

Foraging behaviour and dispersion of eastern grey kangaroos (*Macropus giganteus*) in an ideal free framework

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Abstract

Ideal free distribution (IFD) theory predicts that animals in competitive situations should distribute themselves among available habitat patches according to the density of conspecifics and its regulatory effect on resources. To investigate the applicability of IFD models to free-ranging herbivores, we quantified the dispersion and foraging behaviour of eastern grey kangaroos *Macropus giganteus* among habitat patches of differing suitability, within and outside a reservoir catchment in southern Victoria, Australia. Kangaroo densities within the catchment had a regulatory effect on resource density, while surrounding farmland maintained a higher standing crop despite higher densities of competitors. This difference was slight in autumn, however, when the system was apparently close to equilibrium. Gross bite rates of individuals foraging in farmland were lower than for individuals foraging within the catchment, and vigilance behaviour occurred more frequently in farmland habitat than any other, decreasing time devoted to feeding. Interference competition occurred in only 1.9% of focal samples, although competitive differences based on phenotype were observed. Although resource gains by individual kangaroos are likely to be influenced by other factors, including resource dynamics, predation risk and phenotypic differences, IFD theory provides a valuable analytical framework for this herbivore foraging system.

Introduction

Most field-based studies of resource selection by herbivores have been essentially correlative, matching spatial patterns of population density with heterogeneity in forage abundance and quality (e.g. Catt & Staines, 1987; Licoppe, Efor & de Crombrughe, 2001). A newer approach has been to explore the spatial distribution of a population in terms of individual foraging decisions, taking into account spatial variation in forage suitability and the effects of intra-specific competition. Ideal free distribution (IFD) theory provides a formal framework for this approach. IFD theory describes a set of rules that predict the distribution of a population of free-ranging individuals throughout a foraging environment, where each individual acts to maximize its resource uptake, and consequently its long-term fitness (Fretwell & Lucas, 1970). In patchy environments, composed of spatial units of differing forage suitability (Weins, 1976; Bell, 1991), not every consumer can occupy the most suitable patch. Assuming that competitors are 'ideal', selecting patches that offer the best foraging opportunities, and that they are 'free', and so are not constrained in their choice of habitat, IFD theory predicts that individuals in a population will distribute themselves so that each maximizes its resource intake rate, reaching an equilibrium state when none can

gain by switching patches. Negative feedback reduces patch suitability through the depletion of available forage, so that average payoffs are predicted to become equal for all individuals regardless of the patch they occupy (Fretwell & Lucas, 1970; Sutherland, 1996); This framework can be used to explore how well a foraging population conforms to these predictions, and to identify potential causes of departures from IFD models (see Tregenza, 1995).

Most previous IFD research explores the consumption of prey items that are easily quantifiable as discrete units (Parker, 1970, 1978; Milinski, 1984, 1986); however, in herbivore grazing systems, resources occur as a standing crop of forage. The quality and production rate of this forage will vary among patches in heterogeneous environments. In a grazing system that has reached an equilibrium state, IFD theory predicts that the distribution of consumers should deplete the standing crop of forage to matching levels among patches (Lessells, 1995). Despite the general applicability of IFD models to a grazing system, only a few studies have specifically addressed the predictions of IFD in relation to free-ranging herbivores (e.g. Wahlström & Kjellander, 1995; Kohlmann & Risenhoover, 1997; Conradt, Clutton-Brock & Guinness, 1999; Pettorelli *et al.*, 2001). One herbivore species that appears well-suited to study within an IFD framework is the eastern grey kangaroo *Macropus*

giganteus. Eastern grey kangaroos are selective grazers, preferring forage with high nitrogen content (Taylor, 1984), and their selection of foraging patches is density-dependent (Ramp & Coulson, 2002), suggesting that the species is likely to conform to the general assumptions of IFD theory. Furthermore, eastern grey kangaroos form open-membership groups, which allow individuals the freedom to disperse between foraging patches (Southwell, 1984; Jarman & Coulson, 1989).

