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Ecological specialisation in habitat selection within a macropodid herbivore guild

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Abstract

Specialist species show stronger resource selection, narrower niches, and lower niche overlap than generalist species. We examined ecological specialisation with respect to habitat selection in a macropodid community comprised of the western grey kangaroo *Macropus fuliginosus*, red-necked wallaby *M. rufogriseus* and swamp wallaby *Wallabia bicolor*, in the Grampians National Park, Victoria, Australia. We used radio-tracking to quantify habitat selection. We predicted that because the fitness benefits of generalisation and specialisation differ, there would be a mix of generalised and specialised species in our community. As all three macropodid species show marked sexual dimorphism, we also expected that they should show sex-based specialisation. Finally, because many large herbivores select different habitats for foraging and resting, we predicted that our species would specialise on a subset of their overall selected habitat based on activity period (diurnal or nocturnal). All three species specialised on the available resources to some degree. Western grey kangaroos were specialists, at least during the active period. Niche data for the two wallaby species were harder to interpret, and so we could not determine their degree of specialisation. Within species, we found no evidence of sex-based specialisation. However, we found clear evidence of specialisation by activity period in western grey kangaroos and red-necked wallabies, but not in swamp wallabies. The strength of behavioural decisions made during the foraging period in influencing specialisation points to the likelihood that bottom-up processes regulate this community.

5 key words not included in the title: specialist, generalist, sexual segregation, resource use, foraging

Introduction

There is a fundamental ecological continuum from ‘generalist’ species, which use a broad suite of the available resources, to ‘specialist’ species, which use a narrower subset. Arguments for the fitness benefits of specialisation assume a trade-off in the use of different resources: more effective use of one resource requires reduced effectiveness at using the other (Rosenzweig 1981, Futuyma and Moreno 1988, Poisot et al. 2011). If specialists are more efficient at using a narrower range of resources, why are generalists not excluded? Specialists are favoured under optimal conditions, but in more stochastic environments the costs of being a generalist may be outweighed by the benefits of increased flexibility (Brown 1996, Poisot et al. 2011). Furthermore, the fitness benefits of each strategy show negative density-dependence (Wilson and Yoshimura 1994). For this reason, communities are likely to be comprised of a mix of generalist and specialist species (Rosenzweig 1981, Futuyma and Moreno 1988, but see Julliard et al. 2006).

There are many techniques to estimate the degree to which a species specialises on a given set of resources (Devictor et al. 2010). Measures of niche breadth and overlap offer some of the simplest: specialists have narrow niches, and generalists may show greater niche overlap with specialists than specialists will show with each other (Futuyma and Moreno 1988). Understanding the strength of resource selection, sometimes referred to as the environmental grain size perceived by a species (Brown 1996), is also useful. A fine-grained species uses resources in the proportions they occur because they are either unable to or do not need to discriminate (a low degree of resource selection), whereas a coarse-grained species discriminates and selects only some resources (a high degree of resource selection) (Rosenzweig 1981). Consequently, generalists may coexist with specialists by perceiving their shared environment at a different scale (Morris 1996, Bonesi and Macdonald 2004). For example, generalist American mink (*Mustela vison*) and specialist Eurasian otters (*Lutra lutra*) prefer similar habitats, but mink use habitats unused by otters in sympatry (Bonesi and Macdonald 2004).

Intraspecific specialisation along one resource axis has been reported in over 100 species across a wide range of taxonomic groups (e.g. Bolnick et al. 2003, Patterson et al. 2012, and references within). The broad spatial scale over which specialisations are considered is important, as a species that is a generalist across its geographical range may show local specialisations (Fox and Morrow 1981, Devictor et al. 2010). For example, the red fox (*Vulpes vulpes*) is considered a dietary generalist across its European range, but some populations show specialist foraging behaviour (Russell and Storch 2004). In addition to local specialisations by generalist species (Fox and Morrow 1981), a generalist species may be comprised of specialist sub-groups or individuals (Wilson and Yoshimura 1994, Bolnick et al. 2003). For example, sexual segregation, where males and females use different resources (i.e. habitat or diet), is a form of intraspecific specialisation. Many mammals with pronounced sexual size dimorphism show sexual segregation (Mysterud 2000), and males and females specialise on a subset of the resources used by the species as a whole, for at least some part of the year. Even during the breeding season, when a species is socially aggregated, habitat segregation may be observed. Species may also specialise within the diel period. For example, white-tailed deer (*Odocoileus virginianus*) use closed vegetation types during the day when they are resting, and more open vegetation types at night when they are foraging (Beier and McCullough 1990). These types of specialisations can also be measured by standard niche metrics.

