacerbate threats to forest specialists. Generalist, terrestrial denning species preferring savanna woodlands/shrublands and rugged rocky habitats were more abundant and less restricted in their distributions than forest specialists. **Conclusions.** These results highlight the local importance of small areas of open forest for threatened arboreal mammals in the Kimberley. **Implications.** We suggest that targeted adaptive management interventions to preserve and enhance open forest vegetation and arboreal habitat including den hollows, through application of low intensity prescribed burning for protection from damaging wildfires, would benefit specialist arboreal species.

Keywords: arboreal, critical weight range mammals, fire ecology, habitat specialisation, niche, northern Australia, threatened species, tropical savannas.

Introduction

Australia has very high rates of mammal extinctions in a global context (Loehle and Eschenbach 2012; Wintle *et al.* 2019). Extinctions of mammals in Australia, particularly within the critical weight range (CWR, 35–5000 g) have been the highest of any fauna group since European colonisation (Burbidge and McKenzie 1989; Murphy and Davies 2014). Highest rates of extinction have been in Australia's arid zone, starting as early as the mid 1800's and continuing right through to the present (Johnson 2006). Ongoing extinctions and declines of Australian mammals appear to show no signs of abating (Woinarski *et al.* 2025). One of the more recently reported regions to be affected by broad-scale mammal declines is the tropical savannas of north-western Australia that up until the last few decades had mammal assemblages that were considered largely intact compared to the rest of the continent (McKenzie *et al.* 2007; Woinarski *et al.* 2001, 2010, 2011; Murphy and Davies 2014).

Although CWR mammals as a group have declined across the entire tropical savanna region (Woinarski *et al.* 2011; Ziembicki *et al.* 2015; Stobo-Wilson *et al.* 2025), there are some differences in the expressions of these declines, and possibly the processes driving

them in different regional contexts and among different species or species groups. For example, arboreal species appear to be disproportionately represented among declining mammals of northern Australia (Fitzsimons *et al.* 2010; Woolley *et al.* 2024). There is debate about whether the key drivers of declines are predominantly arboreal or terrestrial for these species (Woolley *et al.* 2018; Stobo-Wilson *et al.* 2019; Penton *et al.* 2020, 2021*a*, 2021*b*; Woolley *et al.* 2024). There are also cross-regional differences in decline patterns among arboreal mammals. While in the Northern Territory the arboreal black-footed tree-rat *Mesembriomys gouldii* and the brush-tailed possum *Trichosurus vulpecula* subsp. *arnhemensis* are still common in some areas (Davies *et al.* 2018; Stobo-Wilson *et al.* 2020; Penton *et al.* 2020, 2021*a*, 2021*b*; Woolley *et al.* 2024), these species are now very rarely detected in the Kimberley (Bradley *et al.* 1987; Start *et al.* 2007; Radford *et al.* 2014, 2015, 2020, 2021*a*; Kerle *et al.* 2024). Conversely, the partially arboreal northern quoll *Dasyurus hallucatus* (Trewella *et al.* 2024) and the golden-backed tree-rat *M. macrurus* are apparently common in parts of the Kimberley (Radford *et al.* 2020, 2021*a*; Kerle *et al.* 2024) but have declined markedly or become extinct in Northern Territory savannas (von Takach *et al.* 2020). Several additional arboreal species, including the brush-tailed phascogale *Phascogale tapoatafa* and the northern brush-tailed phascogale *P. pirata* (Geyle *et al.* 2020), and the brush-tailed rabbit-rat *Conilurus penicillatus*, appear to have declined to low abundance across both savanna regions (Firth *et al.* 2010; Woinarski *et al.* 2014; Davies *et al.* 2017). On the other hand, the recently described arboreal savanna glider *Petaurus ariel* still occurs across extensive parts of the Northern Territory compared to the other arboreal species (Stobo-Wilson *et al.* 2019; Cremona *et al.* 2021).

What processes underlie these apparently disparate observations on arboreal mammals across northern savannas, and are processes the same or different among the various species? One of the key problems in addressing these questions is that for some of these species there is very little information on their distributions or ecological associations because they are seldom detected using standardised survey methods and are seldom seen due to their remote locations and cryptic ecological characteristics (e.g. nocturnal, forage in arboreal habitats). For this reason, we have little basic information about these species upon which to base hypotheses on causes of decline or regional/ecological divergence in these processes.

Several studies have been published on the impacts of threatening processes on abundance and richness of CWR mammals in the Kimberley region (Bradley *et al.* 1987; Start *et al.* 2007; Gibson and McKenzie 2012; Radford 2012; Radford *et al.* 2014, 2015, 2020, 2021*a*; Kerle *et al.* 2024). Despite this, gaps in our understanding, particularly of arboreal species remain. There is currently insufficient species-specific data for many of the arboreal species to test hypotheses concerning reasons for decline or factors supporting persistence. There is little information on current locations of extant populations, species conservation status or population trends, niche partitioning among species or regional differences in niche habitat extent. In this study, we use eight years of survey records to locate current arboreal mammal refugia and assess the effectiveness of different terrestrial and arboreal trapping methods. We compare trap success between ground-based live-trapping, ground-based camera-trapping, arboreal nest-box and camera trapping surveys to investigate relative effectiveness of the different methods and define trapping niche. Using an experimental approach we further define species trapping niche via direct comparison between tree-based vs ground-placed cameras in the same habitats during simultaneous surveys. Species were subsequently classified according to trapping niche, vegetation/habitat preferences during surveys, known denning and foraging preferences, and by geographic distribution and trap success to assess whether common and widespread species differed in their arboreal niche compared to restricted and low abundance species. Finally, we compare the availability of different vegetation/habitat types regionally to elucidate possible interregional habitat limitations as a contributing factor to divergent decline patterns across northern savannas.

Methods

Study region and design

The study area is the north Kimberley region of north-western Western Australia (Figs 1 and S1). All the study locations occur within either government-managed conservation reserves or Indigenous Protected Areas and areas of Exclusive Possession Native Title Determination managed by the associated native title groups. Some survey data in this study were collected prior to Native Title declarations. The region experiences a tropical monsoonal climate, with high temperatures year-round (daily mean maximum temperature 29.6–36.0˚C) and high rainfall (900–1550 mm) occurring predominantly during the warmer months (i.e. November to April). Savanna vegetation is characteristic of this region, with eucalypt species making up most of the tree canopy and C4 grasses dominating the understorey. Stratification of monitoring sites was based on major north Kimberley vegetation types (Beard *et al.* 2013; Mucina and Daniel 2013). The major Kimberley savanna vegetation habitats used to stratify monitoring sites were tall open *Eucalyptus tetrodonta* savanna forest with mixed tussock grasses on laterititic and alluvium/colluvium substrates (tree canopy 30–70%, height up to 20 m), *Eucalyptus tectifica* woodland and scree with tussock grasses on mafic igneous (volcanic) substrates (tree cover 10–30%, height up to 15 m) and eucalypt woodland/shrubland with *Triodia* spp. hummock grasses on

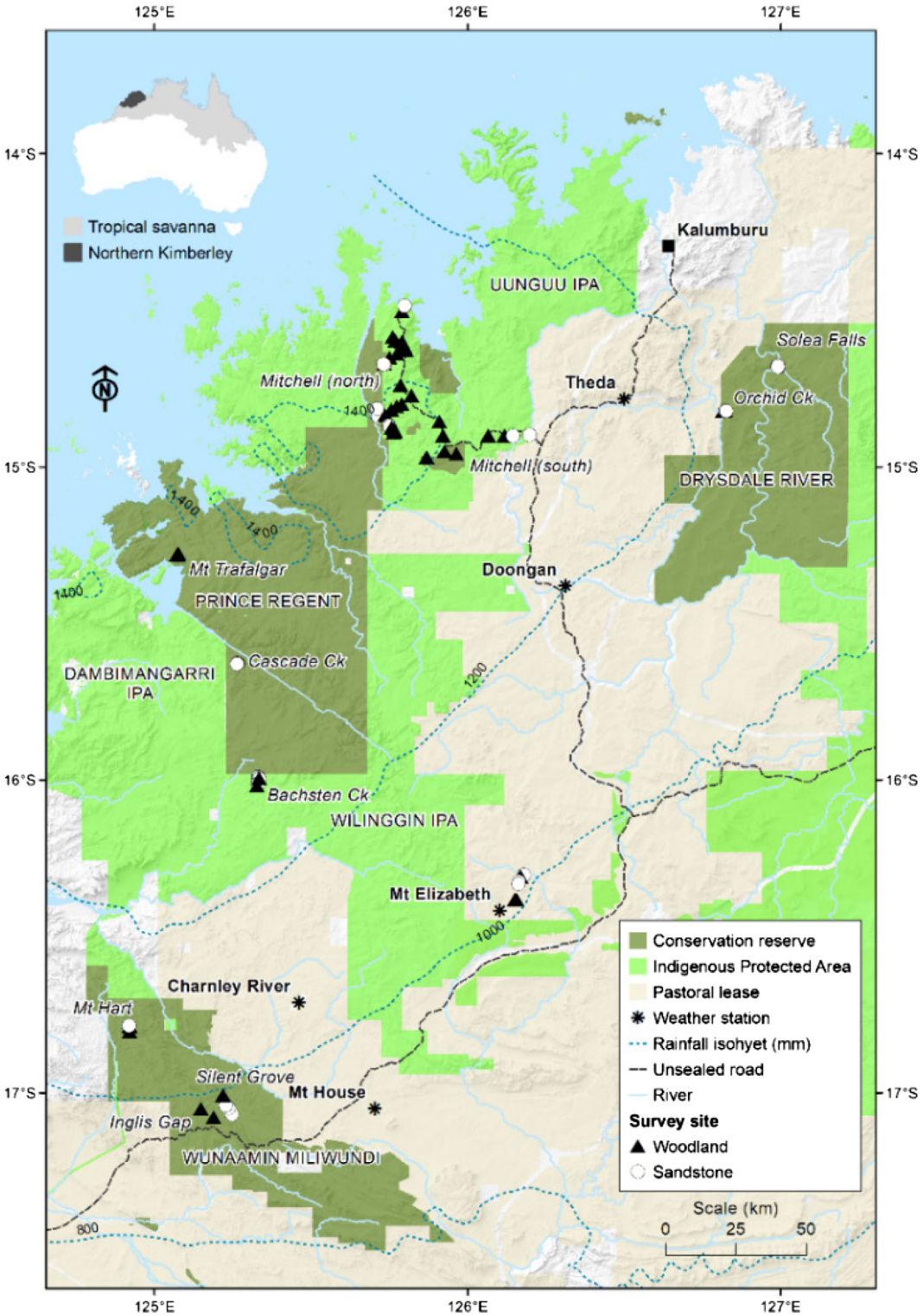

Fig. 1. Locations of monitoring survey locations in the north Kimberley region of northern Western Australia.