Variation in the quality and quantity of forage, however, is unlikely to be the sole influence on the distribution of individual consumers (e.g. Holmgren, 1995; Grand & Dill, 1999; Morris, Lundberg & Ripa, 2001). Ramp & Coulson (2004) found that eastern grey kangaroos underuse better habitat patches than would be expected by an IFD framework, and suggested that these departures stemmed from competitive interactions (interference) and variation in competitive and perceptual abilities. Interference competition, which causes a short-term reversible decline in intake rate by one individual (e.g. Hassell & Varley, 1969; Sutherland, 1983), is predicted to bring about a redistribution of competitors, as it is more profitable for some individuals to move to poorer patches where competition is less intense (Tregenza, 1995). Individuals may also differ in their susceptibility to interference as a consequence of their body size (Croy & Hughes, 1991), age (Goss-Custard & Durell, 1987) or aggressiveness (Harper, 1982). Various IFD models have been developed to explore the effect of unequal competitors on ideal free distributions in populations exhibiting interference, incorporating phenotypic differences in competitive ability (e.g. Sutherland & Parker, 1985, 1992; Tregenza, Hack & Thompson, 1996a; Tregenza & Thompson, 1998; Ruxton & Humphries, 1999). Aggression is known to occur in groups of kangaroos when forage is limited; however, the consequences of this on foraging decisions are unknown (Jaremovic & Croft, 1991a). Furthermore, evidence for differing competitive abilities among phenotypic classes in eastern grey kangaroos is equivocal. Clarke, Jones & Jarman (1989) found no differences between the sexes in bite rates and time spent feeding, whereas Jaremovic & Croft (1991a) reported differences in foraging efficiency among sex-age classes.

We examine the foraging behaviour of a population of eastern grey kangaroos within the theoretical framework of IFD. Forage conditions for this population varied spatially and temporally. Following the predictions of continuous input IFD models for a system in equilibrium, and those of Sutherland & Parker (1992), we assessed the following hypotheses: (1) that the population is distributed in proportion to patch suitability, where suitability refers to the quantity and quality of available resources; (2) that foraging efficiency is equal for all individuals regardless of the patch occupied; (3) that foraging efficiency does not differ between phenotypic classes, or that any differences are equal across patch types; and (4) that phenotypic classes are equal in their susceptibility to interference, which has only a negligible effect on foraging efficiency.

Materials and methods

Study area

We conducted the study within and adjacent to Yan Yean Reservoir catchment (145°09'E, 37°32'S), c. 40 km north-east of Melbourne, Victoria, Australia. The catchment covers an area of 2250 ha, and consists of undulating hills (Coulson *et al.*, 2000). A 1.8-m chain-mesh security fence surrounds the catchment, preventing public access and acting as a partial barrier to the high-density population of eastern grey kangaroos, estimated at 2.2 individuals ha⁻¹ between October 1996 and February 1997 (Coulson *et al.*, 1999). The climate is temperate, with a mean annual rainfall of 667 mm and little variation throughout the year.

The vegetation of the catchment is a mosaic of floristic communities (Moore, Coulson & Way, 2002). The three most preferred by kangaroos are intact open-forest (IOF), disturbed open-forest (DOF) and disturbed open-woodland (DOW) (Ramp & Coulson, 2002). These communities have the same suite of dominant tree species, mostly swamp gum *Eucalyptus ovata*, blue gum *E. globulus* and red stringybark *E. macrorhyncha*, but DOF and DOW also have two introduced tree species, sugar gum *E. cladocalyx* and Monterey pine *Pinus radiata*, scattered throughout. DOW differs from DOF in having more dispersed tree coverage and a shrubby understorey dominated by drooping cassinia *Cassinia arcuata* and wattles *Acacia* spp. The ground layer of each community occurs in discrete, open patches in gaps between the trees, forming a low, uniform sward of native grasses and herbs, predominantly weeping grass *Microlaena stipoides*, kangaroo grass *Themeda triandra*, wallaby grass *Danthonia* spp., spear grass *Stipa* spp. and tussock grass *Poa* spp. These grassy patches are smallest (around 10 m²) within the IOF community, which predominantly consists of remnant native forest, intermediate within DOF and largest (up to 100 m²) within DOW. The patches provide the kangaroos with high-quality resources and are linked by well-worn tracks, created by kangaroos as they move within and among communities. Swamp wallabies *Wallabia bicolor*, common wombats *Vombatus ursinus* and European rabbits *Oryctolagus cuniculus* also inhabit the catchment, but in very low densities, so that kangaroos are the dominant herbivore (Coulson *et al.*, 2000).

