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Potential for dietary competition between the threatened black-flanked rock-wallaby and sympatric western grey kangaroo

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Abstract. An overabundance of western grey kangaroo (*Macropus fuliginosus*) can detrimentally impact agriculture and compete with threatened fauna for food resources. In Paruna Wildlife Sanctuary, south-western Western Australia, kangaroos are common and widespread. By contrast, the endangered black-flanked rock-wallaby (*Petrogale lateralis lateralis*) are spatially constrained to rock refuges. We investigated the potential for dietary competition between these two species by measuring the overlap in their diets, spatial overlap in their foraging patches, and comparing their diets with food resource availability. A combination of scat analysis, passive IR camera trapping and vegetation surveys were employed around rock outcrops used by rock-wallabies within the sanctuary. Rock-wallaby diets were dominated by forbs, overlapping 56% with kangaroo diet, which included mostly browse and forbs. Some of their shared preferred food resources were spatially and/or temporally limited, suggesting potential competition for these food plants. There was also a 33% spatial overlap of foraging patches between the two species. The dietary and spatial overlap detected between rock-wallabies and kangaroos suggest there is potential for resource competition, which may be exacerbated if kangaroo numbers increase. Future conservation actions include monitoring western grey kangaroo densities and food plant availability. Population control for kangaroos may be required, particularly for increasingly hot and dry years, as predicted under climate change.

Keywords: threatened species, sympatric macropod, dietary competition, dietary overlap, spatial overlap, foraging patterns, preference, selectivity index, camera trapping, scat analysis, vegetation availability, conservation.

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Introduction

The endangered black-flanked rock-wallaby (*Petrogale lateralis lateralis*) is a medium-sized macropod (up to 5 kg males, 3.8 kg females: Eldridge and Close 1995) occurring in areas of suitable rocky habitat across Western Australia (Pearson 2013). These rock-wallabies are crepuscular or nocturnal central place foragers (Sharp 2009), returning between foraging trips to a central rock refuge for protection from predators and thermal extremes (Boyd *et al.* 2014; Pentland 2014). Their foraging behaviour is therefore inherently restricted and can be even further constrained by a perceived risk of predation (Pentland 2014). Populations of the subspecies have declined predominantly due to predation by foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), habitat degradation from weed incursion, and dietary competition from introduced herbivores like feral goats (*Capra hircus*) (Kinnear *et al.* 1984, 1988, 1998; Burbidge *et al.* 2014; Pentland 2014; Creese *et al.* 2019; Fleming *et al.* 2020). Additional dietary competition from native herbivores is also suspected to contribute to their decline.

An overabundance of kangaroos can be detrimental for the natural environment. For example, Neave and Tanton (1989) found that eastern grey kangaroo (*Macropus giganteus*) grazing reduced the height of vegetation in Tidbinbilla Nature Reserve (Australian Capital Territory) to the extent that it was no longer suitable habitat for certain birds and invertebrates. Their large adult body size (weighing up to 72 kg, Leishman 2014) and large home ranges (33–70 ha, Arnold *et al.* 1992) reduces predation risk for adults (Banks *et al.* 2000) and allows them to opportunistically exploit resources. Combined with their broad diet of grasses, forbs, browse and sedges (Algar 1986; Barker 1987; Norbury 1987; Shepherd *et al.* 1997; Wann and Bell 1997), these kangaroos therefore have a competitive advantage over smaller sympatric macropods (Tuft *et al.* 2011*a*).

To demonstrate dietary competition between black-flanked rock-wallabies and western grey kangaroos, three aspects need to be observed: (1) dietary overlap, (2) spatial overlap in foraging patch use, and (3) limited field availability of preferred food resources (Wilson 1991; Creese *et al.* 2019). Several studies have examined the respective diets and foraging patterns of these species across their ranges (Halford *et al.* 1984; Algar 1986; Barker 1987; Norbury 1987; Priddel *et al.* 1988; Wilson 1991; Arnold *et al.* 1992; Shepherd *et al.* 1997; Wann and Bell 1997; Pentland 2014; Chauvin 2015; Creese *et al.* 2019). Both species consume the same plant functional groups, some congeneric plants, and follow similar temporal patterns in terms of proportions of groups consumed across seasons (Wann and Bell 1997; Pentland 2014; Chauvin 2015), but spatial overlap in foraging patch use and food resource limitation has not been shown for these two species. However, in Cape Range National Park, black-flanked rock-wallabies and euros (*Osphranter robustus erubescens*) consume some of the same plants and forage within the same patches, and spatial limitation of food resources suggests possible dietary competition between these two species (Creese *et al.* 2019). Other studies have found that western grey kangaroos consume a similar range of plants as western brush wallabies (*Notamacropus irma*) in Whiteman Park (Wann and Bell 1997) and tammar wallabies (*N. eugenii*) in Perup Nature Reserve (Shepherd *et al.* 1997). Such evidence of dietary competition for other macropods suggests the same may hold for black-flanked rock-wallabies and western grey kangaroos.

Paruna Wildlife Sanctuary (Paruna) in south-western Western Australia supports a population of translocated black-flanked rock-wallabies. Their conservation and management depends on reducing threats, which may include dietary competition with resident western grey kangaroos. This study investigated the potential for dietary competition between rock-wallabies and kangaroos using a combination of scat analysis, motion sensor camera trapping and vegetation surveys to quantify dietary overlap, spatial overlap in foraging patch use, and vegetation availability.

Methods

Study area

Paruna Wildlife Sanctuary (31°40′S, 116°8′E) is located in the Avon Valley, ~45 km north-east of Perth in Western Australia (Fig. 1). The 1950 ha partially predator-proof fenced sanctuary is managed by the Australian Wildlife Conservancy and links Avon Valley National Park and Walyunga National Park. Erosion of the valley slopes has resulted in shallow soils and many exposed underlying granite and dolerite dykes (Australian Wildlife Conservancy 1998). The sanctuary experiences warm, dry summers and cool, wet winters and receives an average rainfall of 655 mm (Bureau of Meteorology 2019); the year of study was average in terms of rainfall (682 mm) (Bureau of Meteorology station number 9053). There is ongoing fox and cat control carried out across the sanctuary, but minimal kangaroo control to date.

Black-flanked rock-wallabies were translocated to a rock outcrop within the sanctuary ('release site') between 2001 and 2007 and have subsequently colonised a second rock outcrop ('new site') (Palmer 2018). Both sites provide rock refuges for rock-wallabies within boulder piles over granite outcrops

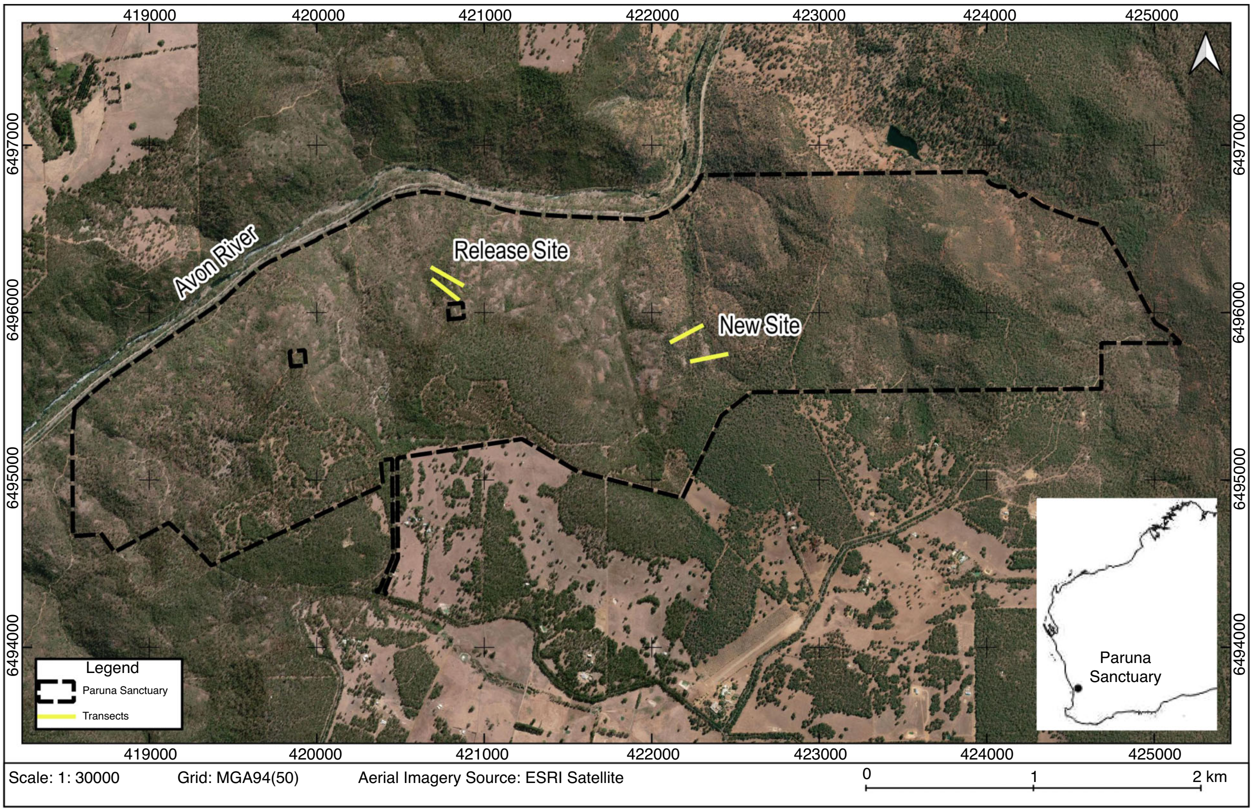

Fig. 1. Map of Paruna Wildlife Sanctuary outcrops and transects, squares represent excised portions of the reserve; inset: location of the sanctuary within Western Australia.

(Lin 2011); those at the release site are more structurally complex, featuring more crevices, extensive multi-entranced caves and overhangs (Pearson 2013). Vegetation transitions from closed heath and/or herblands on the outcrops to open *Eucalyptus* spp. woodlands over shrublands on the slopes (Australian Wildlife Conservancy 1998).

Vegetation availability

Vegetation surveys were undertaken from September to October 2018 at both outcrops to compare the availability of potential food resources. Four transects (100 m each) were laid at each outcrop, beginning near rock refuges and extending upslope and downslope (Fig. 1). Quadrats (5 × 5 m) were established at 20 m intervals along the linear transects (11 quadrats per transect for a total of 44 quadrats); three quadrats were within 20 m of the refuge, four upslope of the refuge and four downslope of the refuge. Within quadrats, percentage cover of each plant species with foliage up to 1 m above ground level (and thereby accessible to rock-wallabies) was recorded using a modified Braun-Blanquet cover-abundance scale (Braun-Blanquet 1932). Plant species were classified into functional groups: browse (i.e. woody shrubs and trees), grass, forb (i.e. non-woody herbaceous plants other than grasses), fern and sedge. Specimens were collected to create a plant reference library. Other observations recorded for quadrats include topography, vegetation type and density versus bare rock, canopy cover and nearby shelter points (boulder piles that provide temporary protection within the foraging range, Tuft *et al.* 2011*a*).