We investigated the extent of ecological specialisation in a macropodid community with respect to both habitat selection and niche breadth and overlap. The community was composed of the western grey kangaroo *Macropus fuliginosus*, red-necked wallaby *Macropus rufogriseus* and swamp wallaby *Wallabia bicolor*, and provides a valuable model for examining ecological specialisation for several reasons. Firstly, phylogeny often affects habitat use (e.g. Lindeman 2000), but nuclear DNA shows that the three species are quite closely related, and could be considered congeneric (Meredith et al. 2008). Secondly, at our study site the vegetation types form a highly heterogeneous mosaic, even at a small scale, so offers significant scope for divergent patterns of habitat selection between specialists and generalists (Kotler and Brown 1988), and for the detection of these patterns. Finally, all three macropodid species show marked sexual size dimorphism (Jarman 1989), and often use different habitats for foraging and resting (e.g. Coulson 1993), so have ample ecological space to show within-species specialisations.

At the interspecific level, we predicted that there would be a mix of generalist and specialist species facilitating coexistence in the Grampians macropod community (Rosenzweig 1981, Futuyma and Moreno

1988), due to the negative density-dependence in the fitness payoff of either strategy (Wilson and Yoshimura 1994). Specialist species will show coarse-grained behaviour (resource selection), whereas generalist species should show fine-grained behaviour (a lower level or no resource selection) (Brown 1996, Morris 1996). Specialist species will have narrower niches than generalists, and generalist species may show niche overlap with specialists and other generalists, but specialists should show little overlap with each other (Futuyma and Moreno 1988). We also expected that there would be intra-specific specialisations (Bolnick et al. 2003). Divergent preferences for resource use between males and females should be apparent over a threshold of 20% difference in body mass (Illius and Gordon 1987). Thus, we expected male and female macropodids to specialise on different subsets of the available resources (Bolnick et al. 2003, MacFarlane and Coulson 2005a). We also predicted that macropodids would specialise on a subset of their overall selected habitat based on whether they were active or non-active.

Materials and methods

Site description and study species

We conducted this study in Victoria Valley, Grampians National Park, south-eastern Australia, between November 2009 and March 2010. This period included the southern hemisphere summer (December to February). The climate is strongly seasonal, with warm dry summers and cool wet winters, and maximum flowering and shoot growth of plants occurs in spring, as dry summer conditions significantly limit plant growth (Specht 1969). Our study period was therefore likely to have coincided with the period of greatest resource limitation for our study species. Victoria Valley is a broad, alluvial plain with poorly-drained, sandy soils. To facilitate macropodid capture, the study site was centred on an unfenced airbase that consisted of two 80 x 800-m grassy runways arranged in a T-shape. The runways were infrequently used but regularly mown to inhibit regeneration of heath species, and supported a low, heterogeneous sward of native and introduced grasses and herbs.

The surrounding vegetation consisted of heathland (low, dense shrub layer and few grasses or herbs) and heathy or shrubby woodland on drier soils. In heathy woodland, the overstorey was dominated by *Eucalyptus* spp., whereas the overstorey in shrubby woodland was composed of *Acacia* species; both supported a diverse range of shrub species, but grasses and herbs were mostly absent. Fertile soils supported open, herb-rich woodlands with a tall *Eucalyptus* spp. overstorey and open grassy clearings containing a high diversity of native and introduced grasses and herbs. Poorly-drained soils supported either damp shrubland or seasonally dry wetlands. Damp shrubland consisted of tall, dense shrubland, with an understorey dominated by smaller shrubs, graminoids and annuals. Seasonally dry wetlands were winter-inundated, nearly treeless, and characterised by large clumps of non-grass graminoids interspersed with patches of largely bare clay. Less-available habitats included the low heathland of the mown airstrip (2% total area), seasonally dry wetlands (2%), herb-rich woodlands (4%) and damp heath (8%); the remaining vegetation types were all more available (>10% total area) (for more details, see Online Resource 1). Abundant free water is available in natural swamps, artificial fire-fighting dams, and an open water supply channel.

Our three study species differ ecologically and morphologically. Western grey kangaroos use heterogeneous habitats (Coulson 1993, Garnick et al. 2014), have grazer dentition (Sanson 1989) and prefer a grass-dominated diet (Coulson et al. 2006, Garnick 2014). Red-necked wallabies use habitats that offer a mix of open grazing areas with patches of denser cover for shelter (Jarman and Calaby 2008, Garnick et al. 2014), have grazer dentition (Sanson 1989) and consume a mixed diet of grass, forbs and browse (Jarman and Calaby 2008, Garnick 2014). Swamp wallabies consistently use dense vegetation, even for foraging (Swan et al. 2008, Di Stefano et al 2009, Garnick et al. 2014), have browser dentition (Sanson 1989) and consume a forb and shrub-dominate diet (Di Stefano and Newell 2008, Garnick 2014). All three species show strong sexual body size dimorphism (Jarman 1989). We collected data during the time period when our study species were socially aggregated for the breeding season, but habitat segregation could still be expected. All three study species are abundant at the study site. Camera trapping surveys in 2011-2012 indicated that all three species were common in the area (Garnick 2014). The vertebrate herbivore community also includes eastern grey kangaroos *M. giganteus* (less common and only associated with specific habitat types), and introduced red deer *Cervus elaphus*, and European rabbits *Oryctolagus cuniculus*.