Outside the catchment, improved pasture on the adjacent farmland (FARM) provides an additional source of forage. Kangaroos gain access to these paddocks via holes in the security fence, with more than 100 passing through a single hole in one evening to forage (Coulson *et al.*, 2000). The pasture is dominated by sweet vernal grass *Anthoxanthum odoratum*, perennial ryegrass *Lolium perenne*, Kentucky bluegrass *Poa pratensis*, brown-top bent *Agrostis capillaris*, wallaby grass and kangaroo grass. The paddocks have a few scattered trees, and clumps of blackberry *Rubus* spp. provide some cover for kangaroos. FARM is grazed periodically by domestic cattle.

Patch suitability and use

We conducted this study from April to September 1998. Sampling was segregated into two seasons: autumn (2 April–31 May) and spring (4 August–30 September). Focusing on the western side of the catchment, we implemented a stratified-random sampling regime to select foraging patches from the DOW, DOF and IOF communities within the catchment, and also within the adjacent farmland. We selected 20 sample points in each vegetation community so that they fell within the average home range of kangaroos at this site (mean = 62.3 ha; Moore *et al.*, 2002). The availability and suitability of resources and their subsequent use by kangaroos were measured at each of these patches.

We sampled the vegetation on two occasions (31 May, autumn, and 29 September, spring). Sampling of the farmland sites occurred only during autumn, as access was not possible during the spring sampling period. At each sampling point, we assessed both the quantity and quality of grass from six 0.25-m² replicates, which we averaged to provide one estimate, as described by Ramp & Coulson (2002). We estimated the above-ground biomass of grass using the comparative yield method (Haydock & Shaw, 1975; Friedel & Bastin, 1988; Friedel, Chewings & Bastin, 1988), a non-destructive sampling technique. Grass quality was assessed subjectively using a seven-point greenness scale (0–100%), with 12.5% increments. Greenness has been shown to be strongly correlated with moisture and nitrogen content (Bailey, Martensz & Barker, 1971; Southwell, 1987), which was confirmed at this site in a pilot study by Ramp (2001).

We estimated the use of a patch using faecal pellet deposition as an index of the time that kangaroos spent grazing at each sampling point (Southwell, 1989). We conducted faecal pellet counts on circular plots of 10 m². We initially cleared the plots of all pellets, and then counted and removed all newly deposited pellets at successive sampling times. Sampling was conducted at fortnightly intervals eight times in autumn and six times in spring in DOW, DOF and IOF. In FARM, however, pellet deposition was sampled only once in autumn and three times in spring because of difficulties with access.

Foraging behaviour

We assessed the foraging behaviour of kangaroos in patches within the four habitats from where we measured resource availability and use. Behavioural sampling was also segregated into two seasonal blocks, with a total of 304 observations conducted in autumn and 368 in spring. We conducted observations 2 h after dawn and 2 h before dusk. Although kangaroos carry out a large proportion of foraging during the night, they also forage actively during the early morning and late evening (Kaufmann, 1975; Clarke *et al.*, 1989), so we assumed that our observations were representative of their foraging behaviour. We used a spotting telescope with a 20–50x-zoom eyepiece to make observations from within hides or from a vehicle overlooking FARM. Visits to patches were alternated to avoid re-sampling individuals that may have remained there overnight.

We stratified selection of the focal animal according to nine of the 10 sex–age classes defined by Jaremovic & Croft (1991b): females with large (FLPY), medium (FMPY), small (FSPY) or no pouch young (FNPY); females with a young-at-foot (FYF); small (SM), medium (MM) or large (LM) males; and sub-adults (SA). We excluded the young-at-foot category, which is still partly dependent on milk, hence violating a critical assumption of freedom of patch choice. Observational data were collected from *c.* 10 animals of each sex–age class per habitat for each time period. Once the allotted number in each sex–age class was obtained, the remaining classes were targeted for observation. If >1 animal was available, selection was randomized by allocating each animal in a group a number relative to its distance and consulting a random number table to determine the order of observation. For recognizable individuals (identified by tags, collars or natural features) sampled on more than one occasion, we used a mean value for that individual (10 individuals; 27 repeated samples).

