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Food choice by western grey kangaroos among plants grown at different nutrient levels

C Rafferty[1] & B B Lamont

Department of Environmental Biology, Curtin University of Technology,
PO Box U1987, Perth WA 6845, Australia.
[1] Corresponding author: ✉ crafferty@bgpa.wa.gov.au).

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Abstract

To test the hypothesis that plant palatability increases with increasing nutritional content, four native Western Australian plant species were treated with differing fertilizer regimes and presented to western grey kangaroos (*Macropus fuliginosus*) at Perth Zoo. Species were *Hardenbergia comptoniana*, *Notodanthonia caespitosa*, *Oxylobium lanceolatum* and *Rhodanthe chlorocephalum rosea*, all commonly browsed in the wild. Kangaroo feeding selection was based on the size of plants independent of nutrient concentrations. Feeding behaviour differed between treatment types, with longer time spent at greater fertilizer levels, which was related to larger plant size.

Keywords: Herbivore selection, kangaroo, nutrient concentration, plant morphology, feeding behaviour.

Introduction

Studies investigating the feeding behaviour of wild western grey kangaroos (*Macropus fuliginosus*) at Whiteman Park Reserve, Perth, Western Australia, revealed a strong positive selection of plants high in nitrogen, potassium and phosphorus (Rafferty *et al.* in press). Reports of selection for plants high in nutritional quality have been observed in a number of herbivore species (Braithwaite et al. 1984). The bridled nailtail wallaby (*Onychogalea fraenata*) showed a positive selection for food items of relatively high nutritional value (Dawson 1995; Evans & Jarman 1999). Similarly, Bergstrom & Berqvist (1997) noted that, for small coniferous and deciduous tree seedlings, grazing by large herbivores was more intense upon planted seedlings than naturally regenerating ones, suggesting it was the result of improved nutrient status of planted seedlings relative to the surrounding vegetation. Waring & Cobb (1992) reported that, for 67% of herbivore nutritional studies, herbivores performed better on fertilized plants, showing greater vigour and health. Tripler *et al.* (2002) showed browse rates to differ between control and fertilised plots for white-tailed deer (*Odocoileus virginianus*). Similarly, Holdo (2003) showed for the African elephant (*Loxodonta africana africana*), a strong preference for tree species occurring on more fertile soils (such as those associated with termite mounds) than those on sandy soils with lower nutrient concentrations.

It remains unclear whether herbivore selection of plants grown in high nutrient level environments is due to increased plant size, decreased plant defences, increased nutrient levels or a combination of these factors. The Plant Vigour Hypothesis (Price 1991) proposes that herbivores perform best on faster growing plants, because plant growth rate is usually correlated with nitrogen levels, although other nutrients may also be important influences of plant palatability (Provenza *et al.* 2003).

The aim of our study was to observe changes in feeding selection of kangaroos upon four palatable native plant species grown under four varying nutrient regimes. Using captive western grey kangaroos at the Perth Zoo, behavioural facets of food selection were monitored to test the hypothesis that plants with high nutritional value are highly palatable, while this palatability declines with decreasing nutrient content. Whether kangaroos actively seek out plants of higher nutritional value, as suggested from our earlier results examining feeding of wild macropod on seedlings of 19 species at Whiteman Park Reserve, was explored here in a controlled environment (Rafferty *et al.*, in press). Whiteman Park Reserve is a conservation and leisure reserve of 3 600 hectares, located 18 km NE of Perth. The primary native herbivore species in the park are the western grey kangaroo (*Macropus fuliginosus*), the black-gloved wallaby (*M. irma*), and the introduced European rabbit (*Oryctolagus cuniculus*). Annual rainfall at the reserve averages 800 mm per year, with most received in the winter months in a typical Mediterranean trend. Vegetation ranges from low woodland to low open forest of *Banksia attenuata* – *B. menziesii* – *B. ilicifolia* on deep pale grey sands, to *Corymbia calophylla* on moister dark grey soils on flatter, lower areas, with local additional species reflecting soil moisture (*Melaleuca preissiana*) or sandier (*Banksia ilicifolia*, *B. menziesii*) soils. Plants species reflect the typically nutrient poor sandplain soils.