Plant reference library

A plant reference library was created for each plant species recorded from the survey quadrats. A permanent slide of leaf and/or stem epidermis was created using a modified methodology from Chauvin (2015). Small sections of leaf and stem were placed in a beaker and boiled in 5 mL of 10% chromic acid (H_2CrO_4) and 5 mL of 10% nitric acid (HNO_3) to digest away mesophyll. Once only epidermal fragments remained, residual acid was extracted from the beaker, before adding water with a few drops of concentrated ammonia (NH_3). Solution was then again extracted, before adding Gentian Violet in 95% ethanol to soak for 30 min. Stained material was washed in water and dehydrated through a series of ethanol solutions (50, 70 and 95%). Epidermal fragments were transferred to a microscope slide, soaked in xylene and sealed with a coverslip coated in Depex mounting solution. Photographs (at 100, 200 and 400× optical magnifications) of each slide were taken to aid identification of epidermal fragments in scats.

Scat analysis

Scats were collected for diet analysis at each quadrat at the same time vegetation surveys were undertaken. The dissimilar size and shape of scats from each species made them distinguishable from each other; rock-wallaby scats have a tapered cylindrical shape (Tuft *et al.* 2011*b*), whereas kangaroo scats are larger and round in shape. Scats were frozen in paper bags before being air dried for analysis. A total of 20 scats (fresh only) were processed for analysis; five from each species from each of the two transects at the release site outcrop (no rock-wallaby scats could be found at the new site). We carried out sample rarefaction (Mao's tau) in PAST 4.03, which indicated that an asymptote was reached by 10 samples for rock-wallaby diet and by 8 samples for kangaroo diet, suggesting that this was an adequate representation of diet. For each scat, a permanent slide of epidermal fragments was created using a modified methodology from Chauvin (2015). Scats were broken up using a mortar and pestle before being transferred to a grinder for 2 min. Samples were transferred into conical flasks with 25 mL of 30% hydrogen peroxide (H_2O_2), two drops of 5% sodium diphosphate ($Na_4P_2O_7$) solution and two drops of concentrated ammonia (NH_3), and heated for ~12 h at 65°C. Samples were then transferred into centrifuge tubes, centrifuged (3000 rpm; ~800*g*) for 10 min, and washed in ethanol (helped by further centrifuging) before being soaked in Gentian Violet in 95% ethanol for 30 min. Stained material was transferred to a 32 mm sieve and washed and dehydrated through a series of ethanol solutions (50, 70 and 95%). A subsample of epidermal fragments from each sample was taken and spread evenly across a microscope slide, soaked in xylene and sealed in Depex mounting solution under a coverslip.

Slides of epidermal fragments were analysed using a point quadrat sampling method at 100× optical magnification whereby, for each field of view, the fragments occurring under the cross-hairs of a 10 × 10 grid eyepiece graticule were identified and counted (Norbury 1988; Poole *et al.* 2014). This methodology accounts for the size of the fragment, which will be proportional to the number of times that fragment occurs under graticule cross-hairs (Poole *et al.* 2014). To ensure even sampling intensity between samples, the field of view was moved across the microscope slide in a linear fashion until 200 fragment-graticule intersections had been recorded for each sample (Poole *et al.* 2014). Photographs of each field of view were taken to aid this process. Where possible, fragments were identified to species, genus or family level through cross-referencing with the key diagnostic characteristics of plant species in the reference collection. Where this was not possible, fragments were classed as unknown Poaceae, unknown monocot, unknown dicot or unknown fragment.

Camera trapping

Motion sensor camera traps (Reconyx Hyperfire HC500) were deployed to monitor activity within quadrats at both outcrops between September and December 2018. For each quadrat, a single camera was mounted to a tree or metal stake 0.3–0.5 m above ground level and positioned to ensure the field of view included the entire survey quadrat (11 cameras per transect for a total of 44 cameras over 128 nights = 5632 camera trap nights). Settings were fixed to rapid fire (five photos after every trigger, with no delay). Camera maintenance (battery and memory card replacement) was undertaken every 6 weeks. Photos were processed in Windows Photo Viewer and ExifPro Image Viewer version 2.1 (Kowalski and Kowalski 2000) and the metadata of every fifth photo of each sequence (representing a single trigger) was exported. To determine the number of independent camera trap events, sequential captures of the same species within 5 min were classified as a single capture event unless multiple individuals were visible in the same photo (classified as multiple capture events). This quiet period of 5 min was chosen with the knowledge that kangaroos can linger for some time while foraging but also can move very quickly past cameras (Green-Barber and Old 2018). Where it was possible to identify plant species, camera trap photos capturing rock-wallabies or kangaroos consuming particular plant species were noted to support scat analysis.

Data analysis

Vegetation availability at the two outcrops was compared using non-metric multidimensional scaling (nMDS) comparing the percentage cover of each plant species at each outcrop with the predictor variables outcrop ('release' and 'new' sites) and location (refuge, upslope and downslope), followed by one-way analysis of similarity (ANOSIM) and a similarity percentage (SIMPER) (PAST 3.0) (Hammer and Harper 2013). The SIMPER determined the contribution of each plant species to the differences found by the nMDS and ANOSIM.

Dietary composition for rock-wallabies and kangaroos were similarly compared using nMDS comparing the counts of epidermal fragments of each plant species in the scats of each macropod species and analysed using a two-way PERMANOVA with species and location as predictor variables. Dietary overlap between rock-wallabies and kangaroos was quantified using the Schoener overlap index (Schoener 1970):

$$\alpha = 1 - 0.5 \times \sum(|\mathrm{Pxi} - \mathrm{Pyi}|), \tag{1}$$

where Pxi is the proportion of plant species i in the diet of rock-wallabies and Pyi is the proportion of plant species i in the diet of kangaroos. Values range from 0 (no overlap) to 1 (total overlap), with values >0.6 considered an indication of significant diet overlap (Wallace and Ramsey 1983; Creese *et al.* 2019).

Dietary selectivity was quantified using Ivlev's Selectivity Index (Lechowicz 1982):

$$\mathrm{Ei} = (\mathrm{ri} - \mathrm{pi})/(\mathrm{ri} + \mathrm{pi}), \tag{2}$$

where ri is the proportion of plant species i in the diets of either rock-wallabies or kangaroos and pi is the abundance of plant species i in the field. The Ei was rounded to –1, 0 or 1, with –1 signifying avoidance, 0 signifying use in proportion to availability and 1 signifying selection (Lechowicz 1982; Poole *et al.* 2014).

To assess the completeness of sampling using each method, species rarefaction curves were created in PAST using Mao's tau sample rarefaction (Hammer *et al.* 2001; Colwell *et al.* 2004).

Spatial overlap in foraging patch use was measured by adding the standardised proportions of photo captures of rock-wallabies and kangaroos at different locations. The proportions of independent camera trap events (captures) of each species at different locations was assessed using Pearson's chi-square tests where expected values were calculated based on the assumption that there was no difference in the proportion of captures of each species by location. Rock-wallaby captures at the new site were excluded from all statistical analyses because only three captures of the same individual (in the same location and distinguished by an ear tag in the right ear) were recorded.

Temporal overlap in foraging activity between rock-wallabies and kangaroos was measured using the timestamp record from photo captures in the Overlap package version 0.3.2 (Meredith and Ridout 2018) in R (R Core Team 2012). Coefficient of overlap values (Δ) range from 0 (no overlap) to 1 (total overlap). The $\Delta 4$ estimator was used because the sample size was >75, and 95% confidence intervals were estimated from 10 000 smoothed bootstrap samples, after correcting for the bootstrap bias (Meredith and Ridout 2018). To determine the significance of the Δ value, a Mardia-Watson-Wheeler test (Batschelet 1981) was performed in the Circular package version 0.4–93 (Lund *et al.* 2017). This test assumes no repeat data so captures recorded at identical times were adjusted by 0.86 seconds (adjusting by 0.00001 resulted in 0.86s). In addition, we also examined a range of variables including whether or not a quadrat occurred within 20 m of a refuge (large rock or boulder pile), had a dense understorey, and/or had any canopy cover.

Results

Vegetation availability

A combined total of 102 plant species were recorded across the outcrops (release site = 67, new site = 93). Of these, 9 were only recorded at the release site and 35 were unique to the new site (Supplementary Table S1). Vegetation availability was significantly different between outcrops (ANOSIM, $R = 0.24$, $P < 0.001$) and also the location on outcrops (refuge, upslope and downslope) (ANOSIM, $R = 0.23$, $P < 0.001$; Fig. 2).

Browse species *Trymalium odoratissimum odoratissimum* and *Darwinia citriodora* contributed most of the difference in vegetation availability between outcrops and locations. *Trymalium odoratissimum odoratissimum* was present at both outcrops, mostly occurring downslope of the refuge (SIMPER, 26% relative availability downslope vs 7% upslope and 5% at the refuge) and was the most available species at the new site (15.5% relative availability). *Darwinia citriodora* was only present at the release site where it was the most available plant species (13.2% relative availability), mostly occurring near and upslope of the refuge (SIMPER, 11% relative availability near the refuge and 9% upslope, vs 1% downslope).

In terms of plant functional groups, forbs were the most available at both outcrops, followed by browse, grasses, ferns and sedges. The new site had more forbs (55 vs 45% relative availability), grasses (18 vs 13% relative availability) and sedges (1 vs <1% relative availability), whereas the release site had more browse (34 vs 22% relative availability) and ferns (7 vs 4% relative availability).

