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Diet of the quokka (*Setonix brachyurus*) (Macropodidae : Marsupialia) in the northern jarrah forest of Western Australia

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Abstract. The diet of the quokka in the northern jarrah forest of Western Australia was investigated by microscopic examination of faecal pellets of known individuals and comparison with a reference collection of plant epidermal tissue. Twenty-nine plant species were identified from the 97 faecal pellet groups collected from 53 individuals, confirming that the quokka is a browsing herbivore that favours leaves and stems. Of those 29 species, 11 made up over 90% of the diet and five species accounted for 71%. *Thomasia* species were the most common in the diet and the most preferred; *Dampiera hederacea* was also preferred and these species, along with *Bossiaea aquifolia*, *Mirbelia dilatata* and *Agonis linearifolia*, were the five most important food items. The seasonal variation in the diet of the quokka, and that between sites, can be attributed to increases in nutrient content associated with fresh growth associated with season or vegetation seral stage after fire. The reduced dietary diversity at sites with younger seral stages (<10 years after fire) and the importance of certain species that are more common in these younger ages explains the cause of the species' habitat preference for sites with a mosaic of young and old (>25 years after fire) age classes. The relatively short availability of sufficient, high-quality, succulent plants in the seral succession of swamps occupied by quokkas is likely to drive a regular pattern of local extinction and recolonisation.

Introduction

The quokka is a threatened, medium-sized macropodid marsupial endemic to the Mediterranean environment of south-west Western Australia (Hayward 2002; Hayward *et al*. 2003). The species is restricted to swamp shrublands dominated by *Agonis linearifolia* in the northern jarrah forest, which occur as isolated habitat patches in the upper reaches of creek systems (Hayward 2002; Hayward *et al*. 2004). The quokka's preference for a mosaic of early seral stage and long unburnt habitat (Christensen and Kimber 1975) is thought to have arisen due to dietary requirements that can be satisfied by the recently burnt areas provided there are refugia from predation nearby (Hayward 2002).

The diet of the quokka on Rottnest Island has been studied previously (Storr 1961*b*, 1964*b*), but extrapolation to the mainland population is unwarranted due to the differences in available habitat between the two regions (Main *et al*. 1959; Hayward 2002). The diet of quokkas on Rottnest Island was dominated by succulents such as *Carpobrotus aequilaterus*, *Arthrocnemum halocnemoides* and *Rhagodia baccata,* grasses and, to a much lesser extent, shrubs such as *Acacia rostellifera* and *Scaevola crassifolia*, and the sedge *Gahnia trifida* (Storr 1964*b*). This diet was deficient in nitrogen (Storr 1964*b*) and was often supplemented by human refuse from the tip and near the settlement of Rottnest Island, introduced stinkwort (*Inula graveolens*) and even snails (Erickson 1951). Quokkas have also been observed climbing into the outer branches of trees and shrubs on Rottnest Island to browse (Wake 1980).

Information on the diet of the quokka on Rottnest Island has been used to elucidate the cause of the seasonal mortality that affects quokkas at the end of summer (Main *et al*. 1959; Barker 1961; Storr 1964*b*). At this time, quokkas lose weight, become dehydrated, decline in body temperature and suffer severe anaemia; however, no single nutritional or physiological feature has been identified as the proximate cause of seasonal mortality (Miller and Bradshaw 1979).

Mainland plants that had evidence of browsing that was attributed to the quokka included *Agonis linearifolia*, *Aotus cordifolia*, *Lepidosperma tetraquentrum*, *Oxylobium lineare*, *Cladium laxum* and *Tetrarrhena laevis* (Storr 1964*a*). In the 1930s quokkas travelled up to 2 km from swamps to browse on seedlings in pine (*Pinus radiata*) plantations (Stewart 1936). This is all that is known about the diet of the quokka on the mainland aside from the fact that captive quokka colonies have been maintained at the University of Western Australia on a diet comprising green herbage, chaff, hay and commercial sheep pellets (Collins 1973). Consequently, the aim of this study was to determine the diet and dietary preferences of the quokka in the northern jarrah forest and to determine

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whether dietary factors are related to the specific habitat preferences of the species or its continued threatened status.