rugged sandstone substrates (tree cover 10–30%, height up to 15 m) (Department of Environment and Conservation 2012; Corey *et al*. 2024). Small patches of non-eucalypt closed vine thicket rainforest (tree cover 70–100%) and open *Callitris intratropica* forest also occur within the savanna matrix and monitoring sites were also established within these. The north Kimberley region is recognised as a relatively intact landscape that has not been subjected to extensive vegetation

clearing (Connor *et al.* 2018). However, the region contains a highly flammable savanna ecosystem in which vegetation structure and composition has likely experienced historical change with Indigenous people implementing purposeful landscape-scale burning that was subsequently disrupted during colonisation. In recent decades reintroduction of Indigenous fire management under the North Kimberley Fire Abatement Project (Vigilante *et al.* 2024) and Traditional Owner Healthy Country Plans (Wunambal Gaambera Aboriginal Corporation 2010; Balanggarra Aboriginal Corporation/Kimberley Land Council 2011; Dambimangari Aboriginal Corporation 2012; Wilinggin Aboriginal Corporation 2012), and increased investment by government agencies in prescribed burning (Department of Environment and Conservation 2012; Radford *et al.* 2020; Corey *et al.* 2024) has led to reductions in high severity late dry season wildfire. Introduced herds of cattle, pigs, horses and donkeys are widespread throughout the region with varying impact on vegetation condition depending on land tenure and management implemented (Ondei *et al.* 2017; Reid *et al.* 2020; Mihailou and Massaro 2021). Both inappropriate fire regimes and introduced ungulates are key threats occurring more broadly across northern Australian savannas (Andersen *et al.* 2005; Legge *et al.* 2011, 2019; Woinarski *et al.* 2011; Stobo-Wilson *et al.* 2020; Radford *et al.* 2020, 2021*a*; Vigilante *et al.* 2024).

Monitoring surveys: ground-based live-trapping

Ground-based live-trapping methodologies within the monitoring program are reported in Radford *et al.* (2015, 2020, 2021*a*). Monitoring sites were situated at least 50 m from roads. Trap effort per site survey was either 72 or 144 trap nights in 2011 (24 traps open for 3 or 6 nights) and was standardised thereafter at 120 trap nights (24 traps open 5 nights). A total of 407 survey sessions was undertaken at 94 sites during the study period between 2011 and 2019. Surveys were conducted in 50 × 50 m quadrats similar to those used as a standard monitoring plot in other parts of northern Australia (Woinarski *et al.* 2010; Legge *et al.* 2011; Radford *et al.* 2015). A total of 10 large (15 × 15.5 × 46 cm) and 10 medium (9 × 10 × 33 cm) metal box traps (Elliotts) were alternatively placed around the perimeter of each quadrat. Four larger wire cage traps (25 × 30 × 73 cm) were placed at the corners. Traps were baited with a mixture of peanut butter and rolled oats. Traps were shaded using grass, leaves or hessian sacks and checked early each morning to prevent overheating. Mammals were identified to species using Menkhorst and Knight (2021), marked using ISO FDX-B Microchips (Mychip) for larger species and permanent marker pens on ears for small species (e.g. rodents) and released immediately on site. Trap success for each species was calculated as a percentage based on the total number of individuals captured (not including recaptures) during 120 trap nights during a survey session.

Vegetation structure at survey sites

Vegetation structure in each plot (50 × 50 m) was assessed during the mammal surveys to provide basic information on arboreal habitat (Radford *et al.* 2015, 2020, 2021*a*; Table 2). Tree height (plants > 4 m) was estimated using a 1% Bitterlich gauge (Lindsey *et al.* 1958). Each plant canopy was assessed as 1% cover if the 10 cm cross-bar, held 50 cm from the observer's eye, was narrower than the canopy width when standing at the quadrat's central point (37 m along the diagonal from the quadrat corner post) in a 360° arc to give total canopy cover percentage. Tree basal area was estimated using a Basal Area Factor 1 Metric Wedge Prism (CruiseMaster). Height of each canopy tree species was measured using an inclinometer at a distance of 15 m from the base of the tree.

Extent of vegetation structural types

Estimates of extent of vegetation types across the north-western Australian savanna region were based on classifications under the National Vegetation Information System (NVIS) (2025). Daniel and Mucina (2013) and Kenneally (2018) were used as sources where the resolution of vegetation mapping under NVIS was insufficiently accurate to detect vegetation types in small patches including open forest and rainforest/vine thicket (e.g. detected using aerial photography, 1:2000).

Ground-based camera trapping

Single cameras were set up to identify additional species not captured in Elliott or cage traps for the five nights of live-trapping. Reconyx PC900 Hyperfire Professional Infra-red (IR) or PC950 Hyperfire Security IR cameras were used in camera surveys, both of which are successful in detecting mammals >1 kg. Cameras were baited using universal bait, as for live-trapping. Cameras were attached to trees, rocks or steel posts at ~1 m above the ground in a horizontal, slightly downward-facing direction allowing detection within a 5 × 2 m area. Ground-layer vegetation was cleared immediately in front of the camera to reduce false triggers and increase visibility, thereby improving ability to identify species. Trap success was calculated as the percentage of days on which each species was recorded on that camera.

Arboreal nestboxes

Nestboxes are used by a range of arboreal mammal species in northern Australian savannas (Woolley *et al.* 2024). Starting in 2015, two nestboxes were deployed in separate trees at monitoring sites that were accessible by road. Half of the nestboxes were large (dimensions 400 × 250 × 250 mm, entrance diameter 100 mm) and half were small (dimensions 400 × 180 × 180 mm, entrance diameter 50 mm), with entrance holes at the front of the nestbox and a lid/awning above the entrance to deter bird occupation. The nestboxes

were made from plywood and external surfaces were weather sealed. Nestboxes were fixed to the tree with brackets ~5–7 m above the ground on a randomly-selected large (>20 cm DBH) eucalypt tree within or adjacent to the monitoring site. Some leaf litter material was placed inside the nestboxes. Nestboxes were checked once during each monitoring survey using a secured ladder tied to the tree (Fig. S1e). Nestbox occupancy was assessed by carefully lifting the hinged lid of the nestbox. If animals were present, the nestbox was taken down from its bracket on the tree, and the animal extracted and handled on the ground as per live-trapping protocols indicated above. Opportunistic hair samples were taken and identified as a record of a local detection event. Nestbox success was the number of times a species was present in a nestbox when checked as a percentage of days checked.

Arboreal cameras

Ad hoc arboreal camera deployments occurred at several locations where previous casual observations, such as spotlighting, had identified rare arboreal mammals in the area. Cameras were fixed on 1.5 m-long brackets attached to tree trunk or branch such that the camera faced towards obvious pathways or hollow/nestbox entrances possibly used by arboreal species. Trap success for camera-trapped species was recorded as a percentage based on the number of days detected over the number of days deployed.

Trapping niche experiment: arboreal vs terrestrial cameras

The experiment to test the degree of arboreality of the various arboreal mammal species was undertaken at Bachsten Creek in the Wilinggin Indigenous Protected Area (Fig. 1) south of Prince Regent National Park, within mixed savanna vegetation types where previous monitoring surveys had highlighted continued occurrence of arboreal mammal species (e.g. *Dasyurus hallucatus*, *Mesembriomys macrurus*, *Petaurus ariel* and *Petropseudes dalhii*), and rock-adapted (e.g. *Isoodon auratus*, *Petrogale burbidgei*, *Wyulda squamicaudata*, *Zyzomys argurus* and *Z. woodwardii*) and terrestrial species (*Isoodon macrurus*, *Rattus tunneyi* and *Pseudomys nanus*). Vegetation was a matrix of open forest, woodland and shrubland. Shrubland vegetation included the shorter-stature species *Eucalyptus brachyandra*, *Ficus platypoda*, *Acacia* spp., *Terminalis* spp. and *Vitex acuminata* with a hummock grass understorey (*Triodia* spp. and *Sorghum stipoideum*) on rugged sandstone ridges. Open forest and woodland trees included *E. tetrodonta*, *E. miniata, E. alba*, *Corymbia* spp. and *Melaleuca leucadendra* with a mixed tussock grass understorey (e.g. *Sorghum plumosum*, *Dichanthium fecundum*, *Eragrostis speciosa* and *Mnesithea rottboellioides*) and occurred in the intervening valley systems of the study area. Both open forest/woodland vegetation and adjacent sandstone ridges were represented in the sampling design to explore local scale niche differentiation.

Cameras were placed both in trees and on the ground to compare the relative detection rates among putative arboreal and terrestrial species. Cameras were placed at previously established monitoring sites for which vegetation structural and habitat measurements were available (see above), and sites represented a gradient of increasing tree cover from sandstone shrubland/woodland through to open forest, and also a range of site rock cover/ruggedness values to quantify adaptation to rocky habitats. Tree cameras were placed 2.5–8 m above the ground on trees, fixed to 1.5 m-long horizontal brackets and trained towards the tree trunk. To test for the benefits of nestboxes in terms of detecting species, half the arboreal cameras were placed on trees with nestboxes ($n = 8$) and the other half were placed on trees without nestboxes. In addition to site-based vegetation and habitat measurements, tree diameter at breast height (DBH), tree height and number of visible natural hollows were measured for trees on which cameras were placed. Ground-based cameras ($n = 17$) were placed on brackets attached to star pickets at ~1 m height facing vertically downwards. At all cameras, a bait station was placed in mid-view with universal bait (peanut butter and oats) that was inaccessible to fauna. Cameras were placed for 9 months, and sites were inaccessible during the wet season (December–May) therefore baits could not be renewed, and only early animal visitation was likely to have been influenced by bait. Detection for each species on each camera was analysed as a count of the number of days (24 h periods) on which each species was detected over the number of days when cameras were deployed and active (batteries still charged). Tests for the effect of differences in camera deployment days among cameras (some batteries did not last the full deployment period) were non-significant ($P > 0.05$) and provided no explanatory power ($R^2 < 2\%$), therefore these were removed from further analyses.