Materials and Methods

Nutrient and morphological analyses were performed upon a subset of 20 native plants endemic to the Swan Coastal Plain near Perth. These species incorporated a variety of leaf types and growth forms, and are commonly browsed in the wild. Of these, four of moderate nutrient content were selected for the selection trial. These were *Hardenbergia comptoniana (*herbaceous climber), *Notodanthonia caespitosa* (grass), *Oxylobium lanceolatum* (herbaceous shrub), and *Rhodanthe chlorocephalum rosea* (herbaceous annual). All species were raised from seeds supplied from Nindethana Seed Service from Western Australian sources. In April 2001, seeds were sown into a 1:1 peat/sand mix. Seedlings were later transplanted when 3–5 cm high into 10 cm × 10 cm square black plastic pots. Pots were watered daily and covered with shade cloth until this was removed in June to allow seedlings to harden-off. Plants were monitored on a weekly basis following planting for signs of invertebrate damage or leaf senescence.

Plants were treated weekly after germination with 100 mL of Thrive® fertilizer, a powdered concentrate made into liquid form by addition to deionised water (27% N, 5.5% P and % K). Four treatment concentrations were used: low, one-eighth scoop to 9 L (approximately 3g) ; moderate, half scoop to 9 L (7g), high; one scoop to 9 L (15g); and very high, two level scoops to 9 L (30g). Attempts were made to use a treatment with no fertilizer addition, although the high mortality of this group led to its omission.

At six months old, plants were presented to a population of eight western grey kangaroos (*Macropus fuliginosus*) in the Australian Bushwalk at Perth Zoo, South Perth during daily visits to the enclosure over one week. Kangaroos typically fed upon pelletised feed and a range of chopped vegetables, but were acquainted with browsing native foliage on a regular basis with branches of a range of native plant species spread in the enclosure as supplementary food items.

Experimental offerings began two weeks after final fertilizer application to ensure no residual fertilizer remained on the foliage. Total leaf number and plant height were recorded prior to presentation. Ten replicates of the each species were presented, with each of the four fertilizer treatments represented in each replicate for the four species. Species were presented to kangaroos in a random arrangement to ensure they did not become acquainted to a particular plant type. Trays containing the four pots were used to assist stabilising pots in the presentation process, and they were presented to one or two kangaroos at a time, with other kangaroos discouraged from participating by accompanying volunteers. This simplified behavioural observations and mimicked natural conditions where fierce competition for small plants would typically be minimal.

Five preliminary trials were undertaken prior to experimental presentations to acquaint animals with the food source. It was decided that cessation of trials upon consumption of half of the plant material was the most suitable measure, rather than a set time interval, to ensure selection was not influenced by plant ‘availability’ and allow for the ability of some kangaroos to process food items at a greater rate. Times therefore varied for each presentation, as determined by kangaroo interest and rate of feeding activity. Following presentation, plant height and leaf number was again recorded. Behavioural responses and time spent feeding were collated.

Chemical and morphological analysis

Nitrogen, potassium, phosphorus, calcium, magnesium and sulfur were analysed for each of the four treatments of each species. Elements selected were analysed due to their high importance in relation to plant growth and morphology. Whole plants of each species (including leaves and stems which were all observed to be consumed in practice trials before commencement of the study) were collected on the first day of presentation, dried at 60° C for 48 hours in an air-forced oven and milled using a coffee grinder, followed by milling to < 1 mm in a cross beater mill (Culatti Pty. Ltd. Michigan, USA). Ten milled plants were bulked and stored in glass sample jars -5°C. Protocols used for each were as follows.

Nitrogen, potassium, phosphorus

For N content determination, 200 mg plant material was digested with H_2SO_4 and H_2O_2 in the presence of salicylic acid (Bradstreet 1965) and analysed using a Technicon segmented analyser with Berthelot colorimetric determination (Searle 1984). Determination of total P and K was undertaken using similar methods, although molybdate/vanadate colorimetric reaction and flame emission spectrometry (Varley 1966) were used respectively.

Calcium, magnesium and sulfur

200 mg of plant material was digested using nitric/perchloric acid in a block digestion at 200–210°C, with nitric acid addition to prevent nutrient loss due to charring. Upon cooling, the mixture was diluted with deionised water and the elements quantified using inductively coupled plasma atomic emission spectroscopy (McQuaker *et al.* 1979).