Once a focal animal had been selected, data on the foraging environment were recorded, including habitat type, distance from nearest neighbour and the size of the group occupied. Nearest-neighbour distance was determined using trigonometry, by measuring the distance to the two animals with a Bushnell laser rangefinder (Lytespeed 400), and the angle of incidence between them with a hand-bearing compass. Group size was defined as the number of individuals within 30 m and able to interact with one another (Jarman, 1987; Jarman & Coulson, 1989). For solitary individuals, group size equalled one. The foraging behaviour of the focal animal was observed continuously for three minutes (after Berger & Cunningham, 1988; Clarke *et al.*, 1989), providing data on four foraging variables (Table 1). Gross bite rate was the closest practical measure of resource intake rate (Clarke *et al.*, 1989; Wallis de Vries & Daleboudt, 1994; Clarke, Jones & Jarman, 1995; Edwards *et al.*, 1995). Feeding time reflected an individual's energetic requirements and trade-offs with vigilance and maternal care (Clarke *et al.*, 1989). Scanning rate reflected an individual's perceived level of predation risk (Pulliam, 1973; Colagross & Cockburn, 1993). Displacement distance reflected the travel costs during foraging (Bernstein, Kacelnik & Krebs, 1991; Croft, 1996).

Whenever the focal individual was involved in an interaction consistent with interference competition, we noted the type of interaction: movement towards an individual, or contact between two individuals by cuffing or kicking, resulting in displacement of the recipient (Croft, 1981; Croft, 1985). The sex–age class of the initiator was also noted.

Statistical analysis

A representation of the quantity and quality of available forage was obtained by multiplying the values of grass biomass by the greenness values. This created a single value of resource density, which we compared among habitats using one-way analysis of variance. *Post hoc* analyses were performed using Student–Newman–Keuls tests. Similar

Table 1 Description of the foraging efficiency variables recorded in 3-min observations of eastern grey kangaroos *Macropus giganteus*

| Variable | Definition |
|---------------------------|--|
| Gross bite rate | The number of bites taken, evident from quick jerky head movements (Watson & Dawson, 1993), expressed per second |
| Feeding rate | The cumulative duration of time with head down biting and selecting bites (Clarke <i>et al.</i> , 1995), expressed as a proportion of the 180-s sampling period. No longer than 5 s must elapse between bites (Bradbury <i>et al.</i> , 1996) |
| Scanning rate | The cumulative duration of time with head up scanning and chewing (Clarke <i>et al.</i> , 1995), expressed as a proportion of the 180-s sampling period |
| Displacement distance (m) | The total distance an animal travels between the beginning and end of the 180-s sample period. This distance was usually in a single direction, but if the direction changed, each distance was measured separately, using trigonometry, and the total distance was summed |

comparisons were made for pellet count data, although they were log-transformed prior to analysis.

Foraging variables were compared among habitats and sex-age classes for each season using one-way ANOVAs. Before analyses, data were transformed to approach normality. Time devoted to feeding was arcsine-transformed, time devoted to scanning and bites per unit foraging time were square-root-transformed and displacement distance, nearest-neighbour distance and group size were log-transformed. Group size was included as a covariate in all analyses, as foraging behaviour varies with increasing group size of eastern grey kangaroos (Banks, 2001). *Post hoc* analyses were conducted using Bonferroni tests to determine specific habitat and sex-age class differences. Linear regression analysis was used to explore relationships between foraging variables. Two-sample *t*-tests were carried out to explore effects on foraging variables for recipients of interference versus individuals experiencing no interference. All data analyses were conducted using SPSS v 10.0.7 (SPSS Inc., Chicago, IL, USA).

Results

Habitat suitability and use

Resource density varied among habitats in both seasons (Fig. 1). In autumn, standing crop \times greenness did not differ within the catchment, where the overall value was 77 ± 8.7 (mean \pm SE), but the standing-crop value in farmland habitat was somewhat higher, with a value of 96 ± 9.1 ($F_{3,80} = 7.65$, $P < 0.001$). In spring, resource density differed among the three habitats within the catchment, having increased almost threefold in the two disturbed habitats ($F_{2,60} = 115.29$, $P < 0.001$; $\text{DOF} > \text{DOW} > \text{IOF}$).