No management culling of macropodids occurs in the park, and macropodids are otherwise protected from hunting (Parks Victoria 2003). It is likely that predation pressure on macropodids is low in Victoria Valley. Dingoes *Canis familiaris* do not occur in the park (Coulson 1999) and introduced red foxes *Vulpes vulpes*, although present, are kept at low density through an extensive baiting and trapping regime (Parks Victoria 2003). However, in the absence or reduced density of predators, many macropod populations retain anti-predator behaviours (Blumstein and Daniel 2005). The combination of low predation pressure and abundant free water means that our macropodid community is likely to be food-limited, particularly during the summer months.

Macropodid capture and radio-tracking

We captured macropodids between August 2008 and February 2010. We darted western grey kangaroos and red-necked wallabies, using either a Wildvet Pro-medic crossbow or an Injek Model P4 syringe projector while the animals were foraging on the runways. Both devices injected Zoletil (1:1 Zolezapam and Tiletamine) into the hindlimb muscle at a rate of 5 mg/kg. Induction of Zoletil was rapid (5 - 10 min) resulting in immobilisation and anaesthesia for approximately 30 min, and full recovery within 2 h. We also captured red-necked and swamp wallabies using soft-walled double-layered traps described by Di Stefano et al. (2005) and sedated them with Zoletil at the same dose rate. Once each macropodid was immobilised, we marked all adult macropodids with paired colour combinations of Allflex ear tags for identification at a distance. We fitted adults of each species with a lightweight (< 1% of body mass) Sirtrack radio-collar transmitting in the 150 – 151 MHz band.

We radio-tracked macropodids between November 2009 and March 2010. We aimed to locate each radio-collared individual on a randomised schedule at least once in a nocturnal and diurnal period during a two-week tracking session each month. During tracking, we homed in on foot using a portable Australis receiver and hand-held Yagi antenna. We ensured at least 12 h had elapsed between successive fixes on each individual, and did not radio-track during darting to avoid influencing their behaviour through frequent disturbance. We tracked in all weather, and at all times of day and night, and defined whether an animal was active or non-active based on the time of day, as we were not always able to observe their behaviour. This definition was based on a well-established pattern of behaviour in this group of animals (e.g. Southwell 1987, Coulson 1999, Di Stefano et al. 2009). As the three species typically show foraging peaks at dawn and dusk but forage throughout the night, we defined active periods as the time between 2 h prior to sunset and 2 h after sunrise (after Southwell 1987). Macropods may also forage at low intensity throughout the day, or rest during the night, and so some minor temporal mixing of behaviours may have occurred within our two classes of data.

Our analysis of habitat selection relied on accurate locations of radio-tracked macropodids. All collars were fitted with motion-sensitive transmitters, which emitted a different pulse rate depending on whether the animal was active or still. This enabled us to discern if we caused the macropodid to move before sighting it, which would potentially bias habitat selection. We used all fixes with a positive visual identification at close range (5 - 10 m), where we were certain of the exact location of the macropodid. We also used some fixes where we did not achieve visual identification, but the macropodid was estimated to be within 15 - 20 m and the habitat type was homogeneous at this scale.

Habitat use and availability

We defined habitat types using a vector-based GIS layer acquired from the local land management agency. This layer defined different vegetation types based on floristic, structural and ecological features (DEPI 2014). To assess habitat use, we classified the habitat in which each macropodid was located using a map of vegetation types, but reclassified the habitat if the on-ground vegetation did not match the map. In the final dataset, we retained only the locations where we could confidently assign a macropodid to one habitat type, yielding records of macropodids in 13 different habitat types. For analysis, we combined some smaller habitat types based on structural and floristic characteristics into seven more general habitat types (Online Resource 1).

Resource selection occurs when animals use resources disproportionately to their availability (Manly et al. 2002), but defining availability can be challenging (Garshelis 2000). While availability is often defined by the boundaries of the home range (Aebischer et al. 1993, Pita et al. 2011), animals have already made selections about which habitats to include within their home range (Kie et al. 2002). To circumvent this concern, many studies define availability as a circle of particular radius around a biologically-meaningful location (e.g. Kie et al. 2002). For western grey kangaroos and red-necked wallabies we defined availability by drawing the smallest circle that encompassed 100% of an individual’s locations in ArcMap v. 9.3 (ESRI 2009). We then generated 1000 random points within each individual’s circle to estimate availability (after Gillies *et. al* 2006).

We had too few locations per individual for swamp wallabies to define availability in this way (Online Resource 2). Instead, we pooled all data for female and male swamp wallabies into two composite ranges. To represent all radio locations from either females or males on the same scale, we set the furthest south-west location of each individual to the same grid reference in order to indicate how far an ‘average’ male or female swamp wallaby might move. We then used these pooled data for each sex to draw the smallest circle that encompassed 100% of an individual’s locations in ArcMap v. 9.3. Using the raw swamp wallaby data, we calculated the geographic mean centre of the radio locations for each individual wallaby in Ranges7 v. 2.7 (South et al. 2008) and overlaid the circle of predetermined size for the corresponding sex around this location to define availability for that individual. No used locations fell outside of our available radii. We then generated random points for each individual swamp wallaby as described before.