Morphological analysis

Leaf : mass area, leaf thickness and dry density were determined as described by Witkowski & Lamont (1991) for treatments, and amendment was made to the formula for leaf : mass area and density for the needle-leaved *Notodanthonia*, by dividing rather than multiplying the standard formula by 0.7854 (Witkowski & Lamont 1991). Leaf area was measured using the Dias system (Delta-T Devices, Cambridge, England). Average plant heights and biomasses were calculated for each treatment of each species by taking the average of ten plants harvested at the time of presentation.

Consumption measures

Consumption measures were dependent upon plant morphology. For all species, except *Notodanthonia*, numbers of leaves consumed were converted to volume for analysis by multiplying percentage leaf number eaten by original biomass. For *Notodanthonia*, leaf number was not representative of selection, as browsing did not always affect leaf number, thus percentage height eaten was multiplied by original biomass. As kangaroos commonly ate only the leaf tips of this species, height was considered a more reliable measure. As biomass values before and after presentation for each treatment and species were non-normal, results were analysed using one-tailed Wilcoxon signed ranks tests (SPSS 11 for Mac, 2002). Feeding times were analysed using ANOVA and Tukey’s pairwise comparisons after removal of zeros and log transformation to normalise the data (SPSS 11 for Mac, 2002). Log-likelihood contingency analyses (Zar 1999) were undertaken upon eaten/not-eaten values to indicate any significant differences in the presence of multiple zero scores for consumption and behavioural measures.

Results

Plant morphology and chemistry

Plant attributes (percentage eaten, height, leaf area, leaf thickness, leaf density, LMA, N, P, K, Ca, Mg and S) for each species at each application level are provided in Table 1. Of all attributes, plant height (Table 1) and biomass (Fig. 1) had the greatest variation between treatments, with greater fertilizer application resulting in increased plant size for all species, although for three species, the highest level of nutrient addition resulted in reduced total biomass (supra-optimal nutrient availability). Leaf nutrient content (N and P) increased with increased fertilizer application for *Rhodanthe*, while for all other species, leaf nutrient concentrations varied independently of fertilizer treatment.

Selection of treatments

Contingency analyses for numbers of plants damaged showed selection was independent of fertilizer treatment for *Hardenbergia*, *Oxylobium* and *Rhodanthe* (Table 2, df = 3, $P > 0.05$). Percentage of plants damaged did not differ significantly for *Hardenbergia*, *Oxylobium* and *Rhodanthe*. A significant difference in the number of plants damaged per treatment was noted for *Notodanthonia* (Table 2, df = 3, $P < 0.05$), with more plants in treatments 2, 3 and 4 consumed than to treatment 1. All species suffered significant loss of biomass following presentation independent of treatment, with the exception of treatment 2 for *Hardenbergia* and treatment 1 for *Oxylobium* (Fig. 1). A significant correlation between amount eaten and plant size was evident for all species combined (Fig. 2, r^2 = 90.7%, $P < 0.0001$, df = 15).

Kangaroo behaviour

Feeding times differed significantly between treatment types for all species (Fig. 3, df = 3, $P < 0.05$). Kangaroos typically fed on closest plants available on all occasions, moving to the next closest when feeding was completed or became difficult, e.g. if all easily accessible foliage was

Table 1

Mean physical and chemical attributes for shoots in the four treatments (Tt) and percentage of plants eaten (%) of the four species. Treatment 1 = 1/8 scoop of Thrive® to 9 L, 2 = 1/2 scoop, 3 = 1 scoop and 4 = 2 scoops. For all attributes, n = 10. Chemical analyses were undertaken on pooled samples. Units of measurement were as follows: height (ht) in cm, consumption: % leaves/height eaten, leaf area in mm^2, leaf thickness in mm, leaf density: mg mm^{-3}, LMA: mg mm^{-2}, N, P, K, Ca, Mg, S: % dry weight. IS: insufficient sample.