The use of foraging patches by kangaroos varied both spatially and temporally (Fig. 2). In autumn, the highest pellet deposition rate was in DOW and FARM habitats ($F_{3,500} = 52.56$, $P < 0.001$; $\text{FARM} = \text{DOW} > \text{DOF} > \text{IOF}$). In spring, deposition rates differed significantly among all four habitats ($F_{3,403} = 88.85$, $P < 0.001$; $\text{FARM} > \text{DOW} > \text{DOF} > \text{IOF}$).

Resource density was similar across the four habitats in autumn, suggesting that the system was close to equilibrium in that season. Spring, in contrast, showed no evidence of equilibrium. Accordingly, only the foraging data obtained in autumn are presented below, so that foraging behaviour

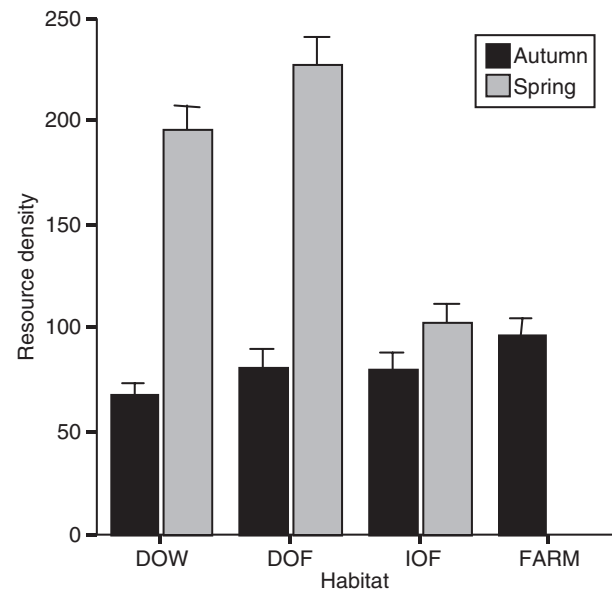


Figure 1 Resource density (mean standing crop \times greenness of grass, g m^{-2}) within each habitat for the two sampling seasons. Error bars represent 95% confidence intervals. Note that values of resource density were obtained within the farmland habitat only in autumn. DOW, disturbed open-woodland; DOF, disturbed open-forest; IOF, intact open-forest; FARM, farmland.

can be compared among different patches without being confounded by differences in resource density.

Group size and spacing

Group sizes varied among most habitats in autumn ($F_{3,305} = 63.44$, $P < 0.001$, $\text{FARM} > \text{DOF} = \text{DOW} > \text{IOF}$), clearly being the largest in FARM habitat (Fig. 3). Nearest-neighbour distances were not different from one another across habitat types ($F_{3,286} = 1.16$, $P = 0.33$) or for groups of varying sizes ($F_{1,286} = 0.94$, $P = 0.33$).

Foraging behaviour

There was a positive relationship between gross bite rates and feeding times ($F_{1,308} = 363.72$, $P < 0.001$). Gross bite rates varied among habitats in autumn (Table 2), being lower in DOW and FARM habitats, and higher in the two open-

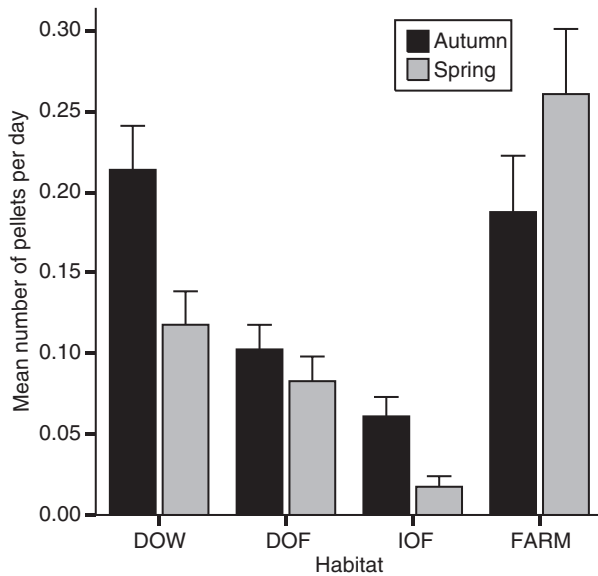


Figure 2 Mean number of pellets deposited (per $\text{m}^2 \text{day}^{-1}$) within each habitat for the two sampling seasons. Error bars represent 95% confidence intervals. DOW, disturbed open-woodland; DOF, disturbed open-forest; IOF, intact open-forest; FARM, farmland.

