Density dependence in foraging habitat preference of eastern grey kangaroos

Daniel Ramp and Graeme Coulson

For a free-ranging forager, the suitability of a patch is dependent on population density, resource supply, resource quality, and the costs of foraging or dispersal. We quantified differences among three foraging habitats and compared this variation to temporal patterns of habitat preference by free-ranging eastern grey kangaroos, *Macropus giganteus*. We investigated selection on a fine-grained spatial scale, and asked whether habitat preference is constrained by density-dependent mechanisms. Variation in the quantity and quality of resources among habitats was greatest during spring, when biomass and quality were highest, and differences among habitats were most pronounced. However, consistent and discernable differences among habitats were not obtained, indicating that the system fluctuated around an equilibrium state. Using isodar regressions to examine the consumer-density relationships among habitats, open-woodland habitat was favoured over the two open-forest habitats for foraging. Seasonal isodars indicated that density dependence regulated preference between the three foraging habitats during autumn, spring and summer, but not during winter, when variability in resources among habitats was lowest.

D. Ramp and G. Coulson, Dept of Zoology, Univ. of Melbourne, Victoria 3010, Australia (present address DR, Inst. of Wildlife Research, School of Biological Sciences, Univ. of Sydney, New South Wales 2006, Australia [dramp@bio.usyd.edu.au]).

A common framework for addressing the relationships between animals and resources, as well as modelling the selection of habitat, stems from optimal foraging and ideal free distribution (IFD) theories (Orians 1969, Fretwell and Lucas 1970). The implicit assumption made by combining these theories is that in environments where habitats vary in the quantity and quality of resources, animals will disperse among habitats to maximise their resource gain, and hence, their reproductive fitness (Fretwell and Lucas 1970, Maynard Smith 1982, Morris and Davidson 2000). For a free-ranging forager, the selection of habitat, at both large ('dispersal') and small ('foraging') scales (sensu Morris 1992), depends upon population density, resource supply, resource quality, and the costs of foraging or dispersal (Rosenzweig 1981, Morris 1987). Habitats are inherently patchy, and can be classified in terms of the quantity and quality of resources they contain (Mor-

rison and Hall 2001). As individuals have the opportunity to move among habitat patches, it is likely that selection of patches varies with population density (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1988). With this in mind, comparison of animal dispersion at both dispersal and foraging scales can provide detailed information on both spatial and temporal variation in habitat selection. This information is critical, as there is currently a lack of understanding of how animals, especially large free-ranging mammals, select habitat at different scales. In addition, little is known about how animals vary their selection of foraging habitat temporally, particularly at the foraging scale.

While the theoretical implications of habitat selection theory are clear, observing these patterns in natural populations has proven elusive (Orians and Wittenberger 1991, Morris 1994). Various analytical procedures have been developed to address this, in essence to

evaluate the effects of density dependence and resource variability on habitat selection (Morris 1987, Pulliam 1988). One such technique, termed isodar analysis, models the distribution of animals among habitats, and seeks to predict variation in the distribution of individuals among habitats at various population densities (Morris 1987, 1988, 1992, Knight and Morris 1996). Isodar analysis enables the investigation of habitat preference by making distinctions between density-dependent and density-independent selection (see Morris 1987, 1988). A significant regression slope of animal density between two habitats of differing suitability implies density-dependent selection. Slopes can also be used to indicate whether habitats vary qualitatively (efficiency of resource use) and/or quantitatively (resource abundance), relative to the foraging species. The technique is suited to distinguishing between different scales of selection, and can be utilised to examine temporal variation in habitat selection.

Isodar analysis has proven fruitful for a range of animal species, with the majority of this work focussing on small mammals (Ovadia and Abramsky 1995, Knight and Morris 1996, Abramsky et al. 1997, Morris 1997, Morris et al. 2000, Shenbrot and Krasnov 2000) but has also included other animals such as stream salmonids (*Salmo salar*) (Rodríguez 1995). To date, no studies have investigated isodars of medium- to large-sized animals. In addition, the impact of seasonality in selection at foraging scales has been ignored.

This paper redresses the lack of research examining habitat selection at small scales, especially with regard to free-ranging foragers. It does this by employing isodar models to investigate habitat selection by eastern grey kangaroos (*Macropus giganteus* Shaw) at the foraging scale. Most of the previous research examining the distribution of kangaroos (*Macropus* spp.) in relation to habitat in Australia has been conducted at the dispersal scale, and has primarily focussed upon correlating vegetation and other environmental parameters with density, exploring population dynamics, regulation of growth rates and carrying capacities (Caughley 1964a, Hill 1981b, Taylor 1984, Priddel 1987, Coulson 1993b, Southwell et al. 1999). This consumer-resource dynamic approach has established that environmental parameters, particularly rainfall, are integral in regulating population growth, at least in semi-arid systems (Caughley et al. 1984, Bayliss 1985, Cairns and Grigg 1993). With their high mobility, complex temporal dynamics, and preference for high quality forage, kangaroos have also been shown to exhibit density-dependent effects at the dispersal scale (Cairns and Grigg 1993, McCarthy 1996). At this scale, the landscape is comprised of a dynamic array of shelter, forage and water resources (McAlpine et al. 1999), which are variously used by kangaroos in relation to seasonal conditions (Bailey 1971, Priddel 1987, Coulson 1993a, Norbury et al. 1994). Dispersion at the dispersal scale is therefore described by both environmental stochasticity and density dependence (Cairns 1989). Selection of habitat at the foraging scale, however, has received little attention.