Species	Tt	% Plants eaten	Ht	Area	Leaf thickness	Density	LMA	N	P	K	Ca	Mg	S
Hardenbergia comptoniana	1	27.5	10.6	478	0.3	12	36	2.56	0.13	1.30	1.01	1.09	0.40
	2	41.9	37.1	713	0.3	16	48	2.10	0.19	0.90	0.57	0.78	0.38
	3	40.2	40.3	145	0.3	13	38	2.51	0.20	0.90	0.46	0.59	0.21
	4	62.4	35.7	772	0.3	15	45	3.65	0.43	1.17	0.37	0.58	0.43
Notodanthonia caespitosa	1	19.4	2.7	6	0.2	31	120	IS	0.08	0.25	0.17	0.27	0.27
	2	43.2	4.6	9	0.5	17	84	1.82	0.20	0.56	0.12	0.16	0.26
	3	44.6	6.5	11	0.3	19	77	1.63	0.13	0.22	0.12	0.15	0.13
	4	38.1	7.1	19	0.2	31	93	2.17	0.22	0.24	0.12	0.17	0.18
Oxylobium lanceolatum	1	33.3	12.0	234	0.3	12	46	2.23	0.14	0.69	0.28	0.51	0.26
	2	42.4	21.9	402	0.2	18	55	3.14	0.40	0.85	0.16	0.30	0.22
	3	31.1	34.2	338	0.2	18	52	1.67	0.018	0.88	0.19	0.33	0.16
	4	45.6	23.4	707	0.2	19	56	2.14	0.44	0.81	0.14	0.31	0.18
Rhodanthec hlorocephalum rosea	1	25.7	13.1	25	0.3	26	63	2.40	0.20	1.23	0.83	0.42	0.31
	2	65.9	14.8	23	0.3	20	56	2.98	0.35	1.51	0.78	0.56	0.40
	3	63.4	13.2	33.2	0.3	18	53	4.79	0.95	2.29	0.54	0.33	0.49
	4	42.7	22.2	25.2	0.3	7	19	4.80	0.93	2.11	0.37	0.27	0.46

Table 2

χ^2 contingency data for the number of plants damaged for each species presentation (n = 10), E = eaten, N = non-eaten. Significance determined using log likelihood analysis, df = 3 for all species.

Treatment	1		2		3		4	
	E	N	E	N	E	N	E	N
Hardenbergia comptoniana	4	6	8	2	6	4	9	1
Notodanthonia caespitosa	3	7	8	2	9	1	8	2
Oxylobium lanceolatum	5	5	8	2	6	4	8	2
Rhodanthe chlorocephalum	4	6	9	1	8	2	6	4

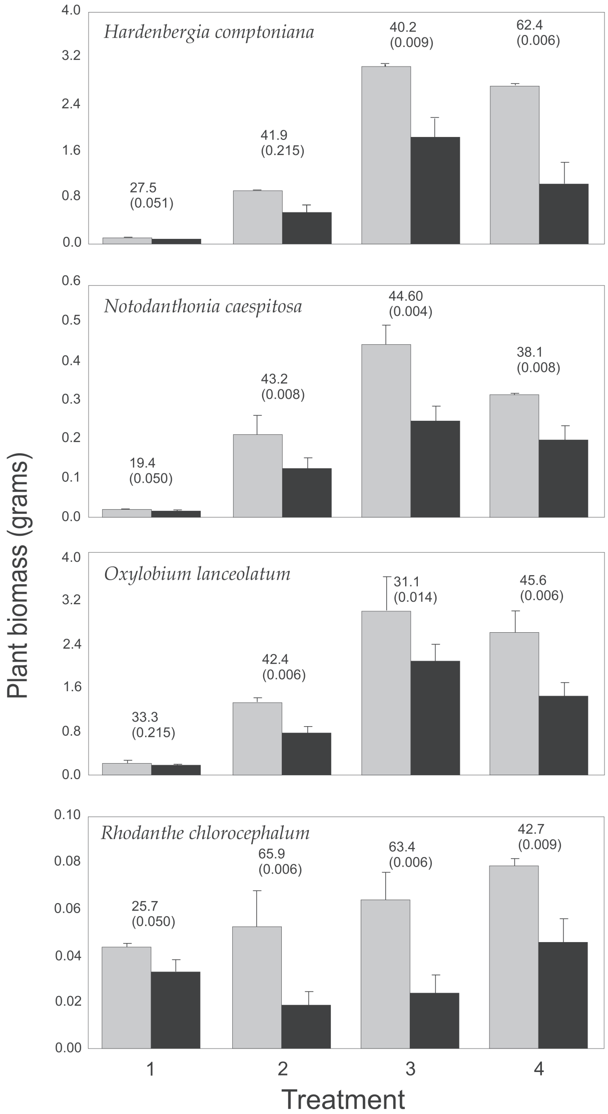

Figure 1. Biomass of plants before (light grey) and after (dark grey) presentation. Percentage biomass of plants consumed for each treatment type provided above standard error bars (fertiliser application: 1 = low, 2 = moderate, 3 = high, 4 = very high). *P* values (in brackets) denote differences between plant biomass before and after presentation.