Materials and methods

Study area

The four study sites (known as Chandler, Kesners, Hadfield and Victor Road) were located in the northern half of the Dale subregion (Beard 1980) of the Jarrah Forest biogeographical zone of Western Australia (Thackway and Cresswell 1995). These sites are among five known extant quokka populations in the region (Fig. 1) (for a map see Hayward *et al*. 2003) and are situated in the broad upper reaches of creek systems containing *Agonis linearifolia* swamp shrublands. A thin strip of bullich (*Eucalyptus megacarpa*) – blackbutt (*E. patens*) open forest surrounds these swamps, with jarrah (*E. marginata*) – marri (*Corymbia calophylla*) communities on the drier slopes and ridges (Havel 1975*a*, 1975*b*). The dominant plant types in each of these communities are shown in Table 1.

Reference collection

The techniques of Storr (1961*a*) and Shepherd *et al*. (1997) were followed to allow comparison with other studies of quokka diet. A reference collection was made of 74 plant species found in and around the *Agonis* swamps of the northern jarrah forest. A 2 cm by 1 cm oblong was cut from large leaves or the edges were trimmed from smaller leaves to facilitate the separation of the two epidermal surfaces.

The leaf material was then boiled for 2–3 min in a test tube containing 5 mL each of 10% nitric and chromic acid, by which time the mesophyll disintegrated and the two surfaces of the leaf separated. This acid digestion method has been found suitable for Western Australian native plants with their high degree of sclerophylly (Halford *et al*. 1984). The contents of the test tubes were transferred to a beaker and washed several times with distilled water. The plant fragments were drained and transferred to a Petri dish where they were dyed with 0.5% gentian violet in 95% ethanol for 24 h. The Petri dishes were allowed to stand for 30 min before they were washed with decreasing concentrations of ethanol (95%, 70%, 50%) and finally distilled water. The epidermal fragments were then transferred to a microscope slide with a small paintbrush and allowed to air dry before being fixed with DPX permanent mount medium.

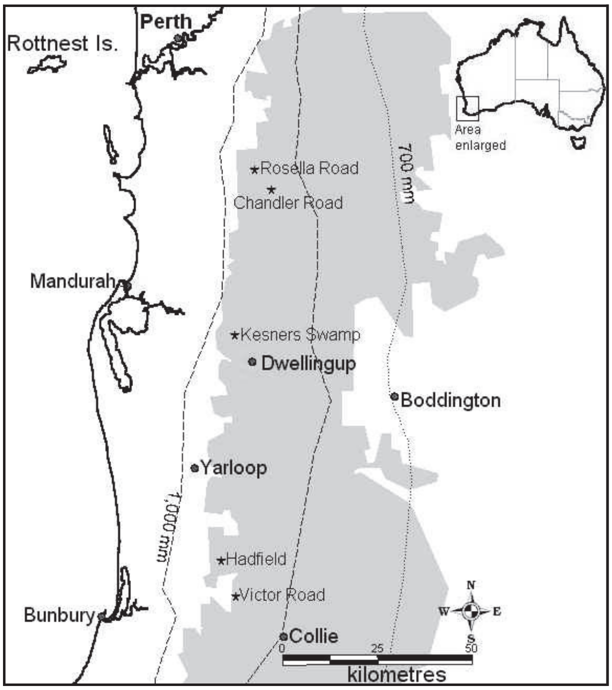

Fig. 1. Location map of the northern jarrah forest (shaded), the study sites (stars) and major towns. The 700-mm and 1000-mm annual rainfall isohyets are shown as dashed and dotted lines respectively.

Line drawings were made of the epidermal tissue patterns and particularly the guard cell complexes to aid identification. A dichotomous key was created based on the arrangement of epidermal cells, the presence of trichomes, stomatal complex types and subsidiary cell variation in a similar fashion to that of Halford *et al*. (1984).

Scat collection

Faecal pellets were collected during seasonal trapping sessions between January 1999 and April 2000 (see Hayward *et al*. 2003 for more details). Faecal pellets left by quokkas in each trap were collected and placed in a labelled paper bag and left to air dry. Pellets containing apple or 'universal' peanut butter mix baits were not collected; these were easy to identify due to their loose texture and unusual colour (pale green for apples or brown for peanut butter mix).

Diet analysis

Three faecal pellets of the first group of pellets collected from an individual during each season were prepared in a similar fashion to the plant reference collection. Dried faecal pellets were separated and then boiled in test tubes of nitric/chromic acid for 1 min. The material from these test tubes was then washed through five sieves with mesh sizes 2.00, 1.00, 0.50, 0.25 and 0.125 mm with distilled water. Any material passing through the smallest sieve was collected on filter paper. Therefore, each sample was divided into six subsamples. Each subsample was transferred into a labelled Petri dish and stained with gentian violet before being permanently mounted on a labelled 25.4 × 76.2 mm slide. The amount of material on each slide was kept to a standard area by minimising the thickness of the leaf fragments to ensure minimal overlap because the scoring method used in estimating dietary composition relied upon each fragment having equal weight in the counting (Luo *et al*. 1994).