This paper aims to assess the applicability of isodar models for large economically significant animals such as kangaroos. It rigorously tests isodar theory by simultaneously measuring habitat quality, so as to corroborate the predictions of the models. It does this principally at the foraging scale, although comparisons with dispersal scale parameters are also considered. Finally, it examines the behavioural mechanisms influencing the selection of habitat by eastern grey kangaroos, and determines whether habitat preference varies with density dependence at the foraging scale, and how this varies on a temporal basis.

Methods

Study area

We conducted the study within the Yan Yean Reservoir Catchment (37° 32′ S, 145° 09′ E), approximately 40 km north-east of Melbourne, Victoria, Australia. This semi-rural water catchment encompasses 2,250 ha of land, with a water body covering an area of 560 ha when filled to capacity (MMBW 1989). As a southern extension of the Kinglake Plateau, the catchment forms a system of undulating hills which are surrounded by farmland. It is closed to the public, with access prevented by a 1.8 m 'Cyclone' chain-mesh security fence (Coulson et al. 2000).

Since quantitative measurement began in 1961, the density of eastern grey kangaroos has been recorded at relatively high levels, ranging from 1770 to 3000 individuals (at either 1.05 or 1.78 individuals per hectare respectively). The kangaroos are effectively competitor free, with only around 20 swamp wallabies (*Wallabia bicolor*), an almost complete absence of rabbits (*Oryctolagus cuniculus*) and the continual removal of predators (mainly dogs) by catchment managers (Ecoplan 1995). As a result, kangaroos are relatively free to select habitat that maximises their access to quality forage.

The vegetation inside the catchment exists as a patchy matrix of remnant and disturbed open-woodland and open-forest communities. These communities were quantitatively segregated into four vegetation habitats on the basis of floristic composition and their level of disturbance (Ramp 2001): Disturbed Open-Woodland (DOW), Disturbed Open-Forest (DOF), Intact Open-Forest (IOF) and Aquatic Verges (AV). The AV habitat was not used in this study as it is periodically flooded. The remaining three habitats contain a mosaic of patches from which kangaroos preferentially forage, regardless of habitat, as indicated by the volume of pellets deposited in these areas when compared to the surrounding area. These foraging patches consist of

structurally open regions of vegetation, and have a low sward of both herbaceous and grass species. Among the habitats foraging patch size varies. The largest patches (up to 100 m^2) occur in DOW, while the smallest (around 20 m^2) occur in IOF. DOF patches are of an intermediate size. The patches also vary in their abundance and occurrence within each of the habitats. In DOW, the patches are distributed in chains, with patches consistently adjacent to one another. In DOF, the patches also form chains but they tend to be smaller and vegetation blocks visibility between patches. Patches within the IOF habitat do not form chains, and are distributed haphazardly. All patches, regardless of habitat, are connected by well-worn tracks created by kangaroos, which run within and between habitats.

Sampling methodology

We selected an area of the catchment for study which had patches representative of all three habitats adjacent to one another. The western side of the catchment satisfied this criterion, as well as possessing the highest kangaroo densities within the catchment area (Coulson et al. 2000). Observation of tagged kangaroos established that movement among habitats was common, with some individuals being observed to forage in patches from each of the habitats on different occasions. A total of 20 permanent sampling points were positioned haphazardly in patches within each of the habitats. Resources were estimated by measuring the quantity and quality of grass plant species from six 0.25-m^2 replicate plots, taken at random within 2 m of each sampling point. A comparative yield technique was used to estimate the standing crop of biomass, as destructive sampling, although more precise, is not practical when sampling permanent sampling points (Catchpole and Wheeler 1992). The comparative method works by comparing the biomass of replicates to a series of photo-standards of known biomass, distributed along a graduated scale (Haydock and Shaw 1975, Friedel and Bastin 1988, Friedel et al. 1988, Norbury et al. 1993). To assess forage quality, a five-point grass 'greenness' scale was used to visually assess replicates, as plant quality (protein content) has been previously linked to moisture content and plant greenness (Bailey et al. 1971, Denny 1980, Southwell 1987). Forage quality was inferred from the colour of the foliage (yellow equals low quality, green equals high quality) and from the health of the foliage (structural integrity, signs of disease and damage). Forage quality was measured as values ranging between 0 and 1, where 0 represented 'very poor' quality and 1 represented 'excellent' quality. Seven categories were recorded: 0, 0.125, 0.25, 0.50, 0.75, 0.875 and 1. Sampling was repeated seven times over a period of ten months on the following dates: 12 March 1998, 1 April 1998, 14 June 1998, 29 September 1998, 29 October 1998, 3 December 1998 and 7 January 1999.

To estimate the use of foraging patches by eastern grey kangaroos, kangaroo abundance was estimated in the 20 foraging patches in each of the three habitats, between March 1998 and March 1999. As direct measurement of kangaroo numbers was impossible to obtain, faecal pellet deposition rates were estimated at each sampling point. The number of pellets deposited provides an indication of the amount of time spent foraging by kangaroos, as they primarily defaecate while feeding (Southwell 1989). Following the methodology of Hill (1981a), 10-m^2 circular plots were situated at each of the sampling points, and faecal pellets were counted and cleared on 18 occasions, every two to three weeks. Individual pellets, rather than pellet groups, were chosen as the preferred method of measurement. Individual pellets have been shown to be more reliable in high density systems (Coulson and Raines 1985), and pellet groups have proven problematical in the past (Perry and Braysher 1986, Johnson and Jarman 1987).

Statistical methodology

For all comparisons of above-ground biomass and quality of grasses, one-way analysis of variance was used to differentiate among habitats at each sampling time. Post-hoc analyses exploring the differences among habitats were conducted using the Student-Newman-Keuls statistic.