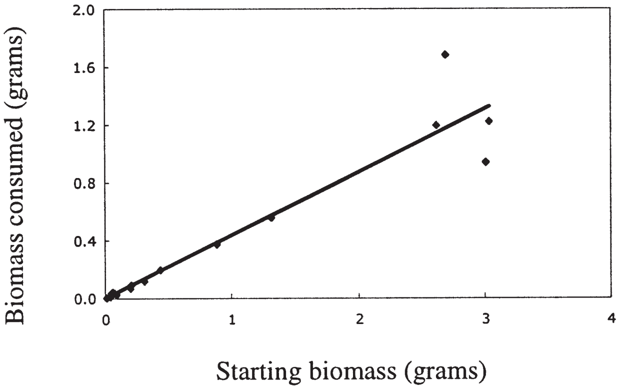

Figure 2. Relationship between starting biomass of plants with biomass consumed for all species.

removed. This trend was only interrupted with the participating of a second kangaroo, in which case the second animal selected the closest accessible after consideration of the initial feeding kangaroo. A significant correlation between time spent eating and plant size was evident (Fig. 4, r^2 = 68.4%, df = 15, $P <$ 0.0001).

Discussion

In a captive setting at Perth Zoo, it appeared plant selection by western grey kangaroos was independent of plant morphology. The extent of plant browsing was similar to the number of plants browsed and the initial size of plants, with kangaroos appearing to eat what was

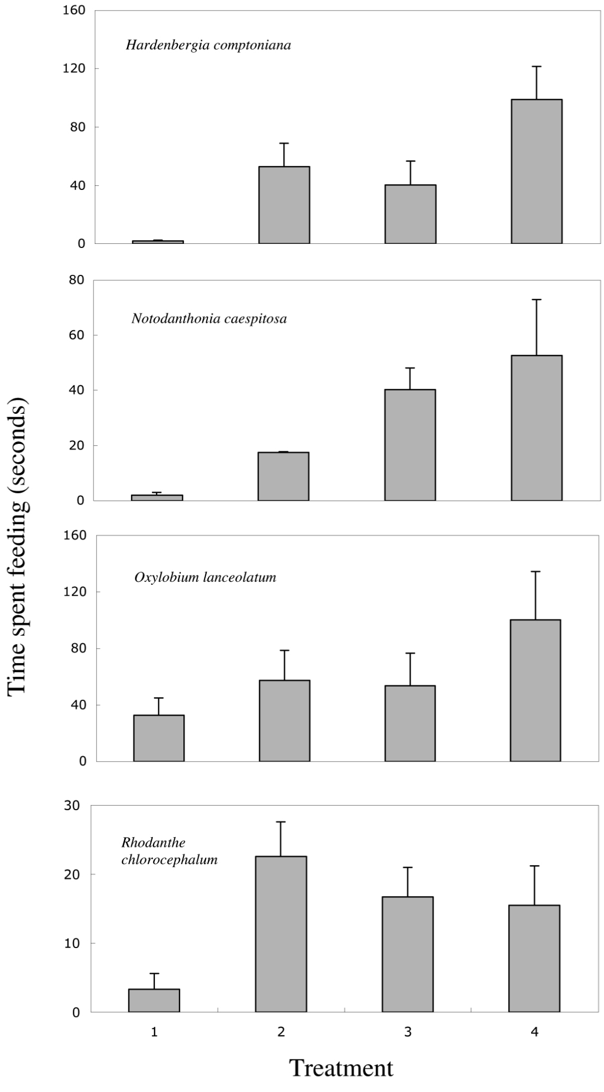

Figure 3. Total time spent feeding upon different treatments (fertilizer application: 1 = low, 2 = moderate, 3 = high, 4 = very high) for a. *Hardenbergia comptoniana*, b. *Notodanthonia caespitosa*, c. *Oxylobium lanceolatum* and d. *Rhodanthe chlorocephalum* (bars denote standard errors).