Dietary compositions and selectivity

Most (80%) of all plant fragments in rock-wallaby scats could be identified to at least family level, with 13% being unknown Poaceae spp., 14% unknown monocotyledons, 5% unknown dicotyledons and 1% unknown fragments. Rock-wallaby scats comprised a total of seven plant species and were dominated by monocots (65.6%), with dicots contributing 26.3% and pteridophytes (ferns) 7.3% (Table S1). Almost half (49.8% occurrence) of the plant material was identified as forbs; pincushions (*Borya sphaerocephala*) being the most common plant species, representing 31.7% occurrence, followed by bellardia (**Bellardia trixago*; asterisks indicate introduced species, i.e. weeds), representing 15.6% occurrence. This was followed by grasses (12.8% occurrence; most common grass being annual

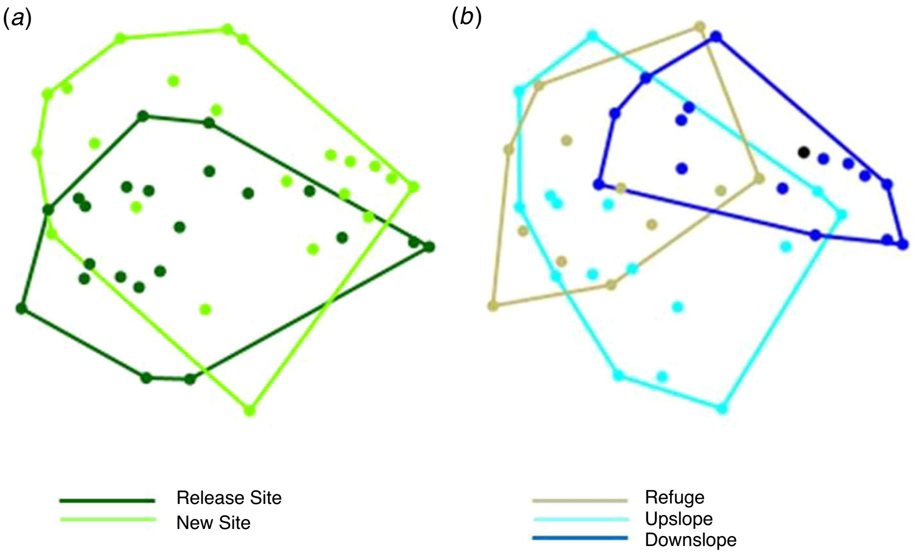

Fig. 2. Non-metric MDS ordination comparing vegetation availability (*a*) between the outcrops and (*b*) between three locations along a transect, centred on rock-wallaby refuges in Paruna Wildlife Sanctuary, Western Australia.

veldtgrass (**Ehrharta longiflora*): 7.0% occurrence), ferns (rock fern (*Cheilanthes austrotenuifolia*): 7.3% occurrence) and browse (3.1% occurrence). Rock-wallabies selected for (Ei = 1) two plant species (pincushions and bellardia), avoided one species (*T. o. odoratissimum*), and consumed four species in proportion to their availability: rock fern, annual veldtgrass (Fig. 3), common sowthistle (**Sonchus oleraceus*) and early hair grass (**Aira praecox*) (Table S1).

About three quarters (72%) of all plant fragments in kangaroo scats could be identified to at least family level, with 8% being unknown Poaceae spp., 21% unknown monocots, 4% unknown dicots and 3% unknown fragments. Kangaroo scats consisted of a total of 13 plant species, with marginally more dicots (47.8%; composed of browse: 22.9% occurrence and forbs: 12.5% occurrence) than monocots (42.2%; composed of grasses: 9.0% occurrence), and a small amount of pteridophytes (rock fern contributing 7.4%) (Table S1). Common sowthistle (forb) was the most common food plant species (17% occurrence), followed by *T. o. odoratissimum* (browse, 14.9% occurrence), rock fern (7.4% occurrence) and yellow autumn lily (*Tricoryne elatior*) (forb, 6.0% occurrence). Kangaroos selected for six species: common sowthistle (Fig. 3), yellow autumn lily, powderbark wandoo (*Eucalyptus accedens*), bellardia, pincushions and morning iris (*Orthrosanthus laxus*). They consumed seven species in proportion to their field availability: *T. o. odoratissimum* (14.9% occurrence), rock fern (7.4% occurrence), annual veldtgrass (4.0% occurrence; Fig. 3), graceful honeymyrtle (*Melaleuca radula*: 1.7% occurrence), foxtail mulga grass (*Neurachne alopecuroidea*: 1.3% occurrence), zamia (*Macrozamia riedlei*: 0.6% occurrence) and snail hakea (*Hakea cristata*: 0.4% occurrence).

Dietary overlap

There was a 56% dietary overlap between rock-wallabies and kangaroos (Schoener index, $\alpha = 0.56$, $P < 0.01$), with six plant species featuring in both of their diets (bellardia, pincushions, rock fern, annual veldtgrass, common sowthistle and *T. o. odoratissimum*; Table S1). This value approached the critical level of $\alpha = 0.6$ that indicates a biologically significant overlap. Furthermore, overall dietary compositions were significantly different (PERMANOVA, F = 5.63, $P = 0.001$) (Fig. 4). Pincushions contributed most of the difference (SIMPER 27.4%), followed by common sowthistle (SIMPER 15.5%), *T. o. odoratissimum* (SIMPER 13.0%) and bellardia (SIMPER 12.4%).

Spatial overlap in foraging patch use

A total of 115 rock-wallaby (release site = 112, new site = 3) and 622 kangaroo (release site = 308, new site = 314) independent photo captures were recorded across a total of 5632 camera trap nights. During this time, a total of three fox (new site only) and 34 feral cat (release site = 14, new site = 20) independent photo captures were also recorded. At least three different feral cat individuals, including a kitten, were identified from photos (Supplementary Fig. S1).

There was some spatial overlap in foraging patch use between rock-wallabies and kangaroos at the release site (33.9% of cameras recording both species; Fig. 5) although foraging activity (percentage of total captures for each species) was disproportionate with location (upslope, refuge and downslope quadrats; transect 1: $\chi^2_2 = = 53.11$, $P < 0.001$ and transect 2: $\chi^2_2 = 103.12$, $P < 0.001$). Rock-wallaby captures were mostly near the refuge (60% of the summed trap capture rate for this species) or downslope of the refuge (37%), with very few (3%) captures upslope of the refuge (Table 1 and Fig. 5). By contrast, kangaroo captures were predominantly upslope of the refuge (60% of captures of this species), with fewer downslope of the refuge (24%) or near the refuge (16%) (Table 1 and Fig. 5). All rock-wallaby captures at the new site were of the same individual and the low number of captures precluded the carrying out of statistical analyses for this outcrop. At the new site, kangaroo captures were similarly fewest at the refuge (27%), but highest downslope of the refuge (42%) rather than upslope of the refuge (31%) (Table 1).

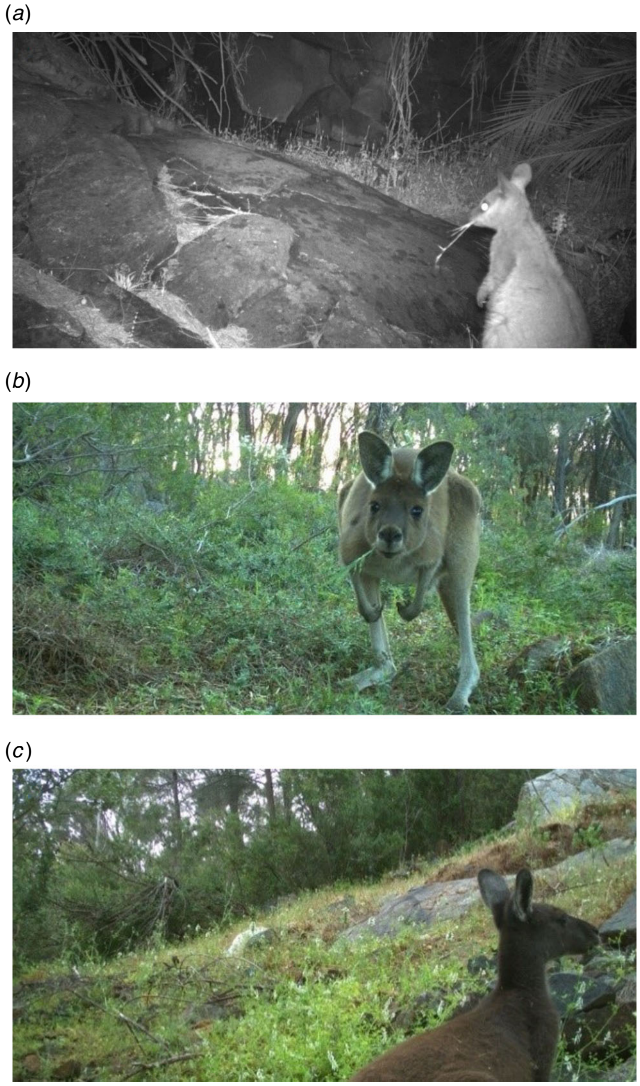

Fig. 3. (*a*) Black-flanked rock-wallaby herbivory of annual veldtgrass. (*b*) Western grey kangaroo herbivory of annual veldtgrass, and (*c*) common sowthistle.

Temporal overlap in foraging activity

In addition to spatial overlap, there was some temporal overlap in foraging activity between rock-wallabies and kangaroos, with both species foraging across the release site outcrop from dusk until dawn (Fig. 5). However, time spent foraging and peak foraging times somewhat varied. Rock-wallabies predominantly began foraging just before dusk (17:00 hours) and ended mid-morning (09:00 hours), peaking between 20:00 and 21:00 hours and then again at midnight (00:00 hours). By contrast, kangaroos foraged throughout the day and night, peaking at 07:00 hours, then between 18:00 and 19:00 hours, and again around midnight (00:00–01:00 hours) (Fig. 5). The largely nocturnal and crepuscular foraging activity patterns of rock-wallabies and kangaroos respectively is documented elsewhere (Sharp 2009; Leishman 2014).

Discussion

A combination of scat analysis, passive IR camera trapping and vegetation surveys around rock outcrops used by black-flanked rock-wallabies in Paruna Wildlife Sanctuary reveals 56.5% dietary overlap and 33.9% spatial overlap with western grey kangaroos. Furthermore, some of their shared preferred food resources were spatially and/or temporally limited, which would indicate potential competition for these food plants. Large populations of kangaroos therefore represent potential food competition with rock-wallabies.

Diet and dietary overlap

Rock-wallabies in Paruna predominantly consumed monocots (in particular forbs such as pincushions). Chauvin (2015) reported a similar finding for populations in the Avon Valley National Park (immediately adjacent to Paruna) and Avon Wheatbelt. Other studies have reported that dicots are the predominant food source for this species in Cape Range National Park (Creese *et al.* 2019) as well as warru (*P. lateralis* MacDonnell Ranges race) in South Australia (Geelen 1999). Comparison between studies carried out at different locations and times of the year (Fig. 6) reveals considerable variation in diet analyses, strongly suggesting that rock-wallabies

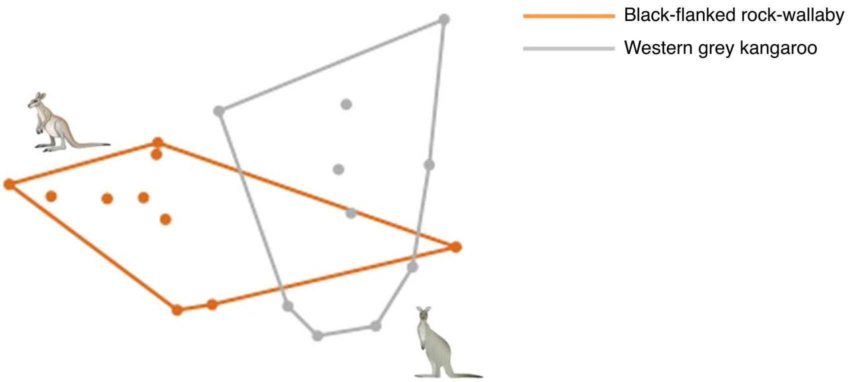

Fig. 4. Non-metric MDS ordination comparing dietary compositions of black-flanked rock-wallaby and western grey kangaroo at Paruna Wildlife Sanctuary, Western Australia.