Denning and foraging niche

Arboreal species from the study region were classified as either arboreal or terrestrial denning and foraging species based on published species-specific ecological literature (e.g. Baker and Gynther 2023, and others). Searches used species name, 'denning', 'foraging' and 'diet'.

Statistical analyses

Statistical analyses of ground-based live-trapping surveys has previously been undertaken (Radford *et al.* 2015, 2020, 2021*a*) and is referred to in this study. Relatively low trap effort during 5-day camera trap deployments during live-trapping surveys, nestbox checks and *ad hoc* arboreal camera trap deployments were of insufficient replication to detect significant regressions with any site-based environmental variables ($P > 0.05$; $R^2 < 5\%$). Therefore, detection data are presented

simply as trap success among the different trapping methods and different vegetation habitat types.

Multivariate Analysis of Variance (MANOVA) was used to test for differences in mammal species assemblages detected in tree versus ground-based cameras (MINITAB Release 14). Non-metric multidimensional scaling (NMDS) ordination using Sorensen Distance was performed on log transformed detections to describe variability in assemblages between tree and ground-based cameras (PC-ORD 7). Non-independence among explanatory variables was tested using Pearson's rank correlations prior to NMDS ordination and highly correlated explanatory variables (Pearson's r between ±0.6 and ±1.0 see Table S1) discarded. A secondary matrix of environmental explanatory variables was used to test for the role of tree and habitat variables camera height, site tree canopy cover, site rock cover and site shrub cover in patterns of mammal assemblage.

Stepwise regressions (MINITAB 14) were used to quantify the most influential explanatory variables among both arboreal and terrestrial cameras for each mammal species separately. Separate stepwise regressions were subsequently used for species detected in arboreal and terrestrial cameras independently to test for the relative importance of arboreal vs terrestrial habitat attributes. Explanatory variables retained for stepwise regression of arboreal and terrestrial cameras included Camera Height, Tree Canopy Cover, Rock Cover and Shrub Cover, with highly correlated variables discarded (Table S1). Explanatory variables included for arboreal regressions were camera tree DBH, camera tree height, camera tree nestbox presence/absence, site tree cover, site rock cover and site shrub cover, with highly correlated variables discarded (Table S2). Explanatory variables retained for ground-based cameras were site tree canopy cover, site rock cover and site shrub canopy cover, and other site level explanatory variables were dropped (see Table S3).

Results

Terrestrial detections

Total terrestrial live trapping effort across North Kimberley monitoring sites during 8 years of surveys represented 48,840 trap nights, whereas terrestrial camera trapping represented much lower total trap effort (2035 trap nights) (Table 1). Despite fewer trap nights represented by camera-trapping, cameras detected the same number of arboreal species (six species each) compared to live-traps and recorded higher trap success. Terrestrial cameras detected two additional arboreal species not detected during live-trapping, including *Petaurus ariel* and *Trichosurus vulpecula* subsp. *arnhemensis* (Table 1, Fig. 2*a*). However, live-trapping also detected two species, *Melomys burtoni* and *Mesembriomys gouldii*, that terrestrial cameras did not detect.

Despite generally low trap success (<1%), terrestrial live-trapping resulted in more terrestrial species being detected than camera trapping (16 spp. for live-trapping vs 7 spp. for camera-traps, Table 1). Terrestrial species not detected using cameras were predominantly small (<50 g) with the exception of the very common rodent *Zyzomys argurus*. (Table 1). It should be noted that *Isoodon auratus* and *I. macrourus*, and *Petrogale burbidgei* and *P. concinna* were not reliably identified based solely on camera trap images due to cryptic diagnostic features. We assumed that smaller *Petrogale* rock wallabies were *P. burbidgei* based on *P. concinna* being very rare on the Kimberley mainland based on recent surveys (Potter *et al.* 2012, 2014). The exclusively terrestrial *Isoodon* spp. could not be reliably distinguished using camera traps. The small terrestrial dasyurid *Sminthopsis butleri* was not detected at all during monitoring surveys. Three additional species, *Leggadina lakedownensis*, *Planigale maculata* and *Sminthopsis macroura* had very low trap success and site detection (t.s. < 0.01%, Table 1) but this may be because the study region was outside their core distributions.

Arboreal detections

Total trap effort for arboreal camera trapping was much higher (tn = 6794) than for nestboxes (tn = 426) (Table 1). Arboreal camera trapping was more successful in detecting arboreal mammal species than checking nestboxes, with 6 of the 10 known arboreal species detected using arboreal cameras, whereas only two arboreal species, *P. ariel* and *M. macrurus*, were detected in nestboxes (Table 1). An additional detection of *M. gouldii* was made in a nestbox using a hair sample from a python scat collected in a nestbox (Table 1). *P. ariel* had a higher detection rate across arboreal camera trapping and nestbox checks (t.s. > 10%) than all other arboreal species (t.s < 2%) (Table 1). Arboreal camera trapping was successful in detecting two species (*Phascogale tapoatafa* and *Petropseudes dahlii*) not detected using terrestrial trapping or nestboxes (Fig. 2*b*, *c*, Table 1). Among putative arboreal species, *D. hallucatus*, *C. penicillatus*, *Melomys burtoni*, *Mesembriomys Macrurus* (Fig. 2*c*), *Petaurus ariel* and *W. squamicaudata* were all commonly detected (>10 trap sessions) using a combination of trapping methods, whereas *Mesembriomys gouldii*, *Petropseudes dahlii* (Fig. 2*c*), *Phascogale tapoatafa* (Fig. 2*b*) and *T. vulpecula* subsp. *arnhemensis* (Fig. 2*a*) were rarely detected (<4 sessions) (Table 1).

Six out of 10 arboreal species (*C. penicillatus*, *D. hallucatus*, *M. burtoni*, *M. macrurus*, *T. vulpecula* and *W. squamicaudata*) were more likely to be trapped using terrestrial trapping methods than arboreal methods (Table 1). Only *P. ariel* and *P. tapoatafa* were exclusively trapped using arboreal methods (Table 1). *M. gouldii* and *P. dahlii* were recorded using both terrestrial and arboreal methods but had higher trap success using arboreal methods (Table 1). None of the known terrestrial mammals were recorded from arboreal captures.

Table 1. Arboreal, semi-arboreal and terrestrial mammal species mean detections during north Kimberley surveys of arboreal nestbox checks (2016–2019), ground-based live-trapping (Elliott and cage traps), terrestrial camera-trapping (2011–2019) and arboreal camera-trapping (2016, 2017–2018) during Kimberley monitoring surveys.

Mammal species	Terrestrial live-trapping		Terrestrial camera-trapping		Arboreal nestboxes		Arboreal camera-trapping		Dominant trapping niche
	Sessions (n = 407)	Trap success % (tn = 48,840)	Sessions (n = 407)	Trap success % (tn = 2035)	Sessions (n = 213)	Nestbox success % (tn = 426)	Sessions (n = 5)	Trap success % (tn = 6794)	
Arboreal									
Conilurus penicillatus (110–190 g)	28	0.23	11	0.49	0	0	0	0	Terrestrial
Dasyurus hallucatus (300–1000 g)	143	1.03	62	5.31	0	0	1	0.45	Terrestrial
Melomys burtoni (30–120 g)	29	0.42	0	0	0	0	0	0	Terrestrial
Mesembriomys gouldii (600–880 g)	1	0.002	0	0	1	0.47[A]	0	0.03	Arboreal
Mesembriomys macrurus (240–330 g)	50	0.21	29	3.84	2	1.41	3	0.39	Terrestrial
Petaurus ariel/sp. C.K. (50–150 g)	0	0	1	0.05	26	28.17	3	13.93	Arboreal
Petropseudes dahlii (1280–2000 g)	0	0	1	0.001	0	0	1	0.03	Arboreal
Phascogale tapoatafa (100–310 g)	0	0	0	0	0	0	1	0.16	Arboreal
Trichosurus vulpecula subsp. *arnhemensis* (1300–4500 g)	0	0	1	0.05	0	0	0	0	Terrestrial
Wyulda squamicaudata (900–2000 g)	28	0.10	13	1.18	0	0	0	0	Terrestrial
Terrestrial									
Hydromys chrysogaster (620–1200 g)	1	0.002	4	0.39	0	0	0	0	Terrestrial
Isoodon auratus (250–650 g)	57	0.28	–	–	0	0	0	0	Terrestrial
Isoodon macrourus (500–3000 g)	117	0.60	–	0	0	0	0	0	Terrestrial
Isoodon spp. (250–3000 g)	–	–	80	7.08	0	0	0	0	Terrestrial
Leggadina lakedownensis (15–25 g)	2	0.004	0	0	0	0	0	0	Terrestrial
Petrogale brachyotis (2200–5500 g)	6	0.02	24	1.87	0	0	0	0	Terrestrial
Petrogale burbidgei (950–1400 g)	17	0.06	27	2.70	0	0	0	0	Terrestrial
Planigale maculata (6–12 g)	1	0.002	0	0	0	0	0	0	Terrestrial
Pseudantechinus ningbing (15–33 g)	9	0.02	0	0	0	0	0	0	Terrestrial
Pseudomys delicatulus (6–12 g)	23	0.09	0	0	0	0	0	0	Terrestrial
Pseudomys johnsoni (9–17 g)	7	0.01	0	0	0	0	0	0	Terrestrial
Pseudomys nanus (25–50 g)	89	0.56	0	0	0	0	0	0	Terrestrial
Rattus tunneyi (50–210 g)	75	0.90	1	0.05	0	0	0	0	Terrestrial
Sminthopsis macroura (15–25 g)	2	0.004	0	0	0	0	0	0	Terrestrial
Sminthopsis virginiae (18–75 g)	23	0.10	0	0	0	0	0	0	Terrestrial
Zyzomys argurus (35–75 g)	159	2.05	8	0.74	0	0	0	0	Terrestrial
Zyzomys woodwardi (80–210 g)	86	0.79	15	1.18	0	0	0	0	Terrestrial

Cameras set up in trees were not part of the regular monitoring program but rather targeted camera placements aimed at detecting arboreal species suspected to be present at specific locations based on *ad hoc* spotlighting activities. Single trapping surveys were classed as a 'session' and trap success was calculated as a percentage of total trap nights (tn) per session.