Preferential selection of foraging habitat by eastern grey kangaroos was investigated using isodar analysis. In isodar analysis, both the slopes of the significant isodar regressions and their y-intercepts are examined in order to obtain information on the mechanisms underlying preference for habitats. If the isodar slope comparing two habitats does not significantly differ from one, the habitats are considered to differ only in the abundance of resources available in each (i.e. quantitatively). If the slope is significantly greater than one, the habitats are considered to differ in the efficiency of foraging individuals that are present in each (i.e. qualitatively). Y-intercepts significantly greater than zero give an indication of the relative differences in habitat suitability perceived by consumers (see Morris 1987, 1988). Isodar regressions were calculated using the pellet densities between each pair of habitats. Mean deposition rates calculated from the 20 replicates in each habitat were used to determine isodar relationships. Isodar regressions were also calculated for each season to explore the lack of fit of some samples. To determine whether the slopes were above, below or equal to one, the 95% confidence intervals around the slopes were calculated.

Results

Resource availability and quality

Above-ground grass biomass differed significantly among habitats at each sampling date (Fig. 1a). In late summer and autumn (February through May), grass biomass was significantly greater in IOF than in the two disturbed habitats (Table 1). While the available biomass remained in both the open-forest habitats during winter (June through August), biomass in DOW was significantly lower, although the actual difference in means were relatively small. With the coming of spring (September through November), the available grass biomass increased, and differences were evident among all habitats. At this time, DOF had the highest quantity of grass biomass available while IOF habitat the lowest. In the summer of 1998–99, available biomass decreased from spring levels and was significantly lower in IOF. Significant differences in grass quality among habitats were apparent only during spring (Fig. 1b). In September, quality was lowest in IOF and highest in DOW, whereas grass quality in IOF was significantly greater than in the two disturbed habitats at the end of October (Table 1). In general, the temporal variation in grass quality was similar to that of the availability of grass, but there was little variation among habitats.

Habitat preference

Faecal pellet deposition rates indicated that eastern grey kangaroos preferentially selected habitat at the microhabitat scale (Fig. 2). Average deposition in DOW consistently outranked the other two habitats,
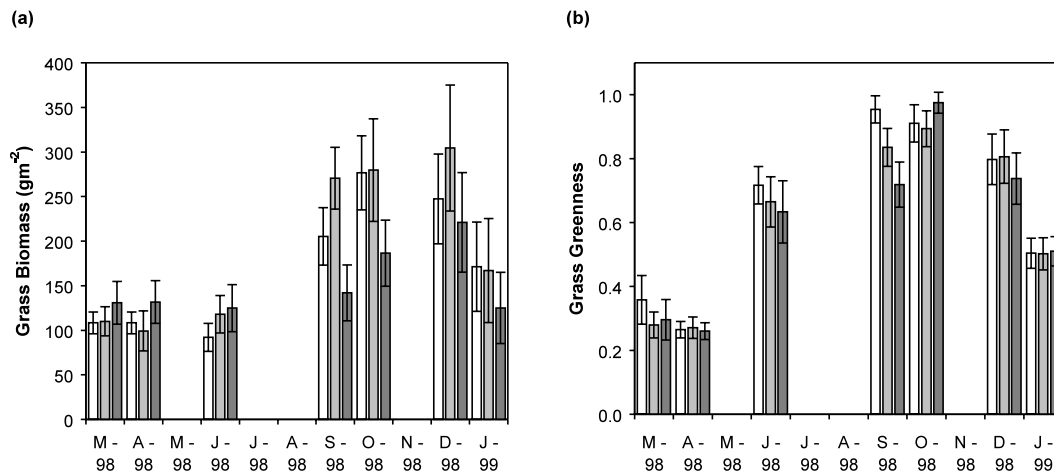

Fig. 1. Change in mean grass biomass (a) and grass greenness (b) in each habitat at seven sampling times, from March 1998 to January 1999. The three habitats are represented as DOW = □, DOF = ▒ and IOF = ■. Error bars represent 95% confidence intervals.

Table 1. One-way ANOVA of log-transformed above-ground biomass and arcsine-transformed forage quality among habitats for each sampling time. Significant differences at 0.05 levels are indicated with an asterisk. Post-hoc analyses were conducted for each sampling time; habitats are ranked from lowest to highest, those not significantly different are identified by = , while those significantly different are identified by <.

Resource	Sampling date	F	p	SNK
Grass quantity	12/3/98	4.061	0.023*	DOW = DOF < DOF = IOF
	30/3/98	5.498	0.007*	DOF = DOW < DOW = IOF
	14/6/98	5.384	0.007*	DOW < DOF = IOF
	29/9/98	26.483	<0.001*	IOF < DOW < DOF
	29/10/98	11.801	<0.001*	IOF < DOW < DOF
	3/12/98	3.251	0.046*	IOF = DOW < DOW = DOF
	7/1/99	3.207	0.048*	IOF = DOF < DOF = DOW
Grass quality	12/3/98	2.572	0.085	DOF = IOF = DOW
	30/3/98	0.398	0.673	IOF = DOW = DOF
	14/6/98	2.103	0.131	IOF = DOF = DOW
	29/9/98	28.929	<0.001*	IOF < DOF < DOW
	29/10/98	5.751	0.005*	DOF = DOW < IOF
	3/12/98	1.357	0.266	IOF = DOW = DOF
	7/1/99	0.057	0.945	DOF = DOW = IOF