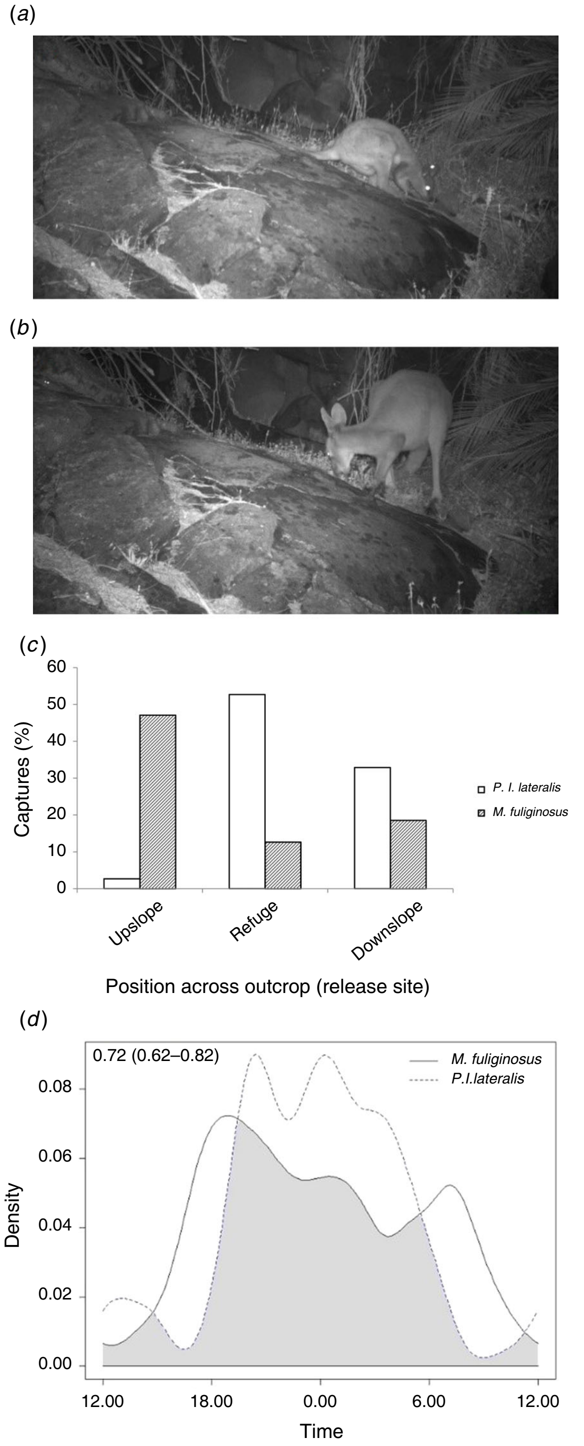

Fig. 5. Black-flanked rock-wallaby (*a*) and western grey kangaroo (*b*) captured using the same foraging patch in Paruna Wildlife Sanctuary. (*c*) Proportion of independent camera trap captures of black-flanked rock-wallaby and western grey kangaroo across the release site outcrop in Paruna Wildlife Sanctuary. (*d*) Temporal overlap in foraging activity between black-flanked rock-wallaby and western grey kangaroo across the release site outcrop in Paruna Wildlife Sanctuary, Western Australia. Shaded area indicates temporal overlap. Value in the top left hand corner represents the proportion overlap in temporal activity (with the 95% confidence interval in brackets).

opportunistically use available forage, including weed species. Rock-wallaby diet seems to vary with plant functional group availability between locations and across seasons (Tuft *et al.* 2011*b*; Pentland 2014; Chauvin 2015). For example, while the present study recorded forbs being mainly eaten in the cooler, wetter conditions of mid-spring when they were most abundant, Chauvin (2015) found that browse was mostly consumed in the drier conditions of late spring through summer in Avon Valley National Park, when forb, grass and fern abundance had declined (Fig. 6). Several other rock-wallaby taxa demonstrate a similar temporal shift in diet (i.e. Dawson and Ellis 1979; Copley and Robinson 1983; Capararo 1994; Telfer and Bowman 2006; Tuft *et al.* 2011*b*).

Western grey kangaroo diet also demonstrates reasonable variation between studies (Fig. 6) and is more diverse (species richness) than that of black-flanked rock-wallabies, comprising monocots and dicots in near equal proportions and more browse than any other plant functional group. Shepherd *et al.* (1997) and Wann and Bell (1997) reported comparable findings in eucalypt forest/woodland (Fig. 6). By contrast, Wilson (1991) and Algar (1986) found that dicots dominate kangaroo diets in mulga (*Acacia aneura*) woodlands and grass, sedge and shrub associations respectively (Fig. 6). In addition to vegetation type, temporal variation in plant functional group availability also seems to influence kangaroo diet. For example, Barker (1987) and Norbury (1987) reported that western grey kangaroo diets comprise mostly monocots in winter, transitioning to mainly dicots in summer. Eastern grey kangaroos are also heavily reliant on grasses in their diets over all seasons (Fig. 6).

Both black-flanked rock-wallabies and western grey kangaroos consumed six of the same plant species, including three forbs, a grass, browse and fern. The dietary overlap between these two species in Paruna was comparable to values of dietary overlap (50–60%) across several published studies (Table 2; see references therein). By contrast, higher degrees of dietary overlap have been reported between black-flanked rock-wallabies with feral goats (*C. hircus*), and between western grey kangaroos with western brush wallabies or tammar wallabies (Table 2).

Availability of preferred food resources

While both black-flanked rock-wallabies and western grey kangaroos consumed plant functional groups according to their availability, they also showed preference for particular plant species. Rock-wallabies strongly selected for pincushions and bellardia, with these two species making up almost half their diet. Chauvin (2015) also found that rock-wallaby populations select for pincushions and rock fern (eaten in proportion to its availability in the present study) in Avon Valley National Park and the Avon Wheatbelt. Both species are resurrection plants capable of withstanding severe desiccation and rehydration (Hopper *et al.* 1997), and likely valuable food resources for rock-wallabies during the wetter months when not in a state of dormancy. Kangaroos also selected for pincushions and bellardia, however these species only made a small contribution to kangaroo diet. Yellow autumn lily, another species selected for in the present study, was also consumed by western grey kangaroos in Whiteman Park (Wann and Bell 1997).

Table 1. Photo captures of black-flanked rock-wallaby (*Petrogale lateralis lateralis*) and western grey kangaroo (*Macropus fuliginosus*) across two rock outcrops in Paruna Wildlife Sanctuary, Western Australia

At each site, two transects, each with 11 Reconyx camera traps, were monitored over a total of 128 days (total 5632 trap nights). Values are numbers of photo captures for individual trap events. The right-hand columns show results of Pearson's Chi tests comparing the actual numbers of trap captures with expected values assuming an equal proportion of captures across upslope, refuge and downslope quadrats. RS = release site, NS = new site, T = transect, Q = quadrat. NA = data not suitable for analysis because only a single rock-wallaby individual was captured at the new site. The darker coloured shading indicates higher numbers of captures

			Upslope				Refuge			Downslope					Chi-square	
			Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10	Q11	Total	χ^2	*P*
P. l. lateralis	RS	T1	0	0	0	3	2	15	6	9	7	13	6	61	26.4	<0.001
		T2	0	0	1	0	1	35	0	6	5	3	0	51	52.8	<0.001
	NS	T3	0	0	0	0	0	0	0	0	0	0	0	0	NA	NA
		T4	0	0	0	0	0	3	0	0	0	0	0	3	NA	NA
M. fuliginosus	RS	T1	11	17	26	20	12	1	11	12	1	7	4	122	31.7	<0.001
		T2	30	62	5	22	15	0	0	7	43	2	0	186	67.8	<0.001
	NS	T3	6	40	8	13	19	11	0	5	23	0	3	128	14.9	0.001
		T4	6	6	20	6	5	5	28	21	30	21	38	186	42.7	<0.001

Of the six preferred food plants in Paruna, three were limited either spatially or temporally. Pincushions were spatially limited, because the species only grows in association with granite rock (Western Australian Herbarium 1998). Bellardia and common sowthistle were temporally limited because they are annual weeds. To an extent, bellardia may also be spatially limited, being only recorded near exposed granite, while common sowthistle was ubiquitously distributed throughout the sanctuary and is a prolific weed across Western Australia (Western Australian Herbarium 1998). It should also be noted that the abundance of pincushions and bellardia may have been underestimated as plants were not flowering at the time of sampling and were therefore less detectable.

The role of weeds in macropod diet

Over a quarter of the plants eaten by rock-wallabies and kangaroos in Paruna were weeds. Similar findings have been reported elsewhere for these species (Wann and Bell 1997; Mayberry 2011; Pearson 2013; Pentland 2014; Chauvin 2015; Creese *et al.* 2019), as well as for other macropod taxa: agile wallaby (*M. agilis*) (Grice 1996), tammar wallaby (McMillan *et al.* 2010), swamp wallaby (de Munk 1999) and eastern grey kangaroo (de Munk 1999; Claridge *et al.* 2016).

Annual veldtgrass is widely consumed by rock-wallabies according to its availability. In Paruna and Avon Valley National Park, which are relatively large and undisturbed reserves, veldtgrass occurs at a low abundance and is eaten in correspondingly low amounts (Chauvin 2015). By contrast, in Nangeen Hill (Avon Wheatbelt), which is a much smaller reserve and more vulnerable to weed invasion, veldtgrass is over twice as prevalent and is consumed in over four times the amount (Chauvin 2015). This suggests that veldtgrass has likely replaced certain native diet items. Any weed control measures would therefore need to be supplemented by revegetation with native forage plants in order to prevent there being a lack of food resources for rock-wallabies.