[A]Detected via diagnostic hair cross-sections undertaken on hairs from python scat found in nestbox.

Denning and foraging niche from the ecological literature

D. halluctaus is reported to use a wide variety of dens both in terrestrial and arboreal habitats including rock crevices, tree hollows, logs, termite mounds and artificial structures (Oakwood 2002, 2023; Moore *et al*. 2021; Cowan *et al*. 2022; Trewella *et al*. 2024) (Table 2). Dietary studies and foraging observations suggest that *D. hallucatus* diets are broad and omnivorous but are dominated by terrestrial invertebrates and small vertebrates (Oakwood 2002, 2023; Radford 2012; Dunlop *et al*. 2017) (Table 2). *M. burtoni* occupies a broad range of vegetation including grasslands, rainforest, swamps and riparian woodlands and is an agile climber usually building nests off the ground in

Fig. 2. Photographs from (*a*) a ground-based camera trap of *Trichosurus vulpecula* subsp. *arnhemensis* at one of the Mitchell Plateau monitoring sites during 2011; (*b*) an arboreal camera image of *Phascogale tapoatafa* during an *ad hoc* deployment at the Mitchell Plateau during 2016; and (*c*) an arboreal camera image of *Petropseudes dahli* (top right) and *Mesembriomys macrurus* (bottom left) at Bachsten Creek in 2016.

grassy or woody vegetation (Kerle 2023). *M. burtoni* eats terrestrial and arboreal foods including grass seeds, fruits and insects (Kerle 2023) (Table 2). *M. macrurus* dens in both rocky and arboreal habitats (e.g. hollows) and forages mainly for arboreal fruits and vegetation (Morton 1992; Hohnen *et al.* 2015; Gibson and McKenzie 2023; Kerle *et al.* 2024) (Table 2). *W. squamicaudata* dens and forages in complex rocky habitats including rainforest and its diet is predominantly arboreal, especially including fruits and leaves (Hohnen *et al.* 2016; Burbidge *et al.* 2023) (Table 2). *P. ariel* is strongly arboreal in both denning and foraging, using tree hollows or nestboxes for denning (Penton *et al.* 2020, 2021*a*, 2021*b*; Woolley *et al.* 2024) and ingesting sap, nectar and invertebrates from tree canopies (Stobo-Wilson *et al.* 2019; Cremona *et al.* 2023) (Table 2). *P. dahlii* den in complex rocky outcrops and escarpments, while foraging mostly for arboreal foliage, fruits and flowers in vine thicket vegetation (Runcie 1999; Webb *et al.* 2023) (Table 2). *C. penicillatus* dens in arboreal or semi-arboreal habitats including tree hollows or hollow logs (Firth *et al.* 2006, 2010; Penton *et al.* 2020, 2021*a*, 2021*b*) but forages mainly on terrestrial foods, especially grass seeds, but also flowers, fruits and invertebrates (Firth *et al.* 2005; Kemper *et al.* 2023; Kerle *et al.* 2024) (Table 2). *M. gouldii* dens mainly in arboreal habitats, especially hollows high up in tall savanna eucalypts (Penton *et al.* 2020, 2021*a*) and forages predominantly for arboreal fruits and flowers (Morton 1992; Kerle *et al.* 2024) (Table 2). *P. tapoatafa* is known to den in tree hollows and forage predominantly on mature trees, large logs, standing dead timber and under bark for large insects, spiders, small vertebrates and nectar (Soderquist and Rhind 2023) (Table 2). Though considered plastic in denning habitat across its entire Australian range, the northern brushtail *T. vulpecula* subsp. *arnhemensis* mainly uses arboreal habitats for denning (e.g. hollows and drays) (Penton *et al.* 2020; Woolley *et al.* 2024) and forages for a broad range of arboreal resources including foliage, flowers and fruits (Kerle and How 2023) (Table 2).

Vegetation linked detections

Vegetation structure differed between the major habitats in terms of tree canopy height, tree basal area and projected tree canopy cover (Table 2). As expected, tall open forest had the highest tree height and basal area, and the second highest projected canopy cover of the vegetation habitats. Vine thicket rainforest had the highest projected canopy cover, and the second highest basal area and tree height (Table 2). *Callitris* groves had the next highest tree height, canopy cover and basal area, followed by volcanic woodlands, sandstone rocky woodlands, volcanic scree and sandstone shrubland scree (Table 2).

Arboreal mammal species were detected most commonly in tall open forest habitats (spp = 9), followed by closed vine thicket/rainforest (spp = 5), rocky sandstone woodlands (spp = 5), rocky sandstone scree shrublands (spp = 4), volcanic scree (spp = 4) and volcanic woodlands (spp = 3). No arboreal mammals were detected in *Callitris* forest groves (Table 2). Combined arboreal mammal trap success was highest in closed vine thicket rainforest, followed by volcanic woodland, sandstone shrubland scree, tall open forest, sandstone woodland, volcanic scree and *Callitris* forest groves (Table 2).

Based on habitats where species have been detected and their geographic spread, Kimberley arboreal mammals can be divided into several ecological groups. Geographically widespread species (detected in >3 subregions) were all species that were detected in rocky shrublands/woodlands (Table 2). These include a group of species found in rocky habitats but also across a broad range of other woodland and forest habitats (*D. hallucatus*, *Mesembriomys macrurus* and *P. ariel*) that we describe here as Rock Generalists (Table 2). The scaly-tailed possum *Wyulda squamicaudata* is also included, detected exclusively in rocky and rainforest habitats (rock/rainforest specialist), and *Melomys burtoni*, detected at high abundance in rainforest but also in a range of forest, woodland and rocky habitats (forest/woodland generalist) (Table 2). Geographically restricted species (detected in only

Table 2. Mean Kimberley arboreal species trap success per hundred trap nights (%) across different vegetation habitats based on monitoring surveys.

Vegetation types (site no.)	Subregions (n = 10, 5[A])	Tropical closed Vine Thicket Rainforest (n = 42, 4[A])	*Eucalyptus tetrodonta* Tall Open Forest (n = 38, 39[A])	*Eucalyptus tectifica* Volcanic Woodland (n = 110, 30[A])	*Eucalyptus tectifica* Volcanic Scree (n = 10, 4[A])	*Callitris intratropica* Forest Grove (n = 18, 0[A])	Eucalypt Sandstone Woodland Rocky (n = 114, 16[A])	Sandstone Shrubland Scree Rocky (n = 75, 16[A])	All vegetation types
Mean canopy height (m) (±s.d.)		10.9 (±3.0)	14.1 (±3.0)	10.0 (±2.6)	7.5 (±2.2)	10.9 (±2.0)	8.8 (±3.2)	7.5 (±3.0)	
Mean basal area (±s.d.)		11.6 (±3.9)	14.8 (±5.8)	4.9 (±3.4)	4.5 (±1.1)	11.5 (±4.8)	6.1 (±2.5)	3.6 (±2.4)	
Mean projected canopy cover (±s.d.)		69.0 (±26.4)	37.2 (±11.0)	20.4 (±10.7)	20.0 (±6.4)	37.7 (±8.9)	25.4 (±10.3)	14.9 (±8.7)	
Widespread									
Dens in rocks, trees/CWD & ground									
Dasyurus hallucatus (T,t)	BC, CC, MN, MH, BG	0.44	0.13	2.75	0.37	0	1.59	1.98	1.04
Melomys burtoni (T,t)	MN, MS, Tr, BG	3.22	0.20	0	0.25	0	0.02	0	0.53
Mesembriomys macrurus (A,t)	BC, CC, MN, MH, Tr	0.77	0.26	0	0.02	0	0.18	0.28	0.22
Wyulda squamicaudata (A,t)	BC, CC, MN, Tr	0.32	0	0	0	0	0.08	0.23	0.09
Dens in trees									
Petaurus ariel (A,a)[A]	BC, MN, MS, MH, BG	0	0.21	0.33	0.50	–	0.06	0.19	0.22
Restricted									
Dens in rocks and trees/CWD									
Petropseudes dahlii (A,a)	BC	0	0.03	0	0	0	0[SP]	0[SP]	0.004
Dens in trees/CWD									
Conilurus penicillatus (T,t)	MN, Tr	0.12	1.27	0.36	0	0	0	0	0.25
Mesembriomys gouldii[A] (A,a)	BC, MN[B]	0.47[B]	0.01	0	0	0	0	0	0.08
Phascogale tapoatafa[A] (A,a)	MN	0	0.16	0	0	0	0	0	0.02
Trichosurus vulpecula subsp. *arnhemensis* (A,t)	MS	0	0.05	0	0	0	0	0	0.007
Total arboreal mammal trap success		5.34	2.32	3.44	1.14	0	1.93	2.68	2.41

Species are classified by denning habitat (headings), predominant arboreal or terrestrial foraging niche based on literature (A, T) and predominant arboreal or terrestrial trapping niche based on trapping data presented in this study (a, t). Mean and standard deviation of tree basal area (m^2 timber/ha) measured using a factor 1 basal area prism and projected tree canopy cover (%) measured using a Bitterlich Gauge is presented to objectively define each vegetation habitat type based on values measured at North Kimberley monitoring sites. Widespread species here were designated as having been detected in three or more regions, with restricted species detected only in one or two regions. [SP]Species detected only from spotlighting and though incidental observations rather than during formal trapping surveys. Subregions were MN (Mitchell Plateau North), MS (Mitchell Plateau South, Mitchell), Tr (Mt Trafalgar, Prince Regent National Park (PRNP)), CC (Cascade Creek, PRNP), BC (Bachsten Creek), MH (Mt Hart, Wunamin Miliwundi National Park) and BG (Bells Gorge, Wunamin Miliwundi National Park).