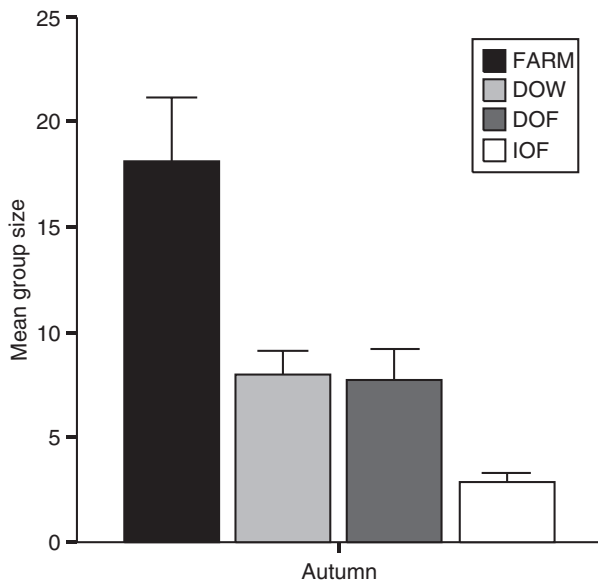


Figure 3 Mean group size within each habitat for autumn. Error bars represent 95% confidence intervals. DOW, disturbed open-woodland; DOF, disturbed open-forest; IOF, intact open-forest; FARM, farmland.

forest habitats. There were differences in the time devoted to feeding and scanning, but only between FARM and the catchment habitats. In FARM, feeding times were lower and scanning times were higher than in any other habitat (Table 2). There was no difference among habitats in the number of bites per unit of foraging time or in displacement distances.

Table 2 Habitat differences in foraging efficiency variables during autumn

| Efficiency variable | Source | $F_{3,1,304}$ | Bonferroni |
|------------------------------|------------|---------------|---------------------|
| Gross bite rate | Site | 9.990* | DOW = F < DOF = IOF |
| | Group size | 7.561* | |
| Bites per unit foraging time | Site | 0.916 | F < DOF = IOF = DOW |
| | Group size | 5.134* | |
| Time devoted to feeding | Site | 4.464* | F > DOF = IOF = DOW |
| | Group size | 7.153* | |
| Time devoted to scanning | Site | 2.916* | F > DOF = IOF = DOW |
| | Group size | 5.372* | |
| Displacement distance | Site | 1.695 | |
| | Group size | 3.320 | |

Group size was included as a covariate.

Significant results were taken as $P < 0.05$ and delineated with an asterisk. Bonferroni *post hoc* tests are presented for significant results.

F, farmland; DOW, disturbed open-woodland; DOF, disturbed open-forest; IOF, intact open-forest.

Phenotypic differences in exploitation ability

There were no significant differences in intake rates among sex-age classes in the two forest habitats (Table 3). However, gross bite rates differed among sex-age classes in FARM ($F_{1,76} = 2.42$, $P = 0.023$) and DOW ($F_{1,87} = 2.99$, $P = 0.006$). In FARM, bite rates were significantly higher for FYF and SM. In DOW, bite rates were also higher for FYF and SM, as well as LM.

Interference competition

The frequency of competitive interactions was low, occurring in only 1.9% of 304 focal samples. Most of these interactions occurred in FARM (47%) and DOF (37%). Overall, SA (53%), SM (21%) and females with no or small pouch young (16%) were the most common recipients of interference. Interference usually occurred through direct contact, when a dominant individual cuffed or kicked, displacing the recipient from its foraging path. Interference was most often initiated by LM or SA. Interference resulted in a decrease in the gross bite rate ($t_{308} = 2.93$, $P = 0.003$) and feeding time ($t_{308} = 3.21$, $P = 0.004$), and an increase in scanning rate ($t_{308} = 2.93$, $P = 0.004$) of recipients.