Rock-wallabies and kangaroos may be contributing to the persistence and spread of existing weed populations in Paruna through several means. First, they may be dispersing viable weed seeds in their scats, as shown by other macropod taxa (eastern grey kangaroo: Claridge *et al.* 2016; agile wallaby: Grice 1996). Given the variable effect of gut passage on seed germination between herbivores (Westcott *et al.* 2008), the proportion of weed seeds ingested by rock-wallabies and kangaroos that remain viable after excretion is unknown. Rock-wallabies may be transporting weed seeds to microsites on the outcrop, where the elevated nutrient and moisture levels facilitate germination (Brown and Archer 1988), although their small population size likely precludes this from being a management concern. Kangaroos, however, are abundant in Paruna and their large home ranges make them a more noteworthy vector for weed spread. Second, foraging by rock-wallabies may be limiting the recruitment (Young *et al.* 1995; Allcock and Hik 2004) or regeneration (Gardiner 1986) of less competitive native plant species (Tuft *et al.* 2011*b*). Third, overgrazing is known to cause soil disturbance and, together with nutrient additions from rock-wallaby scats, can also facilitate weed encroachment (Hobbs and Atkins 1988), as previously reported by Pentland (2014) at Nangeen Hill (although this seems unlikely at Paruna where rock-wallaby foraging ranges are not restricted as they are at Nangeen Hill).

Spatial overlap in foraging patches

We measured 33.9% spatial overlap in rock-wallaby and kangaroo foraging patches, with rock-wallabies (adults and young-at-heel) predominantly foraging near refuges but also regularly venturing considerable distances ($\geq$ 100 m) downslope of their refuges to forage. Kangaroos were more likely to be sighted on cameras upslope or downslope of the refuges and seemed to avoid steep terrain around the refuges (i.e. precarious steep angled smooth rocks). The rock-wallaby's morphological adaptations (i.e. a strong non-prehensile tail, large pads and short

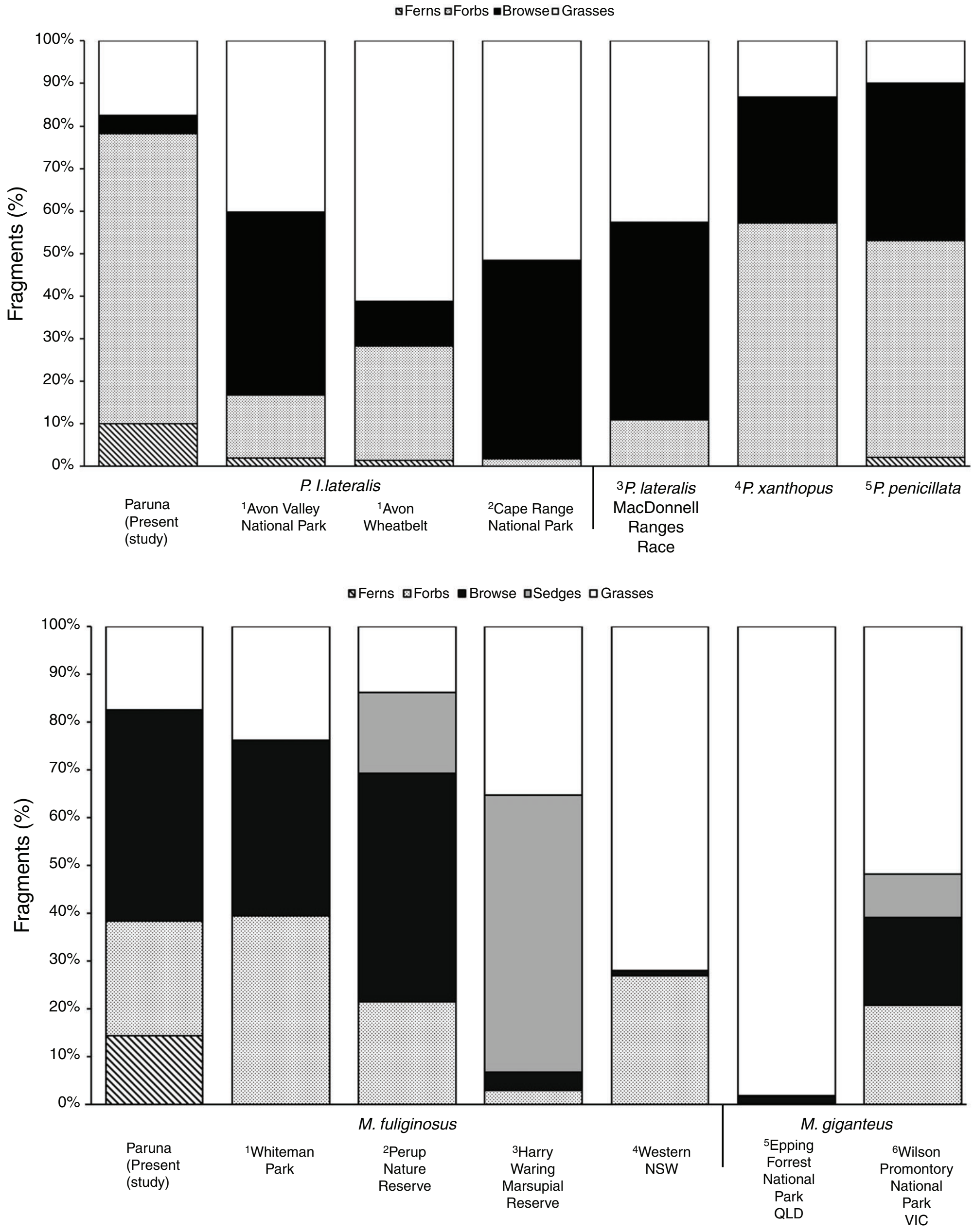

Fig. 6. (*a*) Comparison between black-flanked rock-wallaby dietary composition results of this study with those from other studies, and other rock-wallaby *Petrogale* taxa. Cape Range National Park data is from Pilgonaman Gorge summer sampling. Avon Valley National Park and Avon Wheatbelt sedge data has been incorporated into forb data given no occurrence of Cyperaceae family. Data on forb and browse for *Petrogale xanthopus* excludes round-leaved chenopods. Overall data for *Petrogale penicillata* is the mean of multiple seasons of sampling and sedge data has been incorporated into forb data given no occurrence of Cyperaceae family. References: [1](Chauvin 2015) [2](Creese *et al.* 2019) [3](Geelen 1999) [4](Dawson and Ellis 1979) [5](Tuft *et al.* 2011*b*). (*b*) Comparison between western grey kangaroo dietary composition results of this study with those from other studies, and eastern grey kangaroo (*Macropus giganteus*). With the exception of Wilson (1991) and Algar (1986), all data is the total of multiple seasons of sampling. Wilson's Promontory National Park sedge data may also include other non-grass graminoid species including certain rushes, lilies and forbs. Sedges = Cyperaceae family. References: [1](Wann and Bell 1997) [2](Shepherd *et al.* 1997) [3](Algar 1986) [4](Wilson 1991) [5](Woolnough and Johnson 2000) [6](Davis *et al.* 2008).

Table 2. Comparison between dietary overlap results of this study at Paruna Wildlife Sanctuary with those of published studies for a range of macropod species

Values from similar indices representing dietary overlap: (S) Schoener index (Schoener 1970) and (H) Horns index of niche overlap (Horn 1966). *statistically significant dietary overlap recorded. NS = index value was not significant but was not given

	Western grey kangaroos (*Macropus fuliginosus*)	Eastern grey kangaroos (*Macropus giganteus*)	Euros (*Osphranter robustus erubescens*)	Feral goats (*Capra hircus*)
Black-flanked rock-wallaby (*Petrogale lateralis lateralis*)	0.56 (S)[A]		0.57 (S)[B]	0.85* (S)[B]
MacDonnell Ranges race (*Petrogale lateralis*)			NS[C]	
Brush-tailed rock-wallabies (*Petrogale penicillata*)		(50–60%)[D]		
Western brush wallabies (*Macropus irma*)	0.88* (S)[E,I] 0.33 (H)[F,I] 0.04 (H)[G]			
Tammar wallabies (*Notamacropus eugenii*)	0.95* (H)[F,I]			
Swamp wallabies (*Wallabia bicolor*)		0.61 (H)[H]		

[A] Present study. [B] Pilgonaman Gorge summer sampling: Creese *et al.* (2019). [C] Capararo (1994). [D] Tuft *et al.* (2001*b*). [E] Wann and Bell (1997). [F] Shepherd *et al.* (1997). [G] Algar (1986). [H] Davis *et al.* (2008). [I] Data is the total of multiple seasons of sampling.

nails) enable them to scramble and leap across rocks (Horsup 1986; Barker 1990; Tyndale-Biscoe 2005; Pentland 2014) and may allow for some degree of spatial resource separation from the larger and more competitive kangaroos.

Predation risk

Rock-wallabies spent considerable time foraging, with activity extending from dusk to mid-morning, suggesting that their activity in Paruna was not constrained by a perceived risk of predation, as was observed by Pentland (2014) at Nangeen Hill. However, at least three individual feral cats were present on the outcrops, one of which moved between them. These feral cats visited several rock-wallaby foraging patches, including one nearest a refuge containing a young-at-heel individual. Juvenile rock-wallabies are highly vulnerable to predation by feral cats (Paltridge *et al.* 1997; Fleming *et al.* 2020) and red foxes (Kinnear *et al.* 1984; Pentland 2014). The presence of feral cats (*Felis catus*) around the rock outcrop shelter used by rock-wallabies suggests that predation threat cannot be ignored. Predation was suspected to cause population decline of almost fifty per cent of Paruna rock-wallabies between 2010 and 2014, after which an intensive fox control program was implemented (Palmer 2018). Poison baiting, using 1080 meat baits and canid pest injectors, along with trapping around the outcrops has since reduced predation pressure to the extent that rock-wallaby recruitment had recommenced, although recent annual rock-wallaby capture-mark-recapture monitoring suggests that the population in Paruna is still declining (Palmer 2018).

Pentland (2014) similarly observed feral cats intruding into rock-wallaby refuges at Nangeen Hill. Predator-proof exclosures at Nangeen Hill and in the Musgrave Ranges in South Australia have achieved excellent conservation outcomes for resident black-flanked rock-wallaby and warru respectively (R. Boyland pers. comm; Ruykys 2011; Muhic *et al.* 2012; Chauvin 2015). Feral cats are notoriously difficult to control and will continue to incur into Paruna while it remains only partially protected by a predator-proof fence along its southern boundary. Extension of the fence to encompass the entire sanctuary would support complete predator eradication. In addition to the benefits this would bring resident rock-wallabies, it will also improve the future success of supplementary translocations.

Limitations of this study

There may be errors and biases in the data resulting from the limitations of methods used. Although considered to provide an accurate estimation of diet, scat analysis assumes that all plants have equally digestible epidermal tissues (Dawson and Ellis 1979). This is not the case, with some plants being less digestible and therefore more easily identifiable (i.e. those with stellate trichomes such as browse species *T. o. odoratissimum*: Horsup and Marsh 1992), whereas others may be unidentifiable (forb species *Dioscorea hastifolia* and **Fumaria capreolata* were photographed being eaten by kangaroos but not identified in their scats). Consequently, more easily identifiable plants can be overestimated and grasses underestimated (Creese *et al.* 2019).