Fig. 2. Mean faecal pellet deposition rate (m^{-2} day^{-1}) in each habitat over time, from March 1998 to April 1999. The three habitats are represented as DOW = ♦, DOF = ■ and IOF = ●. Error bars represent 95% confidence intervals.
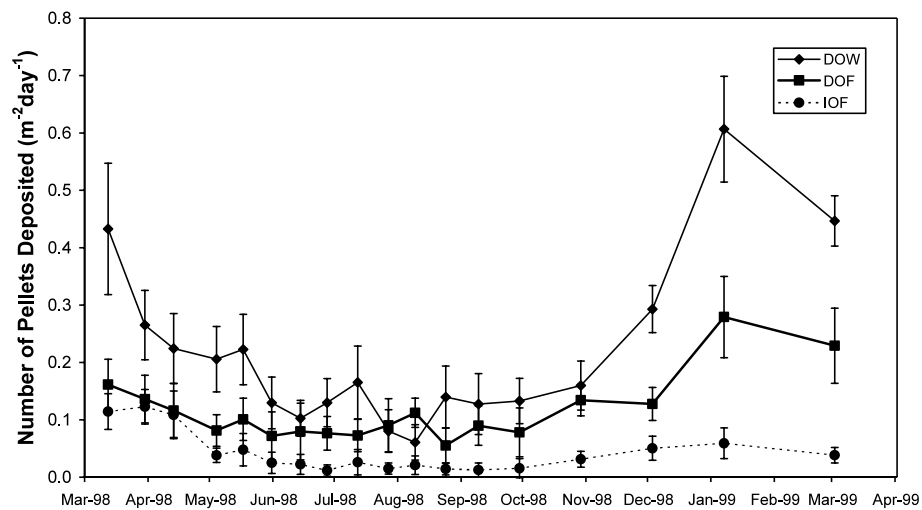
Table 2. Isodars contrasting pellet deposition rates in DOW, DOF and IOF habitats. Results of linear regression are presented for all sampling times and separated into seasons. Significant regressions at 0.05 levels are marked with an asterisk. Slopes which were significantly above, below or equal to 1 and y-intercepts (constants) significantly different from zero are also marked with an asterisk. Upper (UCI) and lower (LCI) 95% confidence intervals are included for both slopes (S) and constants (C).

Contrast	Season	R^2	F	N	Slope	S LCI	S UCI	Constant	C LCI	C UCI
DOW v DOF	ALL	0.810	68.062*	18	2.255*	1.676	2.834	−0.044	−0.119	0.031
DOW v IOF	ALL	0.295	6.701*	18	2.186	0.396	3.977	0.124*	0.025	0.223
DOF v IOF	ALL	0.175	3.387	18	0.671	−0.102	1.444	0.087*	0.044	0.130
DOW v DOF	AUT	0.846	21.969*	6	2.756*	1.123	4.388	−0.060	−0.249	0.128
DOW v DOF	WIN	0.704	9.526*	6	−1.717*	−3.261	−0.172	0.252*	0.124	0.380
DOW v DOF	SPR/SUM	0.934	56.507*	6	2.363*	1.490	3.236	−0.075	−0.226	0.076
DOW v IOF	AUT	0.487	3.801	6	1.619	−0.687	3.925	0.123	−0.075	0.322
DOW v IOF	WIN	0.012	0.050	6	0.785	−8.921	10.490	0.099	−0.086	0.284
DOW v IOF	SPR/SUM	0.714	9.962*	6	8.935*	1.075	16.795	−0.014	−0.317	0.288
DOF v IOF	AUT	0.819	18.129*	6	0.701	0.244	1.158	0.058*	0.019	0.097
DOF v IOF	WIN	0.043	0.180	6	0.713	−3.957	5.384	0.068	−0.021	0.157
DOF v IOF	SPR/SUM	0.617	6.451	6	3.399	−0.316	7.114	0.039	−0.104	0.182

except for two sampling times in August 1998 when average deposition in DOF ranked higher. Average deposition in IOF consistently ranked lowest throughout the period of the study. The amount of time spent grazing by kangaroos on the foraging patches varied over time. Use was lowest during winter and spring, while deposition rates increased in all habitats during summer, tailing off during autumn. Seasonal variation in deposition rates varied most in DOW, ranging from 0.1 to 0.6 pellets m^{-2} day^{-1}, while variation in DOF and IOF was not as extreme.

Isodar analysis

Isodar regressions were analysed over all sampling times and separately for each season (Table 2, Fig. 3). Across all seasons, density-dependent habitat selection was evident between DOW and the other two habitats, but not between DOF and IOF habitats ($p > 0.05$). Given the low power of the test (0.445) and its p-value at less than 0.10, it is plausible that density-dependent habitat selection of foraging patches is also occurring between these two habitats. Significantly different y-intercepts from zero were determined for DOW/IOF and DOF/IOF regressions. This suggests that at low kangaroo density, eastern greys preferentially select against IOF. The DOW/DOF regression returned a non-significant y-intercept, while the slope of the regression line was significantly greater than 1. The reverse was true for the DOF/IOF isodar, where the y-intercept was significantly greater than zero and the slope was not significantly greater than one.