[A]Estimates based on arboreal trap data from the five subregions where arboreal nestboxes and arboreal cameras were used.

[B]Detected as hair samples in predator scats (e.g. python, dingo).

1 or 2 subregions) included species detected only in forest habitats (*Mesembriomys gouldii*, *Phascogale tapoatafa* and *Trichosurus vulpecula* subsp. *arnhemensis*), one species detected in woodlands and forest habitats (forest/woodland generalist *C. penicillatus*), and one species *Petropseudes dahlii* known to be a rock specialist (from spotlighting and based on literature: Runcie 1999; Olds *et al.* 2016, 2017; Webb *et al.* 2023) but only detected in open forest habitat during our surveys (Table 2).

Nine of the ten arboreal species were detected in northern, coastal, high rainfall subregions (MN, BC, Tr, CC, MH and BG) (Table 2). In contrast, only three arboreal species were detected in more inland, lower rainfall subregions (MS) (Table 2).

Arboreal-terrestrial trapping niche experiment

Arboreal and terrestrial cameras differed significantly in the mammal assemblages detected (Wilk's MANOVA: DF 9/23; $F = 19.891$; $P < 0.0001$). NMDS ordination supported segregation of arboreal and terrestrial cameras in terms of mammal assemblage (Fig. 3). Species more likely to be detected by arboreal cameras included *Petaurus ariel*, *Mesembriomys macrurus*, *Wyulda squamicaudata* and *M. gouldii*, while *D. hallucatus*, *Petrogale burbidgei*, *Zyzomys* spp., *Isoodon* spp. and rodents/small dasyurids were more likely to be detected by terrestrial cameras (Fig. 3). *Petaurus ariel* and *M. gouldii* were exclusively detected in arboreal cameras (Fig. 3, 4*a*, *b*). Three species, *M. macrurus* (Fig. 4*c*, *d*), *W. squamicaudata* (Fig. 4*e*, *f*) and *D. hallucatus* (Fig. 4*g*, *h*) were detected in both arboreal and terrestrial cameras. All other species including *Petrogale burbidgei* (Fig. 4*i*) and *Isoodon* spp. (Fig. 4*j*) were detected almost exclusively in terrestrial cameras (or in terrestrial habitats, e.g. one *P. burbidgei* was incidentally detected on the ground in rocky habitat under one of the arboreal cameras). Environmental variables most strongly associated with segregation of mammal assemblages were camera height along Axis 1 and rock cover along Axis 2 (Fig. 3).

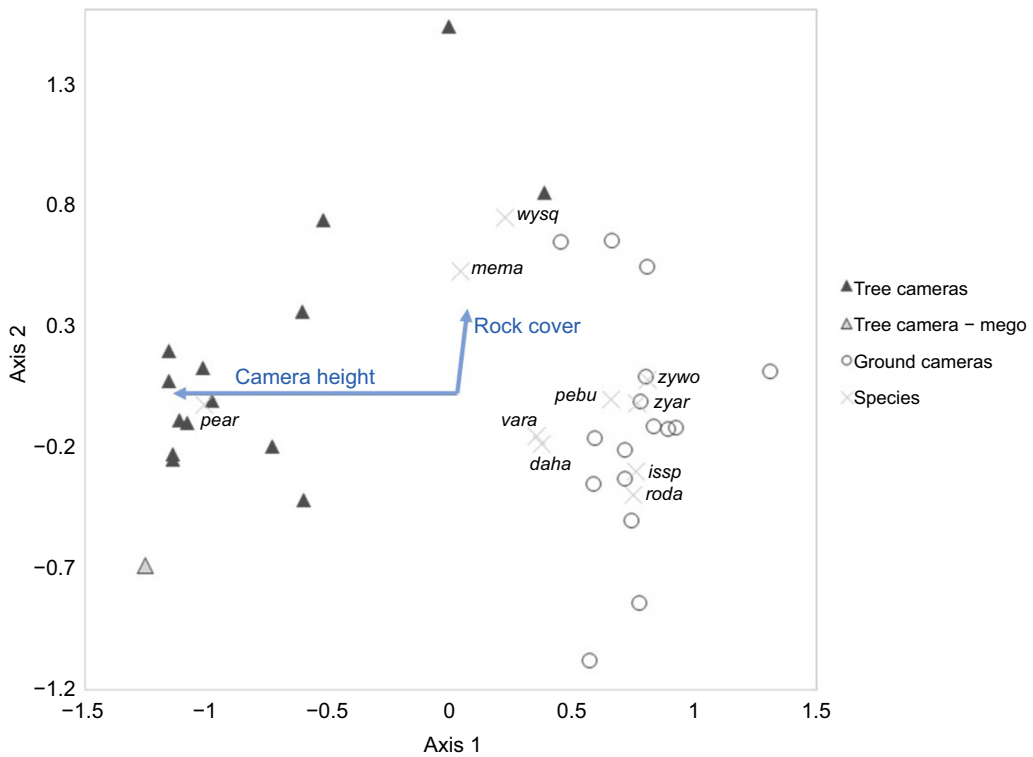

Fig. 3. Non-metric multi-dimensional scaling (NMDS) ordination of mammal assemblages among camera traps. Final NMDS stress was 15.814 and Pearson's correlation cutoff for explanatory variable vectors was $r = 0.200$. Species labels are as follows: *pear* – *Petaurus ariel* (savanna glider), *mema* – *Mesembriomys macrurus* (golden-backed tree-rat), *wysq* – *Wyulda squamicaudata* (scaly tailed possum), *daha* – *Dasyurus hallucatus* (northern quoll), *pebu* – *Petrogale burbidgei* (monjon rock wallaby), *zywo* – *Zyzomys woodwardi* (Kimberley rock rat), *zyar* – *Zyzomys argurus* (common rock rat), *issp* – *Isoodon* spp. (golden and northern brown bandicoots), *roda* – small/medium rodents and dasyurids, and *vara* – *Varanus* spp. (goanna species). 'Camera height' refers to height above ground level (up a tree or on a star picket) of camera placement. 'Rock cover' is the percentage of camera site ground area made up by rock or boulders. Filled triangle symbols denote tree-based camera assemblages while clear circles denote ground-based assemblages. The grey triangle denotes the single tree camera where *Mesembriomys gouldii* (black footed tree rats) was detected.

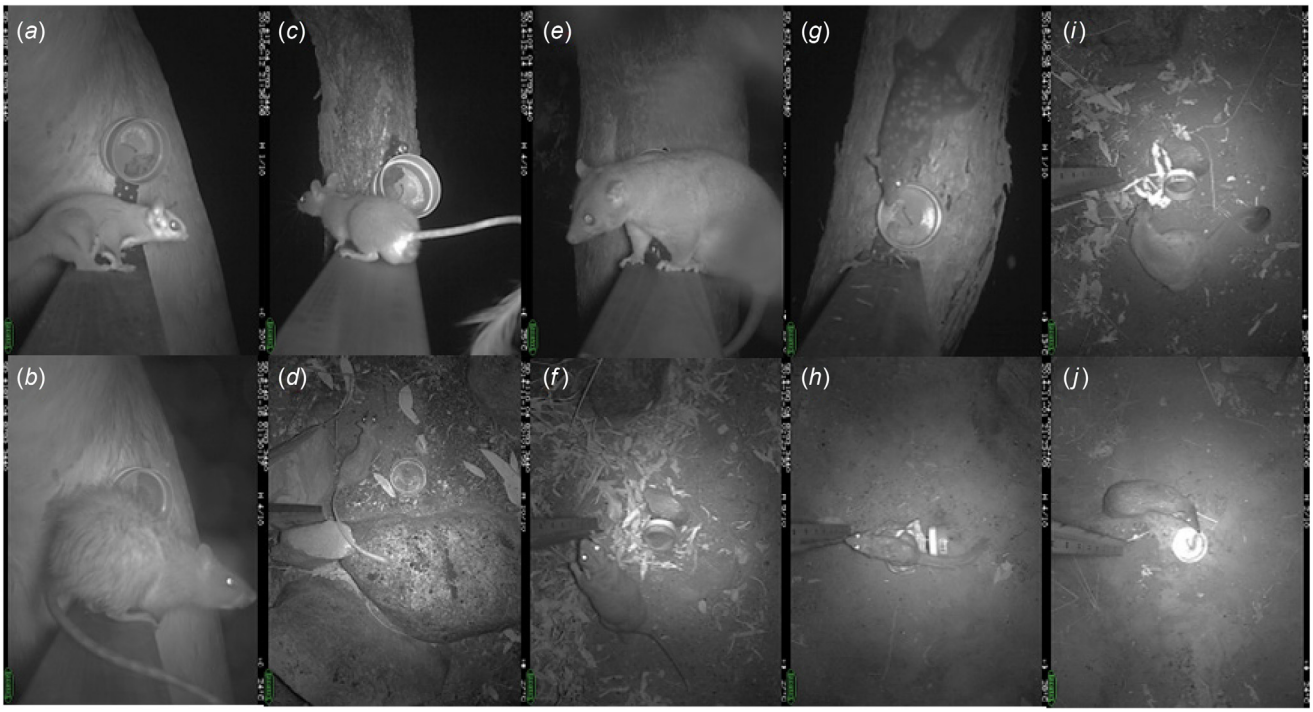

Fig. 4. Mammal species detected during the niche experiment at Bachsten Creek in 2014 and 2015 by arboreal and terrestrial cameras. These include the species (*a*) *Petaurus ariel* and (*b*) *Mesembriomys gouldii,* which were exclusively detected by arboreal cameras. Three species were detected using both arboreal and ground-based cameras, including *M. macrurus* both in a tree (*c*) and on the ground (*d*), *Wyulda squamicaudata* in a tree (*e*) and on the ground (*f*), and *Dasyurus hallucatus* in a tree (*g*) and on the ground (*h*). (*i*) *Petrogale burbidgei* and (*j*) *Isoodon macrourus* were exclusively detected on terrestrial cameras.