Although grasses (Poaceae spp.) could be relatively easily identified based on the presence of silica bodies, elongated long-cells often with crenulated cell walls, and their cells running in rows parallel to venation (Storr 1961; Kok and Van der Schijff 1973), further identification to species level was difficult, likely because of their high proportion of digestible cellulose (Shipley 1999) and absence of other diagnostic features (Ellis *et al.* 1977). Seven Poaceae species were identified in vegetation surveys at the release site but only three (early hair grass, annual veldtgrass and foxtail mulga grass) were identified in the scats sampled, while 62% of grass fragments could only be identified to family.

The method is further limited in that it does not account for the relatively long period between ingestion and excretion, and therefore potential for macropods to have sourced plants from outside the vegetation quadrats (foraging patches) surveyed (Norbury and Sanson 1992), which would influence the identification of selected or avoided plant species. This is more likely the case for kangaroos with their larger foraging ranges (Arnold *et al.* 1992) away from the rock refuges (Creese *et al.* 2019).

Finally, this study was only carried out at one point in time. The collection of additional scats over multiple seasons could extend upon these results. Being able to attribute scats to individuals may also be a powerful advantage to determine whether there are age or sex differences in diet.

Conclusions and conservation management

Spatial and dietary overlap between black-flanked rock-wallabies and western grey kangaroos suggests that the availability of shared food resources could limit expansion of rock-wallaby foraging patches beyond the steep sites where they are more mobile than the kangaroos. Although the energy requirements of the rock-wallabies are smaller (due to their smaller body size) (Illius and Gordon 1987; Tuft *et al.* 2011*a*), if shared food resource quality declines, the kangaroos are likely to have an advantage as they can digest poorer quality forage (Dawson 1989) and also forage further to fulfil their nutrient requirements (Tuft *et al.* 2011*a*). Competition between these two species may become increasingly probable with drought and bushfire intensities predicted to increase across southwest Western Australia as a result of climate change-induced rainfall reduction and temperature increases. Kangaroos may also compete with rock-wallabies through interference competition, preventing them from accessing optimal foraging patches (Tuft *et al.* 2011*a*). Consequently, kangaroos can adversely impact relictual rock-wallaby populations and proactive kangaroo population management may be required, particularly within reserves enclosed by predator-proof fencing (Woolnough and Johnson 2000). This could include reducing kangaroo population densities around existing rock-wallaby populations, as is already occurring at Nangeen Hill (A. Chauvin pers. comm.), as well as at future rock-wallaby translocation sites currently used by kangaroos.

Data availability

The data that support this study are available in the Supplementary Material.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Algar, D. (1986). An ecological study of macropodid marsupial species on a reserve. University of Western Australia: Perth.)

Allcock, K. G., and Hik, D. S. (2004). Survival, growth, and escape from herbivory are determined by habitat and herbivore species for three Australian woodland plants. *Oecologia* **138**, 231–241. doi:10.1007/S00442-003-1420-3

Arnold, G. W., Steven, D. E., Grassia, A., and Weeldenburg, J. (1992). Home-range size and fidelity of western grey kangaroos (*Macropus fuliginosus*) living in remnants of wandoo woodland and adjacent farmland. *Wildlife Research* **19**, 137–143. doi:10.1071/WR9920137

Australian Wildlife Conservancy (1998). 'Paruna Sanctuary Management Plan.' (Australian Wildlife Conservancy: Perth.)

Banks, P. B., Newsome, A. E., and Dickman, C. R. (2000). Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**, 283–291. doi:10.1046/J.1442-9993.2000.01039.X

Barker, R. D. (1987). The diet of herbivores in the sheep rangelands. In 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia'. (Eds G. Caughley, N. Shepherd, J. Short.) pp. 69–83. (Cambridge University Press: Cambridge.)

Barker, S. C. (1990). Behavior and social-organization of the allied rock-wallaby *Petrogale assimilis*, Ramsay, 1877 (Marsupialia, Macropodoidea). *Wildlife Research* **17**, 301–311. doi:10.1071/WR9900301

Batschelet, E. (1981). 'Circular statistics in biology.' (Academic Press: New York.)

Boyd, C., Punt, A. E., Weimerskirch, H., and Bertrand, S. (2014). Movement models provide insights into variation in the foraging effort of central place foragers. *Ecological modelling* **286**, 13–25. doi:10.1016/J.ECOLMODEL.2014.03.015

Braun-Blanquet, J. (1932). 'Plant sociology.' (McGraw-Hill: New York.)

Brown, J. R., and Archer, S. (1988). Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio* **73**, 73–80. doi:10.1007/BF00031854

Burbidge, A., Woinarski, J., and Harrison, P. (2014). 'The Action Plan for Australian Mammals 2012.' (CSIRO Publishing: Melbourne.)

Bureau of Meteorology (2019). Climate Data Online. Available at http://www.bom.gov.au/climate/data/?ref=ftr. [verified 1 October 2019].

Capararo, S. M. (1994). 'Potential dietary overlap between the black-footed rock-wallaby (*Petrogale lateralis*) and two common sympatric herbivores in Central Australia.' The University of New England: Armidale.)

Chauvin, A. (2015). Diet selection by black-flanked rock-wallabies (*Petrogale lateralis lateralis*) in the central wheatbelt and Avon Valley of Western Australia. Honours thesis. Murdoch University, Perth.

Claridge, A. W., Hunt, R., Thrall, P. H., and Mills, D. J. (2016). Germination of native and introduced plants from scats of fallow deer (*Dama dama*) and eastern grey kangaroo (*Macropus giganteus*) in a southeastern Australian woodland landscape. *Ecological Management & Restoration* **17**, 56–62. doi:10.1111/EMR.12193

Colwell, R. K., Mao, C. X., and Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717–2727. doi:10.1890/03-0557

Copley, P. B., and Robinson, A. C. (1983). Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray (Marsupialia: Macropodidae). 2. Diet. *Wildlife Research* **10**, 63–76. doi:10.1071/WR9830063

Creese, S., Davies, S. J. J. F., and Bowen, B. J. (2019). Comparative dietary analysis of the black-flanked rock-wallaby (*Petrogale lateralis lateralis*), the euro (*Macropus robustus erubescens*) and the feral goat (*Capra hircus*) from Cape Range National Park, Western Australia. *Australian Mammalogy* **41**, 220–230. doi:10.1071/AM17059

Davis, N. E., Coulson, G., and Forsyth, D. M. (2008). Diets of native and introduced mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia. *Wildlife Research* **35**, 684–694. doi:10.1071/WR08042

Dawson, T. J. (1989). Diets of macropodoid marsupials: general patterns and environmental influences. In 'Kangaroos, wallabies and rat-kangaroos'. (Eds G. Grigg, P. Jarman, I. Hume.) pp. 129–142. (University of New South Wales: Kensington.)

Dawson, T. J., and Ellis, B. A. (1979). Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. *Wildlife Research* **6**, 245–254. doi:10.1071/WR9790245

de Munk, F. D. (1999). Resource use by the eastern grey kangaroo and black wallaby in a managed remnant woodland community. PhD thesis. Deakin University, Melbourne.

Eldridge, M. and Close, R. (1995). Black-footed Rock-wallaby. In 'The Mammals of Australia'. (Ed. R. Strahan.) pp. 377–381. (Reed Books: Sydney.)

Ellis, B. A., Russell, E. M., Dawson, T. J., and Harrop, C. J. F. (1977). Seasonal changes in diet preferences of free-ranging red kangaroos, euros and sheep in western New South Wales. *Australian wildlife research* **4**, 127–144. doi:10.1071/WR9770127

Fleming, P. A., Crawford, H., Auckland, C. H., and Calver, M. C. (2020). Body size and bite force of stray and feral cats – are bigger or older cats taking the largest or more difficult-to-handle prey?. *Animals* **10**, 707. doi:10.3390/ANI10040707

Gardiner, H. G. (1986). Dynamics of perennial plants in the mulga (*Acacia aneura* F. Muell.) zone of Western Australia. I. Rates of population change. *The Rangeland Journal* **8**, 18–27. doi:10.1071/RJ9860018

Geelen, L. J. (1999). A preliminary study of the black-footed rock-wallaby (*Petrogale lateralis* MacDonnell Ranges race) in the Anangu Pitjanjatjara lands, South Australia. Honours thesis. University of Adelaide, Adelaide.

Green-Barber, J. M., and Old, J. M. (2018). Is camera trap videography suitable for assessing activity patterns in eastern grey kangaroos?. *Pacific Conservation Biology* **24**, 134–141. doi:10.1071/PC17051

Grice, A. C. (1996). Seed production, dispersal and germination in *Cryptostegia grandiflora* and *Ziziphus mauritiana*, two invasive shrubs in tropical woodlands of northern Australia. *Australian Journal of Ecology* **21**, 324–331. doi:10.1111/J.1442-9993.1996.TB00615.X

Halford, D. A., Bell, D. T., and Loneragan, W. A. (1984). Diet of the western grey kangaroo (*Macropus fuliginosus* Desm.) in a mixed pasture-woodland habitat of Western Australia. *Journal of the Royal Society of Western Australia* **66**, 119–128.

Hammer, O. and Harper, D. A. T. (2013). PAST: version 2.17c. Available at http://folk.uio.no/ohammer/past. [verified 1 October 2019].

Hammer, O., Harper, D. A. T., and Ryan, P. D. (2001). PAST: Paleotological Statistics software package for education and data analysis. *Palaeotologia Electronica* **4**, 9.

Hobbs, R. J., and Atkins, L. (1988). Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology* **13**, 171–179. doi:10.1111/J.1442-9993.1988.TB00966.X

Hopper, S. D., Brown, A. P., and Marchant, N. G. (1997). Plants of Western Australian granite outcrops. *Journal of the Royal Society of Western Australia* **80**, 141.

Horn, H. S. (1966). Measurement of "overlap" in comparative ecological studies. *The American Naturalist* **100**, 419–424. doi:10.1086/282436

Horsup, A. B. (1986). The behaviour of the allied rock wallaby, *Petrogale assimilis* (Macropodinae). PhD thesis. James Cook University of North Queensland, Townsville.

Horsup, A., and Marsh, H. (1992). The diet of the allied rock-wallaby, *Petrogale assimilis*, in the wet-dry tropics. *Wildlife Research* **19**, 17–33. doi:10.1071/WR9920017

Illius, A. W., and Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. *The Journal of Animal Ecology* **56**, 989–999. doi:10.2307/4961

Kinnear, J. E., Onus, M. L., and Bromilow, B. (1984). Foxes, feral cats and rock wallabies. *Swans* **14**, 3–8.