Statistical analysis

We used a generalised linear mixed model (GLMM) with a binomial response variable defined by used (1) and available (0) locations, which is similar to a resource selection function (Gillies *et. al* 2006). We built a series of models comparing the effects of habitat type, sex, and activity period on the response variable, and specified individual as a random effect. We considered additive and interactive combinations of variables. Because we were interested in habitat selection, habitat type was included in all models (Table 1). For each individual, we used the number of used points divided by the number of available points as a weighting variable to rescale the outputs, such that a predicted probability of 0.5 corresponded to habitat use in proportion to availability. We generated estimates using the lme4 package (Bates et al. 2012) run in the R statistical environment (R Development Core Team 2013). For each model, we used Akaike information criteria to compare the relative fit of the five models in the set. Each model received an Akaike weight, which is interpreted approximately as the probability that the associated model is the best in the set. We then used the best model to generate predictions and 95% confidence limits for graphical display.

For analyses of niche breadth and overlap, we determined availability at the study site level. Using Ranges7 v 2.7, we defined our study area as the minimum convex polygon that encompassed 95% of all records of radio-collared animals of all species. The total area was 605 ha. We measured the proportional availability at the study site level of each EVC using Arc Map. We calculated niche breadth using Smith's (1982) FT measure, as it takes resource availability into account (Devictor et al. 2010) and is less sensitive to the inclusion of rare resources than other indices (Krebs 1999). Smith's FT = 0 indicates minimal niche breadth and FT = 1 indicates maximal niche breadth. We calculated niche overlap using Horn's (1966) R_o measure, as it is a symmetrical index which shows very little bias (Krebs 1999). Horn's $R_o = 0$ indicates no overlap and $R_o = 1$ indicates complete overlap. We calculated niche breadth and overlap based on biologically relevant levels identified in the resource selection analysis (between species and between species/activity states). We used PopTools 3.2.5 (Hood 2011) to generate bootstrapped 95% confidence intervals for our estimates of niche breath and overlap based on 10000 permutations of the data.

Results

We captured 6 - 7 individuals of each sex of each species, but radio-tracked individuals for different lengths of time, as some died, some dispersed from the study area, and some radio-collars failed. We collected data on 6 female and 6 male red-necked wallabies, and achieved on average 11.5 ± 1.5 and 12.5 ± 1.4 fixes for each sex respectively. We only collected enough data for 4 female and 4 male swamp wallabies, and achieved on average 6.3 ± 1.0 and 7.3 ± 1.3 fixes for each sex respectively. We collected data on 7 female and 7 male western grey kangaroos, and achieved on average 15.1 ± 1.5 and 12.3 ± 1.3 fixes for each sex respectively (for more details see Online Resource 2). The mean (± SE) mass of each species was: red-necked wallaby = 15.1 ± 1.1 kg, swamp wallaby = 17.4 ± 1.0 kg, western grey kangaroo = 34.1 ± 3.7 kg. Sexual dimorphism in body mass [(average male mass – average female mass)/ average female mass x 100] in western grey kangaroos, red-necked wallabies and swamp wallabies was 112%, 34% and 32% respectively (ratios calculated from study animal data, see Figure 1). In these species, adult males grow faster than females (Jarman 1989), so these data were indicative of the minimum dimorphism in our study animals at the time of our study.

Habitat selection

Swamp wallaby habitat selection was unaffected by sex or activity period (Table 1). Swamp wallabies showed strong selection for shrubby woodland (Figure 2) and avoided (used less than expected) low heathland, sedge-rich wetland and heathy woodland. They used the remaining habitat types in proportion to their availability.

The best model for explaining variation in habitat selection for red-necked wallabies included the interactive effect of habitat and activity period, although the model including habitat as a single predictor also has a moderate degree of support (Table 1). During the active period, red-necked wallabies strongly selected low heathland, and selected sedge-rich wetland to a lesser degree (Figure 3). They avoided sand heathland and heathy woodland, and used the remaining habitats according to their availability. During non-active periods, red-necked wallabies used all habitats in proportion to their availability.

The best model for habitat selection in western grey kangaroos also included the interactive effect of habitat and activity (Table 1). During the active period, western grey kangaroos strongly selected low heathland and used seasonally damp heathy scrub according to its availability (Figure 4). All other habitats were avoided during the active period, except herb-rich woodland, which did not occur within the range of any western grey kangaroos. During the non-active period, western grey kangaroos avoided sedge-rich wetland and used all other habitats according to their availability.