Discussion

Habitat matching

IFD models that incorporate standing crops predict that resource density should be equal across all patches once the system has reached equilibrium (Lessells, 1995; Tregenza, Shaw & Thompson, 1996b). Within the catchment at Yan Yean, resource density was close to equilibrium in autumn. Kangaroo density was highest in DOW and FARM, but only in DOW did these high densities deplete resources to a

Table 3 Phenotypic differences in gross bite rates (bites s⁻¹) for each habitat type, presented as mean and standard error values

| Class | FARM | DOW | DOF | IOF |
|-------|---------------------------|---------------------------|-------------|-------------|
| FNPY | 0.46 ± 0.05 ^{*b} | 0.53 ± 0.06 ^{*b} | 0.81 ± 0.09 | 0.69 ± 0.08 |
| FSPY | 0.51 ± 0.09 ^{*b} | 0.45 ± 0.06 ^{*b} | 0.73 ± 0.09 | 0.71 ± 0.09 |
| FMPY | 0.52 ± 0.08 ^{*b} | 0.54 ± 0.06 ^{*b} | 0.78 ± 0.12 | 0.91 ± 0.07 |
| FLPY | 0.58 ± 0.07 ^{*b} | 0.50 ± 0.50 ^{*b} | 0.97 ± 0.09 | 0.56 ± 0.45 |
| FYF | 0.85 ± 0.15 ^{*a} | 0.69 ± 0.15 ^{*a} | 0.84 ± 0.14 | 0.64 ± 0.11 |
| SM | 0.74 ± 0.08 ^{*a} | 0.86 ± 0.12 ^{*a} | 0.63 ± 0.07 | 0.76 ± 0.08 |
| MM | 0.40 ± 0.08 ^{*b} | 0.44 ± 0.07 ^{*b} | 0.70 ± 0.17 | 0.83 ± 0.18 |
| LM | 0.51 ± 0.10 ^{*b} | 0.79 ± 0.13 ^{*a} | 0.54 ± 0.13 | 0.75 ± 0.25 |
| SA | 0.64 ± 0.06 ^{*b} | 0.56 ± 0.04 ^{*b} | 0.75 ± 0.08 | 0.82 ± 0.08 |

Significant results obtained from Dunnett-T3 *post hoc* tests were taken as $P < 0.05$ and those highlighted with an asterisk denotes significant differences, group a being significantly different from group b, but not significantly different from one another.

DOW, disturbed open-woodland; DOF, disturbed open-forest; IOF, intact open-forest; FARM, farmland; FNPY, females with no pouch young; FSPY, females with small pouch young; FLPY, females with large pouch young; FMPY, females with medium pouch young; SM, small males; MM, medium males; LM, large males; SA, sub-adults.

level matching that of the least preferred habitats, IOF and DOF. Outside the catchment, the resource density in FARM was somewhat higher, suggesting that other behavioural mechanisms were contributing to this deviation from the predictions of IFD standing-crop models.

Foraging behaviour

In the present study, only a single estimation of patch quality was made at the end of each seasonal period. As we were unable to measure resource availability and kangaroo behaviour on the same temporal scales, we assumed that the relative patch quality was effectively constant during the 8-week period during which the behavioural data were collected.

We also made the assumption that gross bite rate adequately measured intake rate. In autumn, kangaroos grazed on a closely cropped sward, so little variation in bite size was expected. This measure probably would have been invalid during spring, when growth produced unequal standing crops and bite size could have varied with sward height.

If the population conforms to IFD, the average foraging efficiency of individuals is predicted to be similar within each habitat, regardless of resource suitability and productivity, or the density of consumers (Sutherland, 1983; Milinski & Parker, 1991; Kacelnik, Krebs & Bernstein, 1992; Moody & Houston, 1995). Deviations from this prediction were observed for gross bite rate, as bite rates were higher in the two open-forest communities. While pellet deposition and resource density were both greater in FARM, bite rates were lowest for this habitat type. This suggests that while the average resource intake rate for foraging individuals in FARM may be low, reward payoffs may be higher as the availability and quality of forage are higher.