Kinnear, J. E., Onus, M. L., and Bromilow, R. N. (1988). Fox control and rock-wallaby population dynamics. *Wildlife Research* **15**, 435–450. doi:10.1071/WR9880435

Kinnear, J. E., Onus, M. L., and Sumner, N. R. (1998). Fox control and rock-wallaby population dynamics – II. An update. *Wildlife Research* **25**, 81–88. doi:10.1071/WR96072

Kok, P. D. F., and Van der Schijff, H. P. (1973). A key based on epidermal characteristics for the identification of certain highveld grasses. *Koedoe* **16**, 27–43. doi:10.4102/KOEDOE.V16I1.883

Kowalski, M. and Kowalski, M. (2000). ExifPro. Available at http://www.exifpro.com/. [verified 1 October 2019].

Lechowicz, M. J. (1982). The sampling characteristics of electivity indices. *Oecologia* **52**, 22–30. doi:10.1007/BF00349007

Leishman, M. (2014). 'Preliminary Determination – *Macropus fuliginosus*.' (NSW Scientific Committee: Hurstville.)

Lin, E. (2011). The optimum field approach for monitoring the black-flanked rock-wallabies (*Petrogale lateralis lateralis*) in Paruna Wildlife Sanctuary. Honours thesis. University of Western Australia, Perth.

Lund, U., Agostinelli, C., Arai, H., Gagliardi, A., Portugues, E. G., Giunchi, D., Irisson, J. O., Pocernich, M., and Rotolo, F. (2017). Package 'circular'. Available at https://cran.r-project.org/web/packages/circular/circular.pdf. [verified 1 October 2019].

Mayberry, C. (2011). Management of isolated populations of western grey kangaroos (*Macropus fuliginosus ocydromus*) through fertility control, in south-western Australia. PhD thesis. University of Western Australia, Perth.

McMillan, A., Coupland, G., Chambers, B. K., Hills, H. R., and Bencini, R. (2010). Determining the diet of tammar wallabies on Garden Island, Western Australia, using stable isotope analysis. In 'Macropods: The Biology of Kangaroos, Wallabies and Rat-kangaroos'. (Eds G. Coulson, ad M. Eldridge.) pp. 243–252. (CSIRO Publishing: Melbourne.)

Meredith, M. and Ridout, M. (2018). Package 'overlap'. Available at https://cran.r-project.org/web/packages/overlap/overlap.pdf. [verified 1 October 2019].

Muhic, J., Abbott, E., and Ward, M. J. (2012). The warru (*Petrogale lateralis* MacDonnell Ranges Race) reintroduction project on the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia. *Ecological Management & Restoration* **13**, 89–92. doi:10.1111/J.1442-8903.2011.00620.X

Neave, H. M., and Tanton, M. T. (1989). The effects of grazing by kangaroos and rabbits on the vegetation and habitat of other fauna in the Tidbinbilla Nature Reserve, Australian Capital Territory. *Australian wildlife research* **16**, 337–351. doi:10.1071/WR9890337

Norbury, G. L. (1987). Diet selection by western grey kangaroos in relation to declining food availability. In 'Herbivore Nutrition Research'. (Ed. M. Rose.) pp. 75–76. (Australian Society for Animal Production: Brisbane.)

Norbury, G. L. (1988). Microscopic analysis of herbivore diets – a problem and a solution. *Australian wildlife research* **15**, 51–57. doi:10.1071/WR9880051

Norbury, G. L., and Sanson, G. D. (1992). Problems with measuring diet selection of terrestrial, mammalian herbivores. *Austral ecology* **17**, 1–7. doi:10.1111/J.1442-9993.1992.TB00774.X

Palmer, N. (2018). 'Black-flanked rock-wallaby annual trapping, Paruna Wildlife Sanctuary 2018.' (Australian Wildlife Conservancy: Perth.)

Paltridge, R., Gibson, D., and Edwards, G. (1997). Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* **24**, 67–76. doi:10.1071/WR96023

Pearson, D. J. (2013). Recovery plan for five species of rock wallabies: Black-footed rock wallaby (*Petrogale lateralis*), Rothschild rock wallaby (*Petrogale rothschildi*), Short-eared rock wallaby (*Petrogale brachyotis*), Monjon (*Petrogale burbidgei*) and Nabarlek (*Petrogale concinna*) 2012–2022. (Department of Parks and Wildlife: Perth.)

Pentland, C. (2014). Behavioural ecology of the black-flanked rock-wallaby (*Petrogale lateralis lateralis*): Refuge importance in a variable environment. PhD thesis. Edith Cowan University, Joondalup.

Poole, H. L., Mukaromah, L., Kobryn, H. T., and Fleming, P. A. (2014). Spatial analysis of limiting resources on an island: diet and shelter use reveal sites of conservation importance for the Rottnest Island quokka. *Wildlife Research* **41**, 510–521. doi:10.1071/WR14083

Priddel, D., Shepherd, N., and Wellard, G. (1988). Home ranges of sympatric red kangaroos *Macropus rufus* and western grey kangaroos *Macropus fuliginosus* in western New South Wales. *Wildlife Research* **15**, 405–411. doi:10.1071/WR9880405

R Core Team (2012). 'R: A language and environment for statistical computing. R foundation for statistical computing.' Available at http://www.R-project.org/[verified 1 October 2019].

Ruykys, L. (2011). 'Ecology of warru (*Petrogale lateralis* MacDonnell Ranges race) in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.' (University of Adelaide: Adelaide.)

Schoener, T. W. (1970). Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418. doi:10.2307/1935376

Sharp, A. (2009). Home range dynamics of the yellow-footed rock-wallaby (*Petrogale xanthopus celeris*) in central-western Queensland. *Austral ecology* **34**, 55–68. doi:10.1111/J.1442-9993.2008.01882.X

Shepherd, K. A., Wardell-Johnson, G. W., Loneragan, W. A., and Bell, D. T. (1997). Diet of herbivorous marsupials in a *Eucalyptus marginata* forest and their impact on the understorey vegetation. *Journal of the Royal Society of Western Australia* **80**, 47.

Shipley, L. A. (1999). Grazers and browsers: how digestive morphology affects diet selection. *Grazing behavior of livestock and wildlife* **70**, 20–27.

Storr, G. M. (1961). Microscopic analysis of faeces, a technique for ascertaining the diet of herbivorous, mammals. *Australian Journal of Biological Sciences* **14**, 157–164. doi:10.1071/BI9610157

Telfer, W. R., and Bowman, D. J. S. (2006). Diet of four rock-dwelling macropods in the Australian monsoon tropics. *Austral ecology* **31**, 817–827. doi:10.1111/J.1442-9993.2006.01644.X

Tuft, K. D., Crowther, M. S., Connell, K., Muller, S., and McArthur, C. (2011*a*). Predation risk and competitive interactions affect foraging of an endangered refuge-dependent herbivore. *Animal Conservation* **14**, 447–457. doi:10.1111/J.1469-1795.2011.00446.X

Tuft, K. D., Crowther, M. S., and McArthur, C. (2011*b*). Multiple scales of diet selection by brush-tailed rock-wallabies (*Petrogale penicillata*). *Australian Mammalogy* **33**, 169–180. doi:10.1071/AM10041

Tyndale-Biscoe, C. H. (2005). 'Life of marsupials.' (CSIRO Publishing: Melbourne.)

Wallace, R. K., and Ramsey, J. S. (1983). Reliability in measuring diet overlap. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 347–351. doi:10.1139/F83-050

Wann, J. M., and Bell, D. T. (1997). Dietary preferences of the black-gloved wallaby (*Macropus irma*) and the western grey kangaroo (*M. fuliginosus*) in Whiteman Park, Perth, Western Australia. *Journal of the Royal Society of Western Australia* **80**, 55.

Westcott, D. A., Setter, M., Bradford, M. G., McKeown, A., and Setter, S. (2008). Cassowary dispersal of the invasive pond apple in a tropical rainforest: the contribution of subordinate dispersal modes in invasion. *Diversity and Distributions* **14**, 432–439. doi:10.1111/J.1472-4642.2007.00416.X

Western Australian Herbarium (1998). FloraBase – the Western Australian Flora. Available at https://florabase.dpaw.wa.gov.au/browse/profile/1273. [verified 1 October 2019].

Wilson, A. D. (1991). Forage utilisation by sheep and kangaroos in a semi-arid woodland. *The Rangeland Journal* **13**, 81–90. doi:10.1071/RJ9910081

Woolnough, A. P., and Johnson, A. N. (2000). Assessment of the potential for competition between two sympatric herbivores – the northern hairy-nosed wombat, *Lasiorhinus krefftii*, and the eastern grey kangaroo, *Macropus giganteus*. *Wildlife Research* **27**, 301–308. doi:10.1071/WR99053

Young, T. P., Patridge, N., and Macrae, A. (1995). Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. *Ecological applications* **5**, 97–108. doi:10.2307/1942055

10.1071/AM20049
Australian Mammalogy

Supplementary Material for

Potential for dietary competition between the threatened black-flanked rock-wallaby and sympatric western grey kangaroo

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Fig. S1. Feral cats captured at the outcrops in Paruna Wildlife Sanctuary, Western Australia

Table S1. Selectivity for plant species (Ivlev's Selectivity Index) calculated by comparing the relative abundance of plant species in black-flanked rock-wallaby (*Petrogale lateralis lateralis*) and western grey kangaroo (*Macropus fuliginosus*) scats compared to their the relative abundance at the outcrops in Paruna Wildlife Sanctuary, Western Australia.