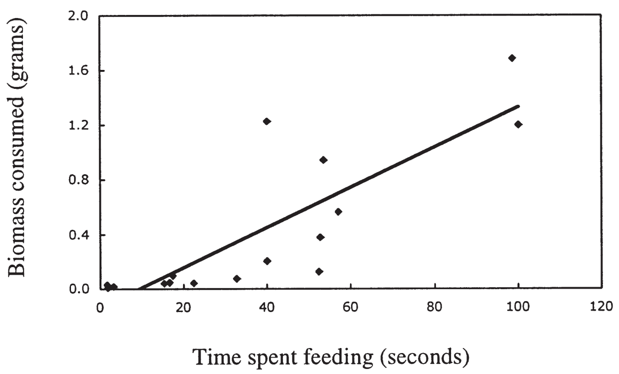

Figure 4. Relationship between starting biomass of plants and time spent feeding for all species.

proportionally available. Once a plant was initially tasted, kangaroos usually continued feeding until foliage was significantly reduced or removed entirely. This was confirmed by time spent feeding and amount consumed. It is difficult to base selection patterns upon plant nutrient concentration however, with concentrations increasing with increased fertilizer application for only one species, despite most plants growing larger with increased fertilizer application. Abrahamson & Caswell (1982) showed that the abundance of most nutrients in the soil showed no correlation with the concentration of that element in shoots. Nutrient application may therefore alter plant morphology but not necessarily nutrient concentration. Thus it is not surprising kangaroos did not select plants on the basis of their nutrient concentrations. The lack of association between nutrient content and selection may also be influenced by the expected satiated nutrient status of captive kangaroos. Animals participating may not ever have been required to base their selection upon nutrient requirement, having unlimited access to a constant, balanced diet. A captive population was selected over presentation in a wild setting, allowing for greater control of conditions and close behavioural observation. While a zoo environment is unnatural in many ways, Bourke (1989) found macropod behaviour was not seriously affected by captivity. Use of plants in the field is difficult as some groups may be eaten in the first night of presentation while others in close proximity may remain untouched for up to six weeks.

Treatments with greater fertilizer applications (i.e. 3 and 4) plants grew faster and larger. According to the Plant Vigour Hypothesis (Price 1991) herbivores perform best on faster growing plants, with growth rate often correlated with high nitrogen. While plants receiving greater fertilizer concentrations were larger, kangaroo selection on this basis was not evident. Belovsky *et al.* (1991) suggest that food selection is not typically based upon protein content of foliage, which is generally well above that thought to be limiting herbivore nutrition, regardless of habitat. Wright *et al.* (2004) reported that at the world level, there appears to be an important relationship between leaf nutrients, particularly N and P, and LMA. They suggest food selection is based on foliage texture rather than chemical content, although in the present study, it appears kangaroos simply ate what was proportionally available, i.e. consuming greater amounts of highly fertilised plants simply due to their greater biomass. With the exception of *Notodanthonia*, kangaroos were always observed to feed upon the closest, most convenient plants for most presentations, suggesting feeding convenience was the driving factor for observed selection patterns, at least in a captive setting. Whether kangaroos in a natural environment would exhibit similar behaviours is difficult to quantify, and controlling for the great number of environmental effects difficult to achieve. Seasonal influences in the wild may also be highly influential, with selectivity often influenced by the abundance of alternative food sources (Atsatt & O'Dowd 1976; Marten 1978). Nutrient content of plants may be irrelevant in summer months when alternatives are scarce and any food item welcome, while in the winter and spring, when abundant pasture land is available for grazing for many kangaroo populations, nutritional content of food items may be equally irrelevant (Murden & Risenhoover 1993).

While it may be true that risk of herbivore damage is maximal on plants growing in nutrient-rich soils (Gowda *et al.* 2003), it is more likely to be a large-scale, overall effect than one of individual plant nutrient content as tested in this study. Concentration of feeding activity by herbivores in regions of high-fertility would undoubtedly provide benefits to herbivores. Plants typically show greater biomass production in these environments; thus it is sensible that herbivores should focus feeding activities in areas of high production where possible (Stephens & Krebs 1986). Individual plants growing in highly fertile substrates may be positively selected for, with risks of damage increased by greater, more prolific growth. It is unlikely, however, that individuals growing nearby in less fertile microsites, would be selected against on the basis of nutrient content given the typically limited nature of forage, particularly in warmer months when wild kangaroos appear to target any suitable food item. While plants grown in less fertile areas may be smaller and less conspicuous, escaping attention to a greater extent than their more fertile counterparts, it is likely they too would be eaten by kangaroos if intercepted while foraging. Visual cues, in conjunction with feeding convenience, may therefore be more important than nutritional content, particularly in forage-limited environments.

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