Seasonal isodars were calculated to examine habitat selection at different times of the year, where data for spring and summer were combined due to a paucity of samples during this period (Table 2). Season was in-

cluded as a predictor variable in a multiple regression comparison of the density relationships among habitats. Season was significant in multiple regressions between DOW/IOF ($p = 0.023$) and DOF/IOF ($p = 0.003$), but not for DOW/DOF ($p = 0.135$). Examining the influence of season in more detail by subdividing the data into seasonal blocks, striking differences in the regression relationships among habitats were apparent among seasons. The DOW/DOF density regressions exhibited significant positive relationships with slopes greater than one during autumn and spring/summer.
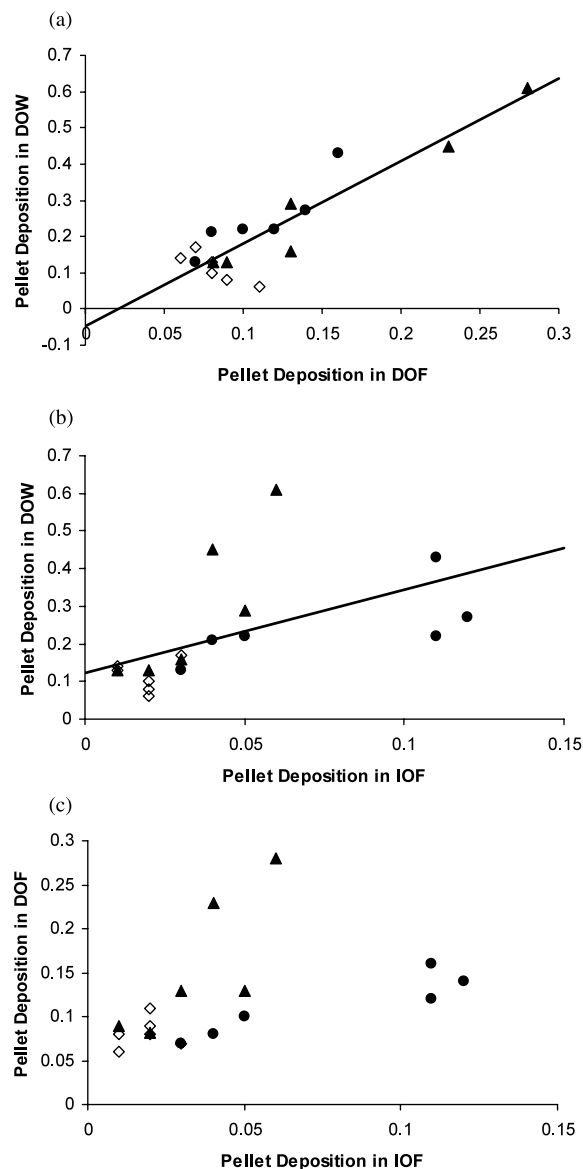

Fig. 3. Density regressions displaying isodars across all sampling times. Isodars comparing DOW to both DOF and IOF were significant at 0.05, while the regression comparing DOF and IOF was not significant. The three seasons are represented as autumn = ●, winter = ▲ and spring/summer = ◇.

During winter, a significant negative relationship was observed, suggesting that selection of preferred habitat during this time was not density-dependent, and perhaps density-independent. A similarly unusual seasonal pattern was evident when comparing DOW and IOF habitats. In autumn, the positive regression was not significant, although the power of this test was poor (0.451). A non-significant regression slope was also evident in winter, where varying densities in DOW were not matched by similar changes in the densities in IOF. However in spring/summer, density-dependent selection occurred, with preference greatly biased in favour of DOW. Seasonal isodar regressions between DOF and IOF habitats exhibited significant regression slopes only during autumn. Slopes during autumn and spring/summer were not significantly different from one, while in winter, no relationship between the densities in each of the habitats was apparent.

Discussion

Resource availability

Availability of quality forage at Yan Yean varied both spatially and temporally at the foraging scale. During spring, when biomass levels were at their highest for the year, forage was most abundant in DOF, while during autumn and winter, forage was generally most abundant in IOF. Similarly, the quality of forage differed little among habitats except during spring, when the quality was highest in DOW in early spring and highest in IOF in late spring. Variation in resource availability can therefore be characterised as occurring mostly during the growing season, when biomass levels are at their highest, quality is at its highest, and differences among habitats are the most pronounced.

This variation in resource availability among habitats has implications for the foraging strategies of eastern grey kangaroos. Eastern grey kangaroos are grazers, foraging primarily on grass (Jarman and Phillips 1989, Duncan 1992, Woolnough and Johnson 2000). It is therefore likely that differences in resources between foraging patches will lead to differences in the time spent grazing at each patch. Better patches will also attract more consumers, leading to a decrease in the availability of forage.

Habitat selection

In order to interpret the preferential selection of habitat by eastern greys, it is useful to examine both spatial and temporal trends at both foraging and dispersal scales. At the foraging scale, the population of kangaroos at Yan Yean can be considered 'closed', where the population is not influenced by dispersal and conforms to the

398

assumptions of an 'ideal' and 'free' distribution (Fretwell and Lucas 1970). Under this foraging-scale scenario, significant differences in kangaroo density among habitats can be considered as genuine preferential selection on the basis of resource availability. Analysis of pellet deposition rates confirmed that eastern greys preferred DOW for foraging over the other two habitats, with IOF preferred the least. This ranking was maintained throughout the year except for a short period in winter, when deposition rates in DOF ranked higher than DOW.

Given the restrictive nature of this scenario, selection of habitat at the foraging scale becomes dependent upon a variety of parameters. Selection processes depend upon the species in question and its environment, and are constrained by the time taken to explore and gather information about the suitability of each habitat (Orians and Wittenberger 1991, Holmgren 1995), by social pressure from conspecifics (Caraco and Giraldeau 1991, Roguet et al. 1998), by pressure from predators (Sinclair and Pech 1996, Abramsky et al. 1997), by movement among habitats, and ultimately by the accessibility of forage (Orians and Wittenberger 1991). Selection processes may also vary temporally. On a fine temporal scale, individuals may make daily movements among available habitats (Caughley 1964b, Southwell 1981, Priddel 1986, Clarke et al. 1989). On a coarse temporal scale, individuals may make selection decisions on a seasonal basis (Priddel 1986, Coulson 1993b). With the data examined at the foraging scale, selection of habitat by eastern greys at Yan Yean conformed to the changing resource attributes of the habitats during the period of the study. This suggests that they are not only aware of the variability in resources on foraging patches from the three habitats, but that they are able to assess the costs and benefits of moving among patches, particularly in relation to exploitation of resources by conspecifics. They were also able to modify their selection criteria depending on the quality and quantity of the resources as they varied among seasons.