Plant			Relative availability (%)		*P. l. lateralis*		*M. fuliginosus*	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Monocot								
Forb	Asparagaceae	*Dichopogon capillipes*	0.6	1.0	0.0	-1	0.0	-1
Forb	Asparagaceae	*Thysanotus manglesianus*	0.1	0.1	0.0	-1	0.0	-1
Forb	Boryaceae	*Borya sphaerocephala*	0.2	0.8	31.7	1	1.3	1
Sedge	Cyperaceae	*Lepidosperma* sp. 1	0.0	0.0	0.0	-1	0.0	-1
Sedge	Cyperaceae	*Lepidosperma* sp. 2	0.0	0.0	0.0	-1	0.0	-1
Sedge	Cyperaceae	*Schoenus nanus*	0.0	0.8	0.0	-1	0.0	-1
Forb	Haemodoraceae	*Haemodorum* sp.	0.2	0.2	0.0	-1	0.0	-1
Forb	Hemerocallidaceae	*Caesia micrantha*	0.3	1.0	0.0	-1	0.0	-1
Forb	Hemerocallidaceae	*Tricoryne elatior*	0.1	0.3	0.0	-1	6.0	1
Forb	Hypoxidaceae	*Pauridia occidentalis*	0.7	0.4	0.0	-1	0.0	-1
Forb	Iridaceae	*Orthrosanthus laxus*	0.0	0.1	0.0	-1	0.7	1
Forb	Iridaceae	**Romulea rosea*	3.2	3.9	0.0	-1	0.0	-1
Forb	Orchidaceae	*Caladenia flava*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Leptoceras menziesii*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Prasophyllum macrostachyum*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Prasophyllum* sp.	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Pterostylis* sp.	0.0	0.1	0.0	-1	0.0	-1
Grass	Poaceae	**Aira cupaniana*	0.0	0.8	0.0	-1	0.0	-1
Grass	Poaceae	**Aira praecox*	0.3	2.5	0.3	0	0.0	-1
Grass	Poaceae	**Bellardia trixago*	0.3	1.3	15.6	1	4.5	1

Plant			Relative availability (%)		*P. l. lateralis*		*M. fuliginosus*	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Grass	Poaceae	**Briza maxima*	0.4	0.4	0.0	-1	0.0	-1
Grass	Poaceae	**Briza minor*	1.9	2.8	0.0	-1	0.0	-1
Grass	Poaceae	**Bromus diandrus*	0.4	2.4	0.0	-1	0.0	-1
Grass	Poaceae	**Ehrharta longiflora*	5.8	2.9	7.0†	0	4.0†	0
Grass	Poaceae	*Microlaena? stipoides*	0.0	0.5	0.0	-1	0.0	-1
Grass	Poaceae	*Neurachne alopecuroidea*	0.5	1.8	0.0	-1	1.3	0
Grass	Poaceae	**Vulpia myuros*	4.0	3.5	0.0	-1	0.0	-1
		Unknown Poaceae			12.5		7.7	
Forb	Restionaceae	*Desmocladus flexuosus*	0.0	0.1	0.0	-1	0.0	-1
Forb	Xanthorrhoeaceae	*Chamaescilla corymbosa*	0.0	0.2	0.0	-1	0.0	-1
Browse	Xanthorrhoeaceae	*Xanthorrhoea preissii*	0.8	0.0	0.0	-1	0.0	-1
Browse	Zamiaceae	*Macrozamia riedlei*	1.5	0.1	0.0	-1	0.6	0
		Unknown monocots			14.1		21.2	
		Total monocots			**65.6**		**42.2**	
Dicot								
Forb	Amaranthaceae	*Ptilotus drummondii*	0.0	0.1	0.0	-1	0.0	-1
Forb	Apiaceae	*Daucus glochidiatus*	3.5	3.9	0.0	-1	0.0	-1
Forb	Apiaceae	*Eryngium pinnatifidum*	0.0	0.3	0.0	-1	0.0	-1
Forb	Araliaceae	*Trachymene? pilosa*	0.0	0.2	0.0	-1	0.0	-1
Forb	Asteraceae	**Arctotheca calendula*	0.4	1.4	0.0	-1	0.0	-1
Forb	Asteraceae	*Brachyscome pusilla*	0.0	0.3	0.0	-1	0.0	-1
Forb	Asteraceae	**Carduus pycnocephalus*	0.5	0.4	0.0	-1	0.0	-1
Forb	Asteraceae	*Helichrysum? luteoalbum*	0.3	0.0	0.0	-1	0.0	-1
Forb	Asteraceae	**Hypochaeris glabra*	4.6	4.4	0.0	-1	0.0	-1
Forb	Asteraceae	**Hypochaeris radicata*	0.0	0.2	0.0	-1	0.0	-1
Forb	Asteraceae	*Plantago? debilis*	0.0	0.7	0.0	-1	0.0	-1

Plant			Relative availability (%)		*P. l. lateralis*		*M. fuliginosus*	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Forb	Asteraceae	*Podolepis lessonii*	0.3	0.5	0.0	-1	0.0	-1
Forb	Asteraceae	*Podotheca gnaphalioides*	0.0	0.1	0.0	-1	0.0	-1
Forb	Asteraceae	**Sigesbeckia orientalis*	0.0	0.8	0.0	-1	0.0	-1
Forb	Asteraceae	**Sonchus oleraceus*	4.7	3.1	2.5	0	17.0†	1
Forb	Asteraceae	**Ursinia anthemoides*	1.3	2.4	0.0	-1	0.0	-1
Forb	Asteraceae	*Lagenophora huegelii*	0.5	0.9	0.0	-1	0.0	-1
Forb	Asteraceae	*Lawrencella rosea*	0.0	0.2	0.0	-1	0.0	-1
Forb	Asteraceae	*Quinetia urvillei*	0.5	2.3	0.0	-1	0.0	-1
Forb	Asteraceae	*Siloxerus humifusus*	0.0	0.4	0.0	-1	0.0	-1
Forb	Asteraceae	*Waitzia nitida*	0.0	0.1	0.0	-1	0.0	-1
Forb	Asteraceae	Unknown Asteraceae	0.0	0.0	0.0	-1	0.0	-1
Browse	Casuarinaceae	*Allocasuarina huegeliana*	0.1	0.2	0.0	-1	0.0	-1
Forb	Caryophyllaceae	**Silene gallica*	0.2	0.2	0.0	-1	0.0	-1
Forb	Crassulaceae	*Crassula colorata*	0.3	0.2	0.0	-1	0.0	-1
Browse	Dilleniaceae	*Hibbertia hypericoides*	0.0	0.2	0.0	-1	0.0	-1
Browse	Dilleniaceae	*Hibbertia lasiopus*	1.1	1.7	0.0	-1	0.0	-1
Forb	Dioscoreaceae	*Dioscorea hastifolia*	7.6	1.5	0.0	-1	0.0	-1
Forb	Droseraceae	*Drosera bulbosa*	0.8	0.5	0.0	-1	0.0	-1
Forb	Droseraceae	*Drosera glanduligera*	0.7	1.2	0.0	-1	0.0	-1
Forb	Droseraceae	*Drosera pallida*	0.0	0.7	0.0	-1	0.0	-1
Browse	Ericaceae	*Astroloma drummondii*	0.0	0.1	0.0	-1	0.0	-1
Browse	Fabaceae	*Acacia pulchella*	0.0	0.0	0.0	-1	0.0	-1
Forb	Fabaceae	**Melilotus indicus*	0.0	0.3	0.0	-1	0.0	-1
Forb	Fabaceae	**Trifolium dubium*	0.0	0.8	0.0	-1	0.0	-1
Forb	Fabaceae	**Trifolium campestre*	0.2	0.5	0.0	-1	0.0	-1
Forb	Fabaceae	**Trifolium subterraneum*	0.3	3.0	0.0	-1	0.0	-1

Plant			Relative availability (%)		*P. l. lateralis*		*M. fuliginosus*	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Forb	Gentianaceae	*Centaurium erythraea*	1.1	1.7	0.0	-1	0.0	-1
Forb	Gentianaceae	**Cicendia filiformis*	0.0	0.4	0.0	-1	0.0	-1
Forb	Geraniaceae	*Erodium cygnorum*	0.1	0.0	0.0	-1	0.0	-1
Forb	Goodeniaceae	*Goodenia pulchella*	0.0	0.0	0.0	-1	0.0	-1
Forb	Lamiaceae	**Stachys arvensis*	1.5	1.6	0.0	-1	0.0	-1
Forb	Montiaceae	*Calandrinia* sp.	0.4	1.9	0.0	-1	0.0	-1
Forb	Mulvaceae	*Thomasia* sp.	0.0	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Corymbia calophylla*	0.1	0.2	0.0	-1	0.0	-1
Browse	Myrtaceae	*Darwinia citriodora*	13.2	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Eucalyptus accedens*	0.0	0.4	0.0	-1	5.3	1
Browse	Myrtaceae	*Hypocalymma angustifolium*	1.1	0.8	0.0	-1	0.0	-1
Browse	Myrtaceae	*Leptospermum erubescens*	0.0	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Melaleuca radula*	1.8	0.0	0.0	-1	1.7	0
Forb	Orobanchaceae	*Parentucellia latifolia*	0.5	1.1	0.0	-1	0.0	-1
Forb	Oxalidaceae	*Oxalis perennans*	0.4	0.4	0.0	-1	0.0	-1
Forb	Papaveraceae	**Fumaria capreolata*	0.8	0.0	0.0	-1	0.0	-1
Browse	Phyllanthaceae	*Phyllanthus calycinus*	2.6	2.2	0.0	-1	0.0	-1
Forb	Phyllanthaceae	*Poranthera microphylla*	0.0	0.2	0.0	-1	0.0	-1
Forb	Primulaceae	**Lysimachia arvensis*	6.6	4.5	0.0	-1	0.0	-1
Browse	Proteaceae	*Hakea cristata*	0.3	0.0	0.0	-1	0.4	0
Browse	Rhamnaceae	*Trymalium o. odoratissimum*	`	15.5	3.1	-1	14.9	0
Forb	Solanaceae	**Solanum nigrum*	0.0	0.0	0.0	-1	0.0	-1
Browse	Solanaceae	*Solanum lasiophyllum*	0.0	0.0	0.0	-1	0.0	-1
Forb	Stylidiaceae	*Levenhookia pusilla*	0.0	0.2	0.0	-1	0.0	-1
Forb	Stylidiaceae	*Stylidium androsaceum*	0.0	0.2	0.0	-1	0.0	-1
Browse	Thymelaeaceae	*Pimelea argentea*	0.4	0.7	0.0	-1	0.0	-1

Plant			Relative availability (%)		*P. l. lateralis*		*M. fuliginosus*	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Forb	Urticaceae	*Parietaria debilis*	0.7	0.1	0.0	-1	0.0	-1
Forb		Unidentified forb 1	0.3	0.8	0.0	-1	0.0	-1
Forb		Unidentified forb 2	0.0	0.2	0.0	-1	0.0	-1
Forb		Unidentified forb 3	0.0	0.0	0.0	-1	0.0	-1
Forb		Unidentified forb 4	0.0	0.2	0.0	-1	0.0	-1
Forb		Unidentified forb 5	0.0	0.2	0.0	-1	0.0	-1
		Unknown dicots			5.2		3.5	
		Total dicots			**26.3**		**47.8**	
Pteridophyte								
Fern	Pteridaceae	*Cheilanthes austrotenuifolia*	7.2	4.1	7.3	0	7.4	0
Fern	Aspleniaceae	*Pleurosorus rutifolius*	0.1	0.2	0.0	-1	0.0	-1
		Unknown fragments			0.9		2.7	

Functional group: browse = woody trees and shrubs, forb = non-woody herbaceous plants other than grasses, grass = Poaceae family. †Camera trap captured a photo of this being consumed. Ivlev's Selectivity Index: used relative abundance values at the release site only because no scats were found at the new site, -1 = avoidance, 0 = use in proportion to availability, 1 = selection (shaded).