Niche breadth

All three species showed clear habitat selection, as no confidence intervals overlapped 1 (Table 2). Consistent with the AIC results, swamp wallabies showed no change in niche breadth between active and non-active periods. Red-necked wallabies and western grey kangaroos used most available habitats during non-active periods, and used a narrower range of habitats during active periods.

Niche overlap

The three species selected habitats differently from each other (Table 3). Red-necked wallabies overlapped with western grey kangaroos and swamp wallabies to a similar extent, and there was much less overlap in habitat selection between swamp wallabies and western grey kangaroos. Between species, niche overlap tended to be smaller during the active period than the non-active period (Table 3). During both the active and non-active period, red-necked wallabies and western grey kangaroos showed the greatest overlap, and western grey kangaroos and swamp wallabies showed the least. Within species, niche overlap between active and non-active periods was generally high (Table 3). There was moderate evidence that red-necked wallabies and western grey kangaroos selected different habitats based on activity period; swamp wallabies did not show such selection.

Discussion

Our study takes a novel approach by examining specialisation in habitat selection both between and within species in the same community. Specialisation plays a role in structuring the Grampians macropodid community, as all species show some degree of specialisation. It is also evident that habitat selection during the active period (when species are likely to be foraging) is a stronger driver of specialisation than habitat selection during the non-active period (when species are likely to be resting). While western grey kangaroos are clearly specialists during the active period, we cannot readily classify the two wallaby species, as different niche metrics suggest different classifications. These data, in combination with the very low predation pressure at our site, suggest that bottom-up regulation may be operating in this community, at least during the summer period when food resources are likely to be limited.

We predicted that some species in our community would specialise on a subset of the available resources (Rosenzweig 1981, Futuyma and Moreno 1988, Wilson and Yoshimura 1994). Indeed, our results indicate that all three species specialised on particular habitat types; no species was a complete generalist. Quantifying the degree of specialisation was challenging, as our measures of niche breadth and overlap returned contradictory outcomes. Based on their higher degree of habitat selection (coarse-grained behaviour: Brown 1996, Morris 1996), and their narrower foraging niches, western grey kangaroos and red-necked wallabies in our community were more specialised than swamp wallabies. This pattern was particularly evident during the active period. Conversely, patterns of niche overlap indicate that western grey kangaroos and swamp wallabies were more specialised than red-necked wallabies. The only consistent signal was that western grey kangaroos are relative specialists, at least during the active period.

As many species specialise within the suite of resources they can use (Bolnick et al. 2003), we predicted that there would be within-species specialisations in our community based on activity period (active or non-active) and sex. Habitat selection in western grey kangaroos and red-necked wallabies was influenced by activity period, and both species had narrower active than non-active niches. The magnitude of difference may not be large, but both species selected open habitats (low heathland, sedge-rich wetland) for activity and were non-active in most of the available habitats. Despite reports of an effect of activity period on habitat selection by swamp wallabies (Swan et al. 2008, Di Stefano et al. 2009), we found no evidence that this species specialised on a subset of habitat over different activity periods. It is possible that temporal specialisation in our community is affected by the spatial arrangement of non-substitutable resources. Swamp wallabies are typically browsers (Di Stefano and Newell 2008), and the shrubby woodland habitat type that swamp wallabies select at our site likely offered co-occurring food and shelter. Thus, swamp wallabies may not have needed to specialise on habitat types by activity period (see also Di Stefano et al. 2010).

It is widely recognised that scale is of critical importance in predicting and understanding ecological processes (Chave 2013). While both diel (Gutman and Dayan 2005) and seasonal (Kotler and Brown 1988, Schleuter and Eckmann 2008) separation of resource use have been well-reported, less attention has been paid to the effects of temporal scale on specialisation within communities. The mismatch between our predictions and data sheds light on both of these dimensions. Our finding that western grey kangaroos and red-necked wallabies were more specialised during the active period than in the non-active period, which met our prediction of activity-based specialisation, highlights the importance of the temporal dimension of ecological specialisation. While we predicted that sex would affect habitat selection, the surprising lack of this effect further highlighted the temporal dimension of specialisation. Other studies of large herbivores similarly report no sex-related differences in resource use (reviewed in Mysterud 2000). However, these were probably due to a modest degree of sexual dimorphism (Illius and Gordon 1987, Mysterud 2000), which did not apply in our system. Our macropodids were highly sexually size dimorphic (Jarman 1989, Fig. 1), particularly compared to ungulates, in which most studies of sexual segregation have been conducted. A more likely explanation is that our study was conducted over the breeding season (Dawson 2012), when the sexes were expected to be aggregating. Western grey and red kangaroos elsewhere show sexual segregation in habitat use in the non-breeding season, but not in the breeding season when they are socially aggregated (MacFarlane and Coulson 2005b). For this reason, it is important to consider not only whether specialisation occurs between the sexes, but also how this might vary across different age and reproductive classes.