Estimation of dietary composition

The frequency-of-occurrence technique was used to ascertain the diet of the quokka after careful consideration of its problems (see Westoby *et al*. 1976; Norbury and Sanson 1992; Luo *et al*. 1994). Where possible, the food materials left in the faeces of the quokka were identified to species under a light microscope; however, broad food categories were also used to confirm that the quokka obtained more food from browsing than from grazing, digging for fungi or insect predation. These broad food categories were leaf, stem, insects, fungi, seed, pollen and flowers. Worms, animal hairs and sand granules were ignored. Trichomes were also ignored unless they were attached to some leaf fragment that provided positive identification.

Fifty fields of view from each of the six slides per animal were scored under ×100 magnification (10 × 10), although searches for pollen grains and fungal spores were carried out under higher power (×400). Each food item was recorded as present or absent in each field according to the methods of Luo *et al*. (1994). The number of scores for each food item and category was summed over all slides and the percentage of each item or category in the diet was calculated as

$$P_i = (f_i / \Sigma f_i) \times 100\%$$

where i is the ith food item, P_i is its percentage occurrence and f_i is its number of scores (Luo *et al*. 1994). Principal components factor analysis was used to reduce the six broad food categories into three to allow comparison of diets between sites using ANOVA. Statview V5.0

Table 1. Dominant plant species within the swamps, in the bullich–blackbutt ecotonal vegetation and in the surrounding jarrah–marri open forest

The rank of each species is based on the number of quadrats within which each was recorded during habitat surveys (Hayward 2002). The order that plants are listed in each column reflects their abundance rank in that vegetation unit while the number in parentheses after the 11 species (shown in bold) commonly found in the quokka's diet reflects its relative abundance rank, which was used in dietary preference analyses. The eucalypts were excluded from this analysis because they were too tall for quokkas to reach to feed on. An asterisk beside a species indicates that it was recorded to some extent in the diet of the quokka

Agonis swamp shrubland	Bullich–blackbutt open forest	Jarrah–marri open forest
_Agonis linearifolia_* (1)	_Lasiopetalum floribundum_*	_Conostylis aculeata_
_Lepidosperma tetraquetrum_*	_Macrozamia reidlii_	_Lasiopetalum floribundum_*
_Astartea fascicularis_*	**_Mirbelia dilatata_* (2)**	_Xanthorrhoea pressii_
_Conostylis aculeata_*	**_Pteridium esculentum_* (3)**	_Macrozamia reidlei_
_Gahnia decomposita_*	**_Bossiaea aquifolium_* (4)**	_Acacia lateriticola_*
_Acacia divergens_* (6)	_Xanthorrhoea pressii_	_Trymalium ledifolium_*
_Boronia molloyiae_*	_Hibbertia montana_	_Conostylis setigera_
Lepidosperma tennue	_Scaevola calliptera_	_Leucopogon pulchella_
Thomasia species* (5)	_Trymalium ledifolium_*	_Lepidosperma tennue_
_Xyris lacera_*	_Conostylis setigera_	_Hibbertia montana_
_Lepidosperma squamatum_*	_Acacia pulchella_	_Acacia pulchella_
_Pteridium esculentum_* (3)	_Astartea fascicularis_*	_Hypocalymna angustifolia_*
_Acacia lateriticola_*	_Lepidosperma tennue_	_Hibbertia acerosa_
_Hypocalymna cordifolium_*	_Acacia lateriticola_*	_Lepidosperma angustatum_
_Oxylobium lineare_*	**_Acacia divergens_* (6)**	**_Allocasuarina fraseriana_* (7.5)**
_Dampiera hederaceae_* (7.5)	_Lepidosperma squamatum_*	_Scaevola calliptera_
_Lomandra seracea_*	**_Allocasuarina fraseriana_* (7.5)**	**_Mirbelia dilatata_* (2)**
_Mirbelia dilatata_* (2)	**_Chorizema illicifolium_* (9)**	**_Chorizema illicifolium_* (9)**
Lepidosperma angustatum	_Astroloma microcalyx_	
Tetraria capillaris	_Acacia extensa_	
_Acacia alata_*	**_Amphipogon turbinatus_* (10.5)**	
Juncus species*	**_Leptocarpus coangustatum_* (10.5)**	
Aotus cordifolia		

(SAS Institute Inc. 1992–98) computer program was used for this and all statistical operations.

Food plant abundance

The vegetation units in and around the