Based on stepwise regressions, *Petaurus ariel* had a positive response to camera height, while *Isoodon* spp., *Petrogale burbidgei*, *Zyzomys* spp., small rodents/dasyurids and total mammal species richness had negative responses to camera height (Table 3). *D. hallucatus* and *W. squamicaudata* had positive responses to percentage rock cover at camera sites, while *Isoodon* spp. and small rodents/dasyurids had negative responses to rock cover (Table 3). Shrub cover was negatively associated with *D. hallucatus* and mammal species richness but positively associated with *M. macrurus* and *Z. woodwardi* detection (Table 3). Tree canopy cover was positively associated with *M. macrurus, Z. argurus* and total mammal species richness (Table 3). The strongest environmental associations ($R^2 > 0.3$) were for the arboreal species *Petaurus ariel*, the terrestrial species *Isoodon* spp. and *Z. argurus*, and for total mammal species richness (Table 3).

For arboreal cameras, only 40.6% of variation in detection of *P. ariel* and 10.1% of variation in detection of *M. macrurus* were explained by arboreal environmental variables (Table 3). *Dasyurus hallucatus*, *M. gouldii* and *W. squamicaudata* showed no significant association with any habitat attributes. Presence of a nestbox in a camera tree was positively associated with detection of *P. ariel* and total arboreal mammal species richness (Table 3). Tree canopy cover was positively associated with *M. macrurus* and arboreal mammal species richness (Table 3). Shrub cover was negatively related to arboreal mammal species richness (Table 3).

Relatively strong explanatory power ($R^2 > 70\%$) was provided by site-based habitat factors for two arboreal species (*Mesembriomys macrurus* and *W. squamicaudata*), while another three species (*Isoodon* spp., *P. burbidgei* and *Z. woodwardi*) showed weak ($R^2 < 15\%$) environmental responses for terrestrial camera detections (Table 3). Tree canopy cover was positively associated with *M. macrurus* detection, while shrub cover was positively associated with both *M. macrurus* and *W. squamicaudata* detection (Table 3). Rock cover was positively associated with detection of *P. burbidgei* and *Z. woodwardi*, while *Isoodon* spp. and small rodents/dasyurids were negatively associated with shrubs (Table 3).

Extent of vegetation types

Forest vegetation is much more restricted in the North Kimberley Region than the Top End of the Northern Territory (Daniel and Mucina 2013; Kenneally 2018; National Vegetation Information System (NVIS) 2025; Table 4). Zero rainforest/vine thicket (NVIS Factsheet MVG 1) or open forest vegetation (NVIS Factsheet MVG 3) were detectable in the North Kimberley Region in areas with >1000 mm annual

Table 3. Stepwise regressions of relationships between detection of mammal species and environmental explanatory variables from an experimental study where both arboreal and terrestrial cameras were deployed to test for differences in arboreal niche.

	Camera Height	Tree Height	Tree DBH	Tree Nestbox	Site Canopy cover	Site Rock cover	Site Shrub cover	R-sq (adjusted)
Combined arboreal/terrestrial cameras								
Arboreal species								
Dasyurus hallucatus						+	–	7.8
Mesembriomys gouldii								
Mesembriomys macrurus					+		+	18.0
Petaurus ariel	+							62.2
Wyulda squamicaudata						+		12.7
Terrestrial species								
Isoodon spp.	–					–		43.7
Petrogale burbidgei	–							19.5
Small mammals (Muridae/Dasyurid)	–					–		11.8
Zyzomys argurus	–				+			38.7
Zyzomys woodwardi	–						+	15.5
Total mammal species richness	–				+			36.8
Arboreal cameras								
Dasyurus hallucatus								
Mesembriomys gouldii								
Mesembriomys macrurus					+			10.1
Petaurus ariel		+		+				40.6
Wyulda squamicaudata								
Arboreal mammal species richness			+	+	+		–	45.4
Terrestrial cameras								
Isoodon spp.						–		13.5
Mesembriomys macrurus					+		+	77.8
Petrogale burbidgei						+		9.5
Small mammals (Muridae/Dasyurid)						–		7.6
Wyulda squamicaudata							+	75.8
Zyzomys argurus								
Zyzomys woodwardi						+		11.3

+ Indicates positive regression between mammal detection and the environmental variable. – indicates a negative regression. A bold symbol indicates a significant regression ($P < 0.05$) and non-bold indicates a non-significant regression ($P > 0.05$). R-sq (adjusted) is the percentage of variation in mammal detection explained by combined regressions.

rainfall using National Vegetation Information System (NVIS) (2025) methodology, whereas 2600 km^2 rainforest/vine thicket, and 52,169 km^2 open forest were detected in the Northern Territory within the same rainfall zone (Table 4). Finer-scale regional structural vegetation mapping using aerial photography however suggests that the extent of Kimberley rainforest/vine thicket is ~70 km^2 (Kenneally 2018) and open forest is ~911 km^2 (Daniel and Mucina 2013), nevertheless this is still much less than in the Northern Territory (Table 4). Eucalypt woodlands (NVIS Factsheet MVG 5) on a range of substrates in the Kimberley including mafic/igneus, lateritic and alluvial/colluvial substrates (Daniel and Mucina 2013) (10,167 km^2) cover approximately a quarter of the area of eucalypt woodlands in the Northern Territory (10,167 km^2 compared to 47,290 km^2) (Table 4). Tropical eucalypt woodlands (NVIS Factsheet MVG 12), mainly on sandstone substrates in the Kimberley (Daniel and Mucina 2013), cover similar-sized areas in the Kimberley (50,713 km^2) and the Northern Territory (53,396 km^2) (Table 4). Relatively small areas (2375 km^2) in the North Kimberley Region constitute shrub-dominated vegetation devoid of a tree canopy (Daniel and Mucina 2013, Table 4).

Table 4. Extent of different vegetation formations based on projected canopy cover (pfc) in the Northern Territory and the North Kimberley Region in areas with >1000 mm annual rainfall.

Vegetation type	NVIS classification	Northern Territory >1000 mm Area (km²)	Kimberley >1000 mm Area (km²)	North Kimberley/Ord Bonapart IBRA Daniel and Mucina (2013), Kenneally (2018)	Area (km²)
Rainforest and Vine Thicket	>70% pfc	2600	0	>70% pfc	70*
Eucalypt Open Forest (e.g. *E. tetrodonta*, *E. miniata*, *Livistona*) – various substrates	30–70% pfc, 10–30 m	52,169	0	Open forest >30% pfc	911
Eucalypt Woodlands (e.g. *E. tetrodonta*/ *E. tectifica*, tussock grasses) – Volcanic/ Laterite/Alluvial/Colluvial substrates	10–30% pfc	47,290	10,167		
Tropical Eucalypt Woodlands/Grasslands (e.g. Eucalypt with C4 tussock including *Sorghum* and hummock grasses) – Sandstone substrates	<30% pfc	53,396	50,713		
Shrubland/Heath (e.g. *Acacia* spp., hummock grasses) – on Sandstone				<1% pfc trees	2375

Discussion

Persistence of threatened North Kimberley arboreal mammals

The higher rainfall (>1000 mm) and coastal parts of the North Kimberley (e.g. northern Mitchell River, Bachsten Creek, Prince Regent River, Wunaamin Miliwundi north of the Gibb River Road) continue to support a full complement of arboreal/scansorial CWR mammal species (Tables 1, 2) identified during historical surveys (Bradley *et al.* 1987; McKenzie *et al.* 2007; Start *et al.* 2007; Radford *et al.* 2014) based on nearly a decade of monitoring surveys (2011–2019) using a range of trapping methods. Data presented here include the first records (during 2015, 2016 and 2018 surveys, Tables 1, 2 and 3) of *Mesembriomys gouldii* since 1987 (Rankmore *et al.* 2023; Kerle *et al.* 2024), with subsequent detections in other parts of the North Kimberley (Young and Potter 2022, during 2019 and 2021) confirming their sparse but continued persistence more widely across the region.

Continued persistence of rare arboreal mammals in the North Kimberley occurs despite ongoing declines across large portions of north-western Australia (McKenzie 1981; Woinarski *et al.* 2010, 2011; Start *et al.* 2012; Ziembicki *et al.* 2015; Davies *et al.* 2018; Neave *et al.* 2024), particularly in more inland and lower rainfall savannas (e.g. inland Mitchell Plateau, Drysdale River National Park, Mount Elizabeth in north central Kimberley). Several arboreal species considered to be declining or extinct elsewhere across their former ranges, including *C. penicillatus* (Firth *et al.* 2010; Davies *et al.* 2017; Penton *et al.* 2021*a*, 2021*b*; Woolley *et al.* 2024), *M. macrurus* (Gibson and McKenzie 2012; Hohnen *et al.* 2015) and *D. hallucatus* (Moore *et al.* 2021; von Takach *et al.* 2022, 2024) continue to be reliably detected. Notably, *D. hallucatus* records presented here pre-date cane toad invasion, a key threat to northern quolls (von Takach *et al.* 2024). However, this species continues to persist following cane toad invasion, albeit at much lower trap success/occupancy (Corey and Radford 2025, unpubl. data; Harrison *et al.*, unpubl. data). In addition, other non-arboreal threatened species including the golden bandicoot *Isoodon auratus* (Rick *et al.* 2023) and the Kimberley rock rat *Z. woodwardi* (McKenzie *et al.* 2023) continue to be reliably detected through our standard monitoring surveys.