The number of bites an individual can obtain within the time it devotes to foraging is a function of its search and handling efficiency. For kangaroos, handling efficiency has a minimal impact on foraging time as most chewing occurs when the head is up scanning, and can occur simultaneously

with searching (Watson & Dawson, 1993). A low number of bites per unit foraging time consequently implies a greater search effort. No difference in the number of bites per unit foraging time was found, indicating that search times remained similar regardless of the quality and structure of the standing crop. Therefore, to maximize intake rates, individuals must maximize the time spent foraging. Intake can increase only to a fixed upper limit, as individuals cannot continue to bite once the mouth cavity is full (Spalinger & Hobbs, 1992; Croft, 1996). To increase foraging time, individuals must minimize the time spent vigilant or in other social activities, such as lying down or grooming. In accordance with this, individuals in FARM exhibited lower gross bite rates, which can be explained by the negative relationship between time allocated to feeding and scanning by individuals occupying this habitat.

Scanning behaviour is seen as a mechanism for assessing predation risk, where increased vigilance enables individuals to detect the presence of predators more quickly (McNamara & Houston, 1992; Brown, 1999; Grand & Dill, 1999; Lima, Zollner & Bednekoff, 1999). In eastern grey kangaroos, group formation is interpreted as an anti-predatory strategy where individuals benefit from a reduction in time spent vigilant, enabling more time to be allocated to feeding (Heathcote, 1987; Jarman, 1987; Jarman & Wright, 1993; Banks, 2001). This negative relationship may, however, be confounded by a number of variables discussed by Elgar (1989). At Yan Yean, group sizes ranged from 1 to 40 and varied among habitats, with the largest group sizes occurring in FARM. With its lack of shelter, and frequent use by predators (e.g. dogs), humans and livestock, FARM has the highest level of disturbance, and yet attracts the highest density of kangaroos. Larger group sizes, however, did not fully offset vigilance costs, a factor contributing to the reduced intake rates experienced by kangaroos foraging in FARM. We conclude that the higher resource suitability of farmland yielded greater benefits per bite in comparison with other habitats, perhaps compensating for lower rates of feeding.

Phenotypic exploitation ability

Given an IFD, we would expect exploitation ability to be equal for all individuals irrespective of phenotype. Comparison of foraging efficiency variables among habitats for different sex–age classes indicated that while there were no consistent trends among habitats, small differences were apparent. Bite rates were consistently higher for FYF and SM in autumn in the two open habitats. This difference may be related to variation in energetic requirements associated with size and reproductive effort (McNamara & Houston, 1992; Colagross & Cockburn, 1993).

Interference competition

At Yan Yean, the frequency of competitive interactions was low, but more likely to occur within the more open communities. Interference is a direct result of competitor spacing, so that if the resource becomes more localized or valuable, tolerance of competitors at closer distances is reduced (Jaremovic & Croft, 1991a). However, there were no differences in the spacing of individuals within and outside the catchment. This suggests that the higher group sizes associated with open habitats may generate higher rates of encounter between foraging individuals (Jarman & Coulson, 1989). Overall, although asymmetry in phenotypes experiencing interference was evident, the consequences of interference were transient and unlikely to be a competitive pressure shaping the distribution of individuals.

Conclusion

IFD theory provided a powerful framework for examining the distribution of a free-ranging herbivore. Within the catchment, equilibrium was achieved through matching of competitor densities to forage availability. The adjacent farmland, however, maintained greater resource density despite higher use by consumers. Behavioural observations highlighted differences in intake rate across habitats, in particular lower bite rates in farmland, related to a trade-off in time allocated to feeding and scanning for predators. It is probable that the higher resource suitability of farmland yielded greater benefits per bite in comparison with other habitats, thus compensating for lower rates of feeding. Measurement of the nutritional benefits of the forage from each habitat, or the fitness benefits (e.g. body mass, number of young produced) experienced by individuals foraging in different habitats, would be needed to clarify this issue. Phenotypic differences were evident in both foraging efficiency and interference competition experienced by individuals, although interference had a transient and apparently negligible effect on foraging behaviour. Comparison of the distribution of phenotypes at Yan Yean should reveal whether competitive differences are significant enough to influence patch choice when the system is in equilibrium.

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