There is little consistency in the literature in the use of measures of niche overlap and breadth in analyses of ecological specialisation. Some authors measure breadth only (Russell and Storch 2004, Peers et al. 2012), some overlap only (Schleuter and Eckmann 2008, Pita et al. 2011), while others report both (Pianka 2014). Our data demonstrate how these two measures generate different conclusions (see also Russell and Storch 2004). For example, two species in a community of interest might use a similar yet narrow range of the available resources. An analysis of niche breadth would assign them as specialists, but an analysis of niche overlap would classify them as generalists. These inconsistencies between niche measures highlight the importance of using multiple niche measures in studies of this type, as interpreting the level of specialisation depends on the response variable under consideration (Devictor et al. 2010, Peers et al. 2012). Furthermore, calculating error estimates for niche measures is crucial (Krebs 1999, Pita et al. 2011), but often ignored (e.g. Schleuter and Eckmann 2008, Pianka 2014). Our conclusions would have been substantially different had we not calculated error estimates.

A combination of top-down processes like predation pressure, and bottom-up processes like forage quality and availability, typically regulate herbivore populations (Sinclair and Krebs 2002). Given that foraging resources are typically more limited than resting resources (Schoener 1971), and predation pressure is low at our site, it is likely that bottom-up processes are more important in our study system, at least during summer when resources are likely to be limited. The influence of the active period in specialisation by western grey kangaroos, and potentially by red-necked wallabies, indicates that foraging is the key to structuring our herbivore community. Our data also highlight the roles of multiple temporal dimensions in shaping ecological specialisation in this herbivore community.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical Approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. This work was conducted under The University of Melbourne's Faculty of Science, School of Land & Environment, and Optometry & Vision Sciences Animal Ethics Committee project number 0810628 and the Department of Sustainability and Environment permit numbers 10004582, 10005421 and 10006116.

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Tables

Table 1 Candidate models and Akaike weights for macropodid habitat selection at the study site in Victoria Valley, Grampians National Park. The best model is indicated by Δ AIC = 0, and Akaike weight is the probability that the associated model is the best in the set.

Species	**Model**	**Δ AIC**	**Akaike weight**
Swamp wallaby	Habitat	0.000	0.879
	Null	4.000	0.119
	Habitat*activity	13.300	0.001
	Habitat*sex	13.400	0.001
	Habitat*sex*activity	37.500	0.000
Red-necked wallaby	Habitat*activity	0.000	0.809
	Habitat	2.900	0.190
	Habitat*sex	14.400	0.001
	Habitat*sex*activity	20.200	0.000
	Null	26.400	0.000
Western grey kangaroo	Habitat*activity	0.000	0.782
	Habitat	3.200	0.158
	Habitat*sex*activity	6.000	0.039
	Habitat*sex	7.200	0.021
	Null	48.600	0.000

Table 2 Smith's niche breadth (FT) in macropodid habitat selection by three species at the study site in Victoria Valley, Grampians National Park. FT calculated for habitat selection across the diel period, then within active and non-active periods separately. FT is represented as means with bootstrapped 95% confidence intervals below in italics.

Time period	**Red-necked wallaby**	**Swamp wallaby**	**Western grey kangaroo**
All	0.85 *0.81 – 0.88*	0.87 *0.81 – 0.92*	0.84 *0.81 – 0.87*
Active	0.68 *0.63 – 0.75*	0.83 *0.73 – 0.89*	0.72 *0.64 – 0.76*
Non-active	0.95 *0.92 – 0.97*	0.83 *0.74 – 0.89*	0.94 *0.90 – 0.96*

Table 3 Horn's niche overlap (H_0) for selection of habitat types by three species of macropodid at the study site in Victoria Valley, Grampians National Park. H_o was calculated between activity states within and between species, represented as means with bootstrapped 95% confidence intervals below in italics. H_0 is symmetrical, such that the extent to which A overlaps B is the same as B overlaps A. Reciprocal or biologically meaningless comparisons indicated by –. If the confidence interval includes 1, complete overlap in resource use is indicated.

	RN non-active	**SW active**	**SW non-active**	**WG active**	**WG non-active**
RN active	0.76 *0.66 – 0.84*	0.56 *0.44 – 0.66*	–	0.72 *0.65 – 0.78*	–
RN non-active	–	–	0.77 *0.63 – 0.88*	–	0.81 *0.76 – 0.86*
SW active	–	–	0.95 *0.87 – 1.00*	0.36 *0.23 – 0.45*	–
SW non-active	–	–	–	–	0.56 *0.41 – 0.69*
WG active	–	–	–	–	0.81 *0.73 – 0.88*

RN = red-necked wallaby, SW = swamp wallaby, WG = western grey kangaroo

Figure legends

Figure 1. Mass of macropodids radio-tracked for analysis of habitat selection in Victoria Valley, Grampians National Park, Australia. Boxes show median and spread of data, whiskers indicate outer 25% quartiles, asterisks represent outliers. RN = red-necked wallaby, SW = swamp wallaby, WG = western grey kangaroo.