But the magnitude of habitat preference was not the only variable to fluctuate over time; total deposition rates among habitats also varied. By treating the system 'closed' at the foraging scale, it is assumed that the total deposition rate among habitats should not vary. Without incorporating dispersal, the significant variation observed in deposition rates must be caused by either changing behavioural responses and/or demographic trends. Eastern grey kangaroos have been reported to increase their frequency of movement during foraging in summer (Southwell 1981, Clarke et al. 1989), presumably to find shelter for thermoregulation and to enhance encounter rates with high quality forage. Eastern greys have also been shown to spend more time foraging during winter

than summer. These seasonal patterns of movement and foraging are likely to have some impact on deposition rates among seasons. Frequent movement in summer would result in a more even deposition of faecal pellets within a foraging patch, while less faecal pellets would be deposited as less time is spent foraging. While studies of the defaecation rates of eastern greys have so far not incorporated seasonal variation (Hill 1978, Coulson and Raines 1985, Johnson et al. 1987), trends from similar species suggest that defaecation rates become significantly lower during summer (Southwell 1989). However pellet deposition rates in all three habitats increased over summer, suggesting that seasonal variation in deposition rates was not a simple effect of changes in diurnal and seasonal foraging behaviour patterns and/or varying defaecation rates.

The assumption of a demographically stable population at the foraging scale is tenuous. Studies of dynamics of the kangaroo population at Yan Yean by Dempster (1964) and Quin (1989) have shown that fecundity and mortality are seasonally dependent, with births peaking in summer and deaths peaking in winter. Mortality was found to be relatively high, with many juveniles succumbing to parasitic nematodes, cold stress and poor nutrition during the winter months. These demographic fluctuations appear to be correlated with the observed temporal pattern in use of foraging patches. It is unlikely, however, that these fluctuations account for all of the observed variation in use, as the deposition rates recorded during winter were almost five times lower than those recorded in early summer.

An alternative explanation for the dramatic temporal variation in deposition rates is required. By considering the abundance of kangaroos at the dispersal scale, a scenario can be envisaged where spatial constraints on the population are removed. The foraging patches examined in this study represent only a portion of the habitat available within the catchment. A mosaic of forage and shelter exists beyond these patches, providing an alternative supply of resources. Kangaroos can therefore enter and leave the designated study system at will. In studies of habitat use by kangaroos over time at the dispersal scale (i.e. incorporating foraging patches and shelter patches), differential selection of habitat has been observed (Hill 1981b, Southwell 1987, Terpstra and Wilson 1989). However unlike this study at the foraging scale, these studies did not document any seasonal fluctuations in habitat use and kangaroo abundance. It is likely that this discrepancy is primarily scale-induced. Therefore by relaxing the assumption of a 'closed' system, a reasonable explanation of the increase in summer deposition rates across all habitats can be attained.

Density dependence

Preferential selection of habitat by eastern grey kangaroos has been shown to be density-dependent at the foraging scale at Yan Yean. Following the procedure for isodar analysis outlined by Morris (1987, 1988), regression analysis implied that kangaroos prefer DOW twice as much as the two open-forest habitats, with IOF least favoured. Comparisons that include DOW all return slopes greater than 1, indicating that the difference among habitats is qualitative, such that they do not necessarily differ in resource availability but rather differ in terms of the ability of individuals to exploit the resource (Morris 1987). This is reflected in the analysis of the spatial and temporal availability and quality of resources, which indicated that DOW does not possess consistently better forage (although this is confounded somewhat by the heavier grazing pressure). In contrast, the slope of the DOF/IOF isodar did not differ significantly from 1, indicating that the principle difference between these habitats was the availability of resources (Morris 1987). The isodar analysis suggests, therefore, that DOW foraging patches are preferred over open-forest patches as foraging is more efficient, while DOF is preferred over IOF as resources are frequently more abundant in DOF.

When isodars were constructed separately for each season, density dependence appeared to regulate preference between the three foraging habitats during autumn, spring and summer, but not during winter, when the variability in resource availability among habitats was lowest.

Implications for behavioural strategies

The fundamental 'aim' of any optimal forager is to maximise its reproductive fitness. This means being able to respond to the relative costs and benefits associated with foraging in a particular habitat at any given time. Selection of habitat is therefore dependent upon a multitude of factors, including variation in resource availability, the presence of competitors, the perceived risks associated with each habitat, the ability of an individual to assess all of these factors for every available habitat and, ultimately, the freedom of individuals to choose their preferred habitat. As has been observed for a gerbil (*Gerbillus henleyi*) in the Negev Desert, Israel (Shenbrot and Krasnov 2000), and now for eastern grey kangaroos at Yan Yean, seasonal patterns in density dependence imply that different strategies of habitat selection may be applied on coarse time scales. These strategies are likely to be responses to stochasticity in both demographic parameters and environmental conditions.

Observations made of eastern grey kangaroos at Yan Yean in this study provide some insight into the strategies employed in the selection of habitat at a foraging scale. The apparent change in the density dependence of eastern greys in selecting habitat in different seasons corresponded with seasonal variation in resource availability and quality. However the number of pellets deposited in each of the habitats differed considerably between seasons. Treating the system as 'closed' makes interpretation of this discrepancy difficult. Allowing movement of individuals into and out of the system (i.e. examining abundance at the dispersal scale) enables the derivation of a wider perspective of the dispersion of kangaroos in relation to environmental conditions. Therefore while identifying habitat preference at small scales is essential for understanding the behavioural strategies of free-ranging foraging animals, these strategies must be considered within a broader population framework.