Despite detecting all expected arboreal species at least once during the study period, relatively little data are available for the rarest species to allow determination of status, distribution or population trends. For example, although there are currently several records for *M. gouldii* in the Kimberley (Tables 1, 2; spotlighting in 2014, cameras Bachsten Creek during 2015 and 2016, and live-trapping in 2018, also Young and Potter 2022), little is known about their density, sub-population extent or distribution, nor their long-term dynamics. Similar to recent detection of *Phascogale pirata* on Melville Island (Geyle *et al.* 2020), our three detections of *P. tapoatafa* on one of eight arboreal cameras deployed at the Mitchell Plateau in 2016, along with a handful of other sightings at the Mitchell Plateau (J. Hayward and L. Baker 2009, pers. comm.; B. Stuart 2010, pers. comm.; D. Bettini 2011, pers. comm.; S. van Barneveld and T. Vigilante 2016, pers. comm.; Wunambal Gaambera Aboriginal Corporation unpublished camera trapping data 2016–2023) and reported sightings from the Yampi Peninsula in the south-western Kimberley, give us little understanding of current population status, threats or trends. *Petropseudes dahlii* was only recorded once during terrestrial camera trapping and once during targeted arboreal camera placements (Bachsten Creek 2016). Subsequent camera records from Prince Regent and Wunaamin Miliwundi National Parks ($n = 4$), a hair sample from a dingo scat collected in Drysdale River National Park and records from several other North Kimberley studies (Runcie 1999; Start *et al.* 2007; Olds *et al.* 2016, 2017;

Wunambal Gaambera Aboriginal Corporation unpublished spotlighting observations 2025) suggest that this species may be more widespread than indicated by data presented here. Only a single detection of *Trichosurus vulpecula* subsp. *arnhemensis* was made during the study period (Table 1), though further camera/live trap records have since been made at the Mitchell Plateau (Wunambal Gaambera Aboriginal Corporation 2016–2025) and Wunamin Miliwundi National Park (Corey and Radford 2024, unpubl. data). The poor detectability using standard trapping methods (e.g. *M. gouldii* and *T. vulpecula*) occurred despite these species being readily detected using standard methods in nearby Northern Territory savannas (Kerle 1998; Penton *et al.* 2020, 2021*a*, 2021*b*; Davies *et al.* 2022; Woolley *et al.* 2024).

The lack of *Mesembriomys gouldii*, *Petropseudes dahlii*, *Phascogale tapoatafa* and *Trichusurus vulpecula* subsp. *arnhemensis* after considerable trapping effort over 8 years, irrespective of species differences in relative detectability, is highly concerning from a conservation perspective. This lack of data certainly suggests that these species are under grave threat. Surveys by Stobo-Wilson *et al.* (2019) estimate that *T. vulpecula* subsp. *arnhemensis* has declined by up to 75% across Northern Territory savannas, particularly from more inland, lower rainfall areas. Even greater declines have likely occurred in the Kimberley Region given the extreme rarity of detections here (Radford *et al.* 2014, 2020, 2021*a*; Woinarski *et al.* 2014; Olds *et al.* 2016, 2017). Recent combined observations from multiple organisations and individuals (Woinarski *et al.* 2014) for *Mesembriomys gouldii* and *Phascogale tapoatafa* confirm very low detection in the Kimberley in recent decades. Continued spotlighting observations of *Petropseudes dahlii* in the Bachsten Creek up until recent years (2018) and on Theda Station (Olds *et al.* 2016, 2017), and the reportedly rugged and inaccessible habitat (Runcie 1999) may well obscure the degree of decline of this species. However, extensive trapping effort in rocky habitats is represented during this study (Table 2), suggesting that we should have detected the species if present within rugged sandstone habitats. Targeted surveys and ecological studies of these species in known remnant habitat are recommended to highlight key remaining population size, key refugia and local threats, and design adaptive management threat mitigation programs if these species are to be rescued from their current dire state.

Effectiveness of arboreal versus terrestrial trapping methods

Terrestrial camera trapping proved more effective than live-trapping for detecting larger arboreal species, consistent with findings elsewhere in northern Australia (Einoder *et al.* 2018; Smith *et al.* 2020). Despite their arboreal behaviour, species including tree-rats *C. penicillatus* and *M. macrurus*, the partially arboreal *M. burtoni*, and the rock inhabiting *D. hallucatus* and *W. squamicaudata* were all regularly trapped using ground-based live-trapping or camera trapping. However, for most of these species camera trapping resulted in higher trap success (Table 1). Using ground-based camera trapping for detection of most arboreal species is therefore more efficient for larger species. It should be noted that camera trapping cannot be easily used to make population size and density estimates because recapture of individuals cannot be determined (although see Palencia *et al.* 2021; Santini *et al.* 2022; Nakashima and Yajima 2025 for methods that do not rely on recaptures). The northern quoll *D. hallucatus* is the exception among Kimberley arboreal species where individuals can be identified based on their spot patterns (Hohnen *et al.* 2013).

It should be noted here that for some species, especially for similar-looking terrestrial species, only live-trapping can be used to confidently attribute species identity (Potter *et al.* 2019). Small rodents and dasyurids are often difficult to identify using camera trapping (e.g. *Sminthopsis butleri* and *S. virginiae*, Potter *et al.* 2019). Improved identification is sometimes possible when cameras are deployed facing downwards for small terrestrial species to allow for comparisons of features including head/body and tail length and tail morphology among similar-sized species (e.g. *Rattus tunneyi*, *Melomys burtoni* and *R. rattus*). However terrestrial species including the bandicoots *Isoodon auratus* and *I. macrourus*, and the rock wallabies *Petrogale burbidgei* and *P. concinna* cannot be reliably differentiated based only on cameras.

Despite the effectiveness of terrestrial trapping methods in detecting most arboreal mammals, not all were able to be detected in this way. *Petaurus ariel* and *Phascogale tapoatafa* were only detected using arboreal methods. These species were detected using camera traps deployed in trees, either facing at bait stations placed on the tree trunk or branch, or facing tree hollow entrances, nestbox entrances or worn areas on the tree indicating frequent use by arboreal species. Nestboxes deployed in arboreal habitat, while successful for savanna gliders, had limitations in remote regions where infrequent checks are possible (also see Woolley *et al.* 2024). Nestboxes were most effective when used in conjunction with an additional trapping method, especially arboreal cameras (e.g. Woolley *et al.* 2024, Tables 1 and 2). Nestboxes combined with cameras provide data on nestbox use over time, thereby effectively increasing trap effort. In contrast, checking arboreal nestboxes once-off during each site visit only provides a single trap night snapshot of occurrence of an arboreal mammal. Hollows are a communal forest resource for arboreal hollow-denning species, therefore use of arboreal cameras in conjunction with hollows and nestboxes can provide additional data on multi-species use and interactions among species including predators, and whether this also occurs in hollow-limited regions (Penton *et al.* 2021*a*; Woolley *et al.* 2024).

This study highlights the importance of targeted active searches in optimal habitats, in addition to standard trapping methods, to identify additional rare arboreal species locations. Targeted arboreal camera trapping in this study was

undertaken after initial spotlight observations or expert local knowledge alerted us to the possible presence of these species (Table 1). In addition, recent studies have shown that new technological applications such as thermal imaging can increase the effectiveness of spotlighting surveys (Underwood *et al.* 2022; Dawlings *et al.* 2023). An example is the detection of three *Mesembriomys gouldii* in a single night at Bachsten Creek (R. Clarke, unpublished observations 2018) where it had previously taken 5 years of standard trapping, targeted arboreal camera surveys and spotlighting to confirm the presence of this species. Based on our observations, spotlighting is ineffective in many Kimberley savanna habitats due to the scarcity of arboreal species, their cryptic nature and also possibly the unsuitability of many Kimberley savanna vegetation types for more specialist arboreal species (Table 2, see below). However, in optimal arboreal habitat and rugged rocky habitat in high rainfall areas, spotlighting (and thermal imaging), possibly even deployed by autonomous drone (e.g. Howell *et al.* 2022), may be a highly valuable additional tool for detecting some of the rarer and more cryptic species.

Arboreal niche defined by trapping, denning and foraging niches

Based on trapping results and previous observations, northern arboreal savanna mammals fall into several distinct niches (Tables 1, 2). The first of these is a more or less strictly arboreal niche. In the North Kimberley Region, species including the savanna glider *P. ariel* (Stobo-Wilson *et al.* 2019; Penton *et al.* 2020, 2021*a*; Cremona *et al.* 2023; Woolley *et al.* 2024) and the black-footed tree-rat *M. gouldii* (Morton 1992; Penton *et al.* 2020, 2021*a*; Kerle *et al.* 2024), the brushtail possum (Penton *et al.* 2020, 2021*a*; Woolley *et al.* 2024) and the brush-tailed phascogale *P. tapoatafa* (Soderquist and Rhind 2023) could be described as strictly arboreal. These species were mainly detected using arboreal trapping methods (Tables 1, 3; Figs 2, 3, and 4), den mainly in tree hollows and feed mainly on arboreal resources (sap, nectar and arboreal invertebrates; fruits and flowers; arboreal invertebrates/vertebrates and nectar respectively). Despite this, both *T. vulpecula* and *M. gouldii* are caught on the ground (Davies *et al.* 2018; Stobo-Wilson *et al.* 2019, 2020; Penton *et al.* 2021*b*, Table 1) presumably when moving between denning and foraging trees. In contrast, *P. ariel* and *P. tapoatafa* are rarely seen or trapped on the ground (Table 1) presumably because gliders can glide directly between trees without descending to the ground (Stobo-Wilson *et al.* 2019; Cremona *et al.* 2023). Phascogales may also be able to leap between tree canopies (Soderquist and Rhind 2023).

Based on evidence presented here, there are two additional semi-arboreal niches among Kimberley mammals defined by trapping, denning and foraging niches. These include an arboreal denning and terrestrial foraging niche, and an arboreal foraging and terrestrial denning niche. The brush-tailed rabbit-rat *C. penicillatus* falls into the former category, denning in tree hollows, often near the ground and occasionally in hollow logs (Firth *et al.* 2006, 2010; Penton *et al.* 2020, 2021*a*; Woolley *et al.* 2024). Despite preferring arboreal dens, *C. penicillatus* forages on the ground for grass seeds, fruits, flowers and invertebrates (Morton 1992; Firth *et al.* 2005; Kemper *et al.* 2023; Kerle *et al.* 2024). This species' trapping niche is mainly on the ground (Davies *et al.* 2017; Radford *et al.* 2020; Table 1) although it is also detected in nestboxes (Woolley *et al.* 2024). Arboreal foraging/terrestrial denning species in the North Kimberley Region include *W. squamicaudata*, *M. macrurus* and *P. dahlii* that forage for fruits, blossums and leaves from a range of tropical and vine thicket trees and shrubs (Morton 1992; Runcie 1999; Hohnen *et al.* 2015, 2016; Webb *et al.* 2023) while denning in complex rugged rocky habitats including rock crevices, rock piles and escarpments but also tree hollows and vine thicket vegetation (Runcie 1999; Hohnen *et al.* 2015, 2016, Table 1). *W. squamicaudata* and *M. macrurus* were more readily trapped on the ground (Table 1, Bradley *et al.* 1987; Start *et al.* 2007; Hohnen *et al.* 2015, 2016; Radford *et al.* 2020) while detections/observations of *P. dahlii* were mainly in arboreal habitats (Table 1, Runcie 1999; Olds *et al.* 2017; Webb *et al.* 2023).