Figure 2. Habitat selection by swamp wallabies at the study site in Victoria Valley, Grampians National Park. When probability of use = 0.5, a habitat type is used equal to availability. Probability of use > 0.5 indicates selection for, and probability of use < 0.5 indicates selection against a vegetation type. Error bars show 95% confidence intervals.

Figure . Habitat selection by red-necked wallabies at the study site in Victoria Valley, Grampians National Park, Australia separated by activity period. When probability of use = 0.5, a habitat type is used equal to availability. Probability of use > 0.5 indicates selection for, and probability of use < 0.5 indicates selection against a vegetation type. Error bars show 95% confidence intervals.

Figure 4. Habitat selection by western grey kangaroos at the study site in Victoria Valley, Grampians National Park, Australia separated by activity period. When probability of use = 0.5, a habitat type is used equal to availability. Probability of use > 0.5 indicates selection for, and probability of use < 0.5 indicates selection against a vegetation type. Error bars show 95% confidence intervals.

Figures

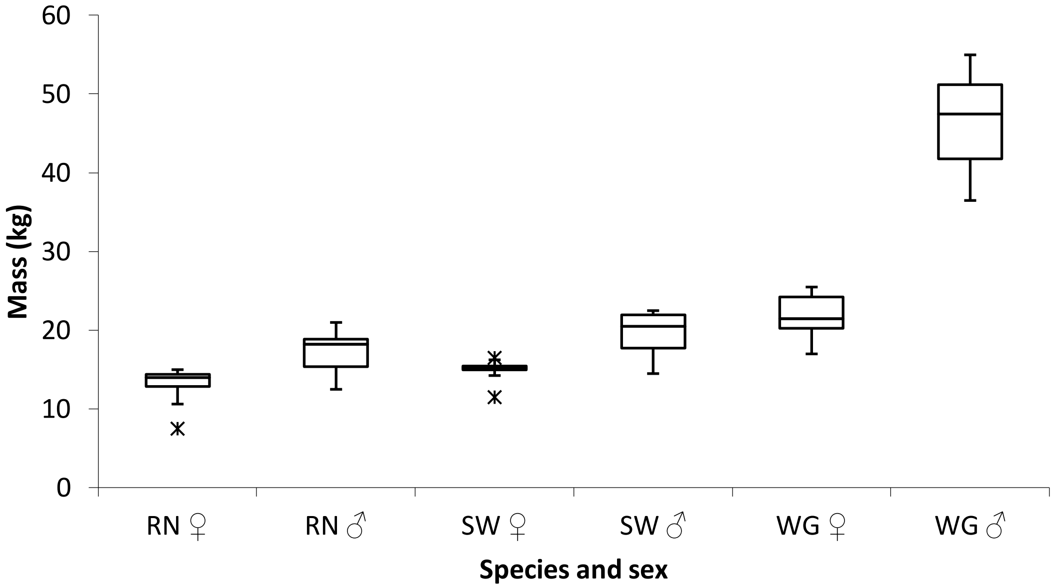
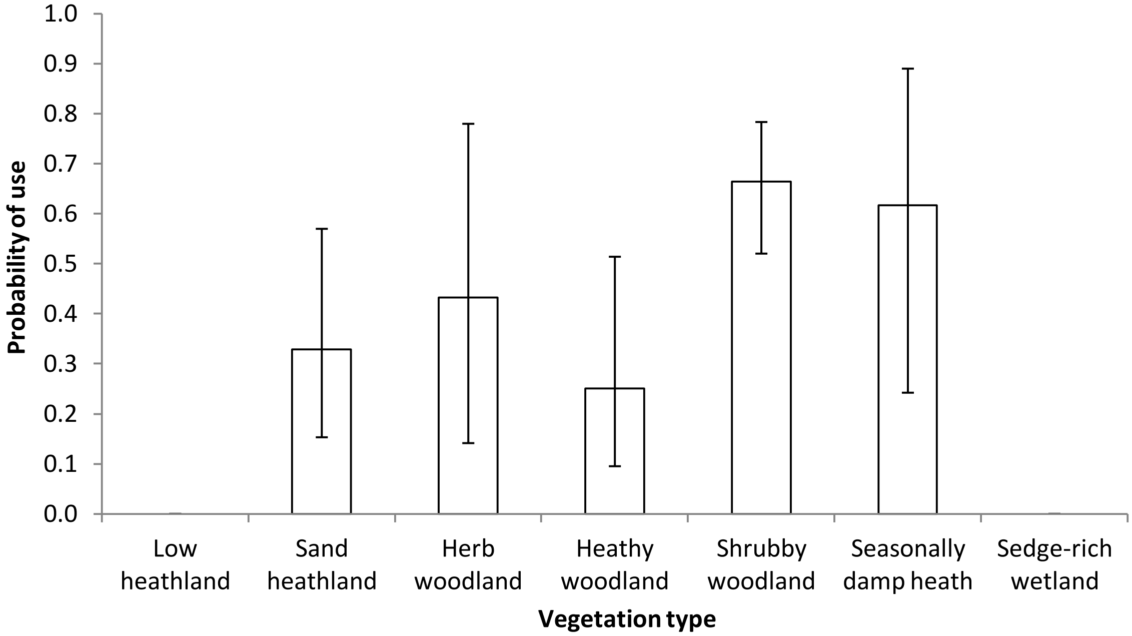