References

Abramsky, Z., Rosenzweig, M. L. and Subach, A. 1997. Gerbils under threat of owl predation – isoclines and isodars. – Oikos 78: 81–90.

Bailey, P. T. 1971. The red kangaroo, *Megaleia rufa* (Desmarest), in north-western New South Wales I. Movements. – CSIRO Wildl. Res. 16: 11–28.

Bailey, P. T., Martensz, P. N. and Barker, R. 1971. The red kangaroo, *Megaleia rufa* (Desmarest), in north-western New South Wales II. Food. – CSIRO Wildl. Res. 16: 29–39.

Bayliss, P. 1985. The population dynamics of red and western grey kangaroos in arid New South Wales, Australia. II. The numerical response function. – J. Anim. Ecol. 54: 127–135.

Cairns, S. C. 1989. Models of macropodid populations. – In: Grigg, G., Jarman, P. and Hume, I. (eds), Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons, pp. 695–704.

Cairns, S. C. and Grigg, G. C. 1993. Population dynamics of red kangaroos (*Macropus rufus*) in relation to rainfall in the South Australian pastoral zone. – J. Appl. Ecol. 30: 444–458.

Caraco, T. and Giraldeau, L.-A. 1991. Social foraging: producing and scrounging in a stochastic environment. – J. Theor. Biol. 153: 559–583.

Catchpole, W. R. and Wheeler, C. J. 1992. Estimating plant biomass: a review of techniques. – Aust. J. Ecol. 17: 121–131.

Caughley, G. J. 1964a. Density and dispersion of two species of kangaroo in relation to habitat. – Aust. J. Zool. 12: 238–249.

Caughley, G. J. 1964b. Social organisation and daily activity of the red kangaroo and the grey kangaroo. – J. Mammal. 45: 429–436.

Caughley, G. J., Bayliss, P. and Giles, P. 1984. Trends in kangaroo numbers in western New South Wales and their relation to rainfall. – Aust. Wildl. Res. 11: 415–422.

Clarke, J. L., Jones, M. E. and Jarman, P. J. 1989. A day in the life of a kangaroo: activities and movements of eastern

grey kangaroos *Macropus giganteus* at Wallaby Creek. – In: Grigg, G., Jarman, P. and Hume, I. (eds), Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons, pp. 611–618.

Coulson, G. 1993a. The influence on population density and habitat on grouping in the western grey kangaroo, *Macropus fuliginosus*. – Wildl. Res. 20: 151–162.

Coulson, G. 1993b. Use of heterogeneous habitat by the western grey kangaroo, *Macropus fuliginosus*. – Wildl. Res. 20: 137–149.

Coulson, G. M. and Raines, J. A. 1985. Methods for small-scale surveys of grey kangaroo populations. – Aust. Wildl. Res. 12: 119–125.

Coulson, G., Alviano, P., Ramp, D. et al. 2000. The kangaroos of Yan Yean: issues for a forested water catchment in a semi-rural matrix. – In: Craig, J. L., Mitchell, N. and Saunders, D. A. (eds), Nature conservation 5: nature conservation in production environments: managing the matrix. Surrey Beatty & Sons, pp. 146–156.

Dempster, J. K. 1964. Control and conservation of kangaroos in Victoria. – In: Australian Vermin Control Conference 1964. CSIRO.

Denny, M. 1980. Red kangaroo arid zone study. – Final report to Australian National Parks and Wildlife Service.

Duncan, A. 1992. The winter diets of fallow deer (*Dama dama*) and forester kangaroos (*Macropus giganteus*) in the midlands of Tasmania. – Tas. Nat. 110: 1–6.

Ecoplan, A. 1995. Macropod and rabbit study report: Yan Yean Catchment and Reservoir Park, Plenty Gorge Park, Cardinia Catchment and Reservoir Park and Sugarloaf Catchment and Reservoir Park. – Ecoplan Australia Pty. Ltd., Melbourne.

Fretwell, S. D. and Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

Friedel, M. H. and Bastin, G. N. 1988. Photographic standards for estimating comparative yield in arid rangelands. – Aust. Range. J. 10: 34–38.

Friedel, M. H., Chewings, V. H. and Bastin, G. N. 1988. The use of comparative yield and dry-weight-rank techniques for monitoring arid rangeland. – J. Range. Manage. 41: 430–435.

Haydock, K. P. and Shaw, N. H. 1975. The comparative yield method for estimating dry matter yield of pasture. – Aust. J. Exp. Agric. Anim. Husbandry 15: 663–670.

Hill, G. J. E. 1978. Preliminary assessment of defecation patterns for the eastern grey kangaroo (*Macropus giganteus*). – Aust. Zool. 19: 291–300.

Hill, G. J. E. 1981a. A study of grey kangaroo density using pellet counts. – Aust. Wildl. Res. 8: 237–243.

Hill, G. J. E. 1981b. A study of habitat preferences in the grey kangaroo. – Aust. Wildl. Res. 8: 245–254.

Holmgren, N. 1995. The ideal free distribution of unequal competitors-predictions from a behaviour-based functional response. – J. Anim. Ecol. 64: 197–212.

Jarman, P. J. and Phillips, C. M. 1989. Diets in a community of macropod species. – In: Grigg, G., Jarman, P. and Hume, I. (eds), Kangaroos, wallabies and rat-kangaroos. Surrey Beatty, pp. 143–149.

Johnson, C. N. and Jarman, P. J. 1987. Macropod studies at Wallaby Creek VI. A validation of the use of dung-pellet counts for measuring absolute densities of populations of macropodids. – Aust. Wildl. Res. 14: 139–145.