The final niche category can be described as an opportunistic arboreal niche. This includes *D. hallucatus* and *M. burtoni* that mainly den, forage and are trapped in terrestrial habitats (Oakwood 2002; Moore *et al.* 2021) but are proficient climbers and known to occasionally den in arboreal habitats (Kerle 2023; Trewella *et al.* 2023, 2024). These species are readily trapped on the ground but also readily observed using arboreal habitats (Table 1, Radford *et al.* 2020; Moore *et al.* 2021).

Kimberley link between vegetation niche and extinction risk

Our results suggest that arboreal denning species with a strong preference for open forest vegetation are currently the group most at risk of decline and extinction in the North Kimberley Region (Table 2). Arboreal open forest specialists had the most regionally restricted distributions based on our monitoring and trial trapping survey locations and also had the lowest measures of abundance of any of the species (Table 3). In contrast, species with broader denning requirements, for example species denning in rocky habitats or on the ground, or species that had broader vegetation habitat requirements including a broader range of savanna woodland and shrubland habitats, had more widespread distributions and were recorded at greater abundance (trap success).

Clearly not only open forest specialists are threatened and declining across northern Australia and in the Kimberley. For example, *P. dahlii*, a rocky habitat specialist is also extremely rare based on the data presented here. Based on recent literature, the whole suite of the CWR savanna mammals has

declined and continues to do so across northern Australia, even in areas that constitute their last major refuges. Nevertheless open forest arboreal specialists including *M. gouldii*, *T. vulpecula*, *P. tapoatafa* and *C. penicillatus* that are among the most restricted and least abundant in the Kimberley, but remain widespread and common in extensive parts of the Top End of the Northern Territory including the greater Darwin region, Cobourg Peninsula, Melville, Bathurst and Groote Islands (Davies *et al.* 2018; Heiniger *et al.* 2020; Stobo-Wilson *et al.* 2020; Penton *et al.* 2021*b*; Neave *et al.* 2024; Woolley *et al.* 2024). Rock denning species, and species with broad woodland/shrubland habitat requirements that remain widespread and common in the North Kimberley (e.g. *M. macrurus* and *D. hallucatus*) are now relatively rare or extinct in the Northern Territory (Ibbett *et al.* 2018; von Takach *et al.* 2020, 2022; Burbidge *et al.* 2023). Which factors might explain this regional divergence in arboreal niche linked declines?

Several recent studies on savanna mammals suggest that many of our threatened species, including arboreal species, have now contracted to the less disturbed, higher production, more coastal parts of their historical ranges (McKenzie *et al.* 2007; Woinarski *et al.* 2011; Murphy and Davies 2014; Stobo-Wilson *et al.* 2020). This is considered to be for several reasons but includes higher productivity and reduced impact of local disturbance regimes (e.g. fire) in humid coastal areas leading to greater population resilience (McKenzie *et al.* 2007; Lawes *et al.* 2015; Radford *et al.* 2015; Stobo-Wilson *et al.* 2020). Additionally, in recent decades, these near-coastal regions in the Kimberley and Northern Territory have experienced implementation of broad landscape-scale prescribed burning and feral herbivore management programs initiated by conservation and Indigenous land managers (Murphy *et al.* 2015; Corey *et al.* 2020; Legge *et al* 2019; Radford *et al.* 2020, 2021*a*; Vigilante *et al.* 2024). These programs have led to demonstrable amelioration of fire regimes in these areas (Murphy *et al.* 2015; Edwards *et al.* 2021; Vigilante *et al.* 2024) and this has been linked to improved outcomes for threatened mammals (Radford *et al.* 2020). For these reasons, key current refugia for threatened savanna mammals are concentrated in near-coastal and island savanna regions of both the Kimberley and Northern Territory.

Despite the similarities in management of these near-coastal refugia, the regions themselves contrast in the near-coastal extent of different vegetation types and structure (Department of the Environment and Water Resources 2007; Beard *et al.* 2013; Daniel and Mucina 2013; National Vegetation Information System (NVIS) 2025). In the Kimberley, a large proportion of the near-coastal vegetation is dominated by savanna woodlands on extensive rugged rocky sandstone ridges, and among igneous hills and ranges (e.g. large areas of Mitchell River National Park, Prince Regent National Park, Artesian Range, northern Wunamin Miliwundi and Yampi) (Department of the Environment and Water Resources 2007; National Vegetation Information System (NVIS) 2025) including on the off-shore Islands (Gibson and McKenzie 2012). Tall open forest here is relatively restricted to small, isolated areas of alluvial valley systems intersecting sandstone ranges or restricted areas of lateritic/bauxite plateaux (e.g. Mitchell Plateau and Bouganville Peninsula, Table 4). It is perhaps not surprising then, that local rock-adapted generalist arboreal species (e.g. *D. hallucatus*, *M. macrurus* and *W squamicaudata*) have relatively high extent and abundance in a landscape dominated by extensive (>50,000 km^2) woodlands on rugged sandstone substrates, while forest specialists have low extent and abundance. Despite landscape management, relatively small areas of tall open forest (<1000 km^2, Table 4) may mean that open forest specialists including *T. vulpecula*, *C. penicillatus* and *M. gouldii* are significantly more limited in their potential areas of suitable high quality habitat (Kerle *et al.* 2024).

In the Top End of the Northern Territory, the opposite situation occurs. Well-managed Top End savannas are dominated by extensive areas (52,000 km^2) of tall open forest on relatively productive substrates (National Vegetation Information System (NVIS) 2025) and rugged sandstone largely restricted to the Arnhem Plateau. In these circumstances, open forest arboreal specialists including *T. vulpecula*, *M. gouldii* and *C. penicillatus* continue to be relatively common (Stobo-Wilson *et al.* 2020) despite showing evidence of continuing decline (Firth *et al.* 2010; Davies *et al.* 2018; Neave *et al.* 2024; Woolley *et al.* 2024).

The very small areas and populations of arboreal specialists in currently suitable open forest vegetation in the North Kimberley Region compared to the nearby Northern Territory, makes such areas highly vulnerable to local operation of threatening processes and stochastic disturbance events that further threaten persistence of these species. Nevertheless extents of distributions of these species were historically much greater than at present (e.g. Stobo-Wilson *et al.* 2019; Baker and Gynther 2023). In addition to generic declines of many savanna mammals associated with terrestrial disturbance regimes and predation by introduced cats (Frank *et al.* 2014; McGregor *et al.* 2014; Leahy *et al.* 2016; Davies *et al.* 2017; Penton *et al.* 2021*b*), perhaps arboreal mammals have also been influenced in their distributions by declines in extent and condition of open forest vegetation – including transitions to more open woodland vegetation – under wildfire-dominated fire regimes, and under pastoralism and invasion of introduced feral herbivores. Several studies allude to the possibility that major changes in vegetation structure and composition have been associated with transition from indigenous-managed to pastoral-managed/unmanaged landscapes including transitions from heavily wooded to more open grass-dominated vegetation (e.g. Connor *et al.* 2018; Rowe *et al.* 2019; Bird *et al.* 2024). Management that seeks to reduce the severity and frequency of fire and herbivore disturbance regimes may have the additional effect in the long term of allowing transition to vegetation with higher forest cover.

Management implications of vegetation niche-linked declines

The relatively small areas of tall open savanna forest in the North Kimberley Region where rare forest specialists still occur may facilitate targeted conservation management intervention. As we described above, arboreal forest specialists require key high quality arboreal vegetation structures including fallen timber, standing dead timber, dense shrub layers and large trees with many denning hollows (Firth *et al.* 2010; Davies *et al.* 2017; Geyle *et al.* 2020; Penton *et al.* 2020, 2021*a*; Woolley *et al.* 2024). Such habitat attributes are considered to persist only in areas managed to mitigate extensive, high severity wildfires (Woolley *et al.* 2018; Penton *et al.* 2021*b*). Targeted fire management that applies broad-scale networks of low intensity, patchy, early dry season burning are the only known management approach that reliably reduces the extent and impact of high severity late dry season wildfires (Radford *et al.* 2020; Vigilante *et al.* 2024). Fire exclusion as a method for preservation of quality forest vegetation is likely to be ineffective in maintaining high tree hollow density and associated habitat structures because fuel accumulation and accidental ignition under frequent lightning and anthropological fire regimes in northern Australia are likely to lead to high impact wildfire associated with the net loss of tree hollows (Woolley *et al.* 2018; Radford *et al.* 2021*b*; Taylor *et al.* 2025). Application of broad-scale, patchy, early dry season prescribed burning is known to benefit savanna mammals more generally (Andersen *et al.* 2005; Legge *et al.* 2008, 2019; Radford *et al.* 2020). Targeted on-ground applications of burning may also have a role in maintaining high-quality arboreal habitat features. Open forest arboreal specialists are known to benefit from the absence of feral herbivores despite their limited period utilising ground level vegetation (Davies *et al.* 2018; Stobo-Wilson *et al.* 2020; Penton *et al.* 2021*b*; Neave *et al.* 2024) as do more generalist savanna mammals (Legge *et al.* 2008, 2019; Radford *et al.* 2015). While the effects of large, introduced herbivores such as cattle on savanna vegetation are often subtle (Vincent *et al.* 2024), impacts including the formation of trails through ground layer vegetation may facilitate hunting by introduced cats in high vegetation cover savanna forests (Davies *et al.* 2018; Stobo-Wilson *et al.* 2020; Penton *et al.* 2021*b*; Neave *et al.* 2024, 2025). We recommend that targeted adaptive management be accompanied by monitoring and evaluation of target mammal populations as an evidence-base for ongoing improvement of conservation management outcomes for these rare arboreal species.

Supplementary material

Supplementary material is available online.

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Data availability. The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://naturemap.dbca.wa.gov.au.

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