Figure 1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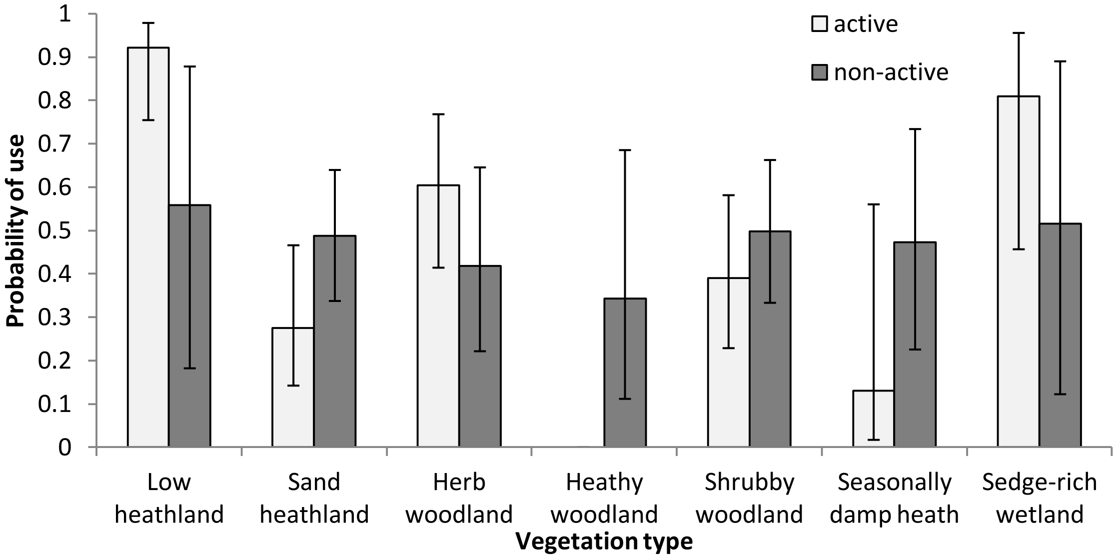
Probability of use
Low heathland
Sand heathland
Herb woodland
Heathy woodland
Shrubby woodland
Seasonally damp heath
Sedge-rich wetland
Vegetation type

Figure 2



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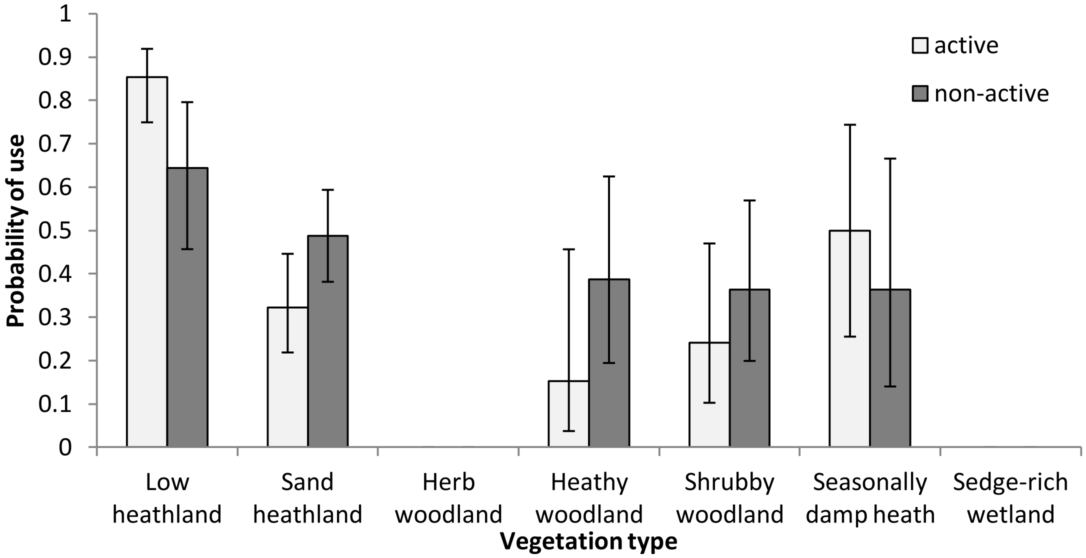
Probability of use
☐ active
▨ non-active
Low heathland
Sand heathland
Herb woodland
Heathy woodland
Shrubby woodland
Seasonally damp heath
Sedge-rich wetland
Vegetation type

Figure 3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Probability of use
active
non-active
Low heathland
Sand heathland
Herb woodland
Heathy woodland
Shrubby woodland
Seasonally damp heath
Sedge-rich wetland
Vegetation type

Figure 4