Johnson, C. N., Jarman, P. J. and Southwell, C. J. 1987. Macropod studies at Wallaby Creek V. Patterns of defaecation by eastern grey kangaroos and red-necked wallabies. – Aust. Wildl. Res. 14: 133–138.

Knight, T. W. and Morris, D. W. 1996. How many habitats do landscapes contain. – Ecology 77: 1756–1764.

Maynard Smith, J. 1982. Evolution and the theory of games. – Cambridge Univ. Press.

McAlpine, C. A., Grigg, G. C., Mott, J. J. and Sharma, P. 1999. Influence of landscape structure on kangaroo abundance in a disturbed semi-arid woodland of Queensland. – Range. J. 21: 104–134.

McCarthy, M. A. 1996. Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. – J. Appl. Ecol. 33: 45–53.

MMBW 1989. Water for Melbourne (brochure). – Melbourne and Metropolitan Board of Works, Melbourne.

Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy environment. – Ecol. Monogr. 57: 269–281.

Morris, D. W. 1988. Habitat-dependent population regulation and community structure. – Evol. Ecol. 2: 253–269.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. – Evol. Ecol. 6: 412–432.

Morris, D. W. 1994. Habitat matching – alternatives and implications to populations and communities. – Evol. Ecol. 8: 387–406.

Morris, D. W. 1997. Optimally foraging deer mice in prairie mosaics – a test of habitat theory and absence of landscape effects. – Oikos 80: 31–42.

Morris, D. W. and Davidson, D. L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. – Ecology 81: 2061–2066.

Morris, D. W., Davidson, D. L. and Krebs, C. J. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. – Evol. Ecol. Res. 2: 41–67.

Morrison, M. L. and Hall, L. S. 2001. Standard terminology: toward a common language to advance ecological understanding and applications. – In: Scott, J. M., Heglund, P. J. and Morrison, M. L. (eds), Predicting species occurrences: issues of accuracy and scale. Island Press.

Norbury, G. L., Norbury, D. C. and Hacker, R. B. 1993. Impact of red kangaroos on the pasture layer in the Western Australian arid zone. – Range. J. 15: 12–23.

Norbury, G. L., Norbury, D. C. and Oliver, A. J. 1994. Facultative behaviour in unpredictable environments – mobility of red kangaroos in arid Western-Australia. – J. Anim. Ecol. 63: 410–418.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. – Am. Nat. 103: 589–603.

Orians, G. H. and Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. – Am. Nat. 137: S29–S49.

Ovadia, O. and Abramsky, Z. 1995. Density-dependent habitat selection: evaluation of the isodar method. – Oikos 73: 86–94.

Perry, R. J. and Braysher, M. L. 1986. A technique for estimating the numbers of eastern grey kangaroos, *Macropus giganteus*, grazing a given area of pasture. – Aust. Wildl. Res. 13: 335–338.

Priddel, D. 1986. The diurnal and seasonal patterns of grazing of the red kangaroo, *Macropus rufus*, and the western grey kangaroo, *M. fuliginosus*. – Aust. Wildl. Res. 13: 113–120.

Priddel, D. 1987. The mobility and habitat utilisation of red kangaroos. – In: Caughley, G., Shepherd, N. and Short, J. (eds), Kangaroos: their ecology and management in the sheep rangelands of Australia. University Press, pp. 84–98.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.

Quin, D. G. 1989. Age structures, reproduction and mortality of the eastern grey kangaroo (*Macropus giganteus* Shaw) from Yan Yean, Victoria. – In: Grigg, G., Jarman, P. and Hume, I. (eds), Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons, pp. 787–794.

Ramp, D. 2001. Dispersion of eastern grey kangaroos and their impacts on vegetation in semi-rural environments. Ph.D. thesis. – Univ. of Melbourne, Melbourne.

Rodríguez, M. A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. – Evol. Ecol. 9: 169–184.

Roguet, C., Dumont, B. and Prache, S. 1998. Selection and use of feeding sites and feeding stations by herbivores – a review. – Ann. Zootechnie 47: 225–244.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335.

Shenbrot, G. and Krasnov, B. 2000. Habitat selection along an environmental gradient: theoretical models with an example of Negev Desert rodents. – Evol. Ecol. Res. 2: 257–277.

Sinclair, A. R. E. and Pech, R. P. 1996. Density dependence, stochasticity, compensation and predator regulation. – Oikos 75: 164–173.

Southwell, C. J. 1981. Sociobiology of the eastern grey kangaroo, *Macropus giganteus*. Ph.D. – Univ. of New England, Armidale.

Southwell, C. J. 1987. Macropod studies at Wallaby Creek II. Density and distribution of macropod species in relation to environmental variables. – Aust. Wildl. Res. 14: 15–33.

Southwell, C. 1989. Techniques for monitoring the abundance of kangaroo and wallaby populations. – In: Grigg, G., Jarman, P. and Hume, I. (eds), Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons, pp. 659–693.

Southwell, C. J., Cairns, S. C., Pople, A. R. and Delaney, R. 1999. Gradient analysis of macropod distribution in open forest and woodland of eastern Australia. – Aust. J. Ecol. 24: 132–143.

Taylor, R. J. 1984. Foraging in the eastern grey kangaroo and the wallaroo. – J. Anim. Ecol. 53: 65–74.

Terpstra, J. W. and Wilson, A. D. 1989. Grazing distribution of sheep and kangaroos in a semi-arid woodland. – Appl. Anim. Behav. Sci. 24: 343–352.

Woolnough, A. P. and Johnson, C. 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*. – Wildl. Res. 27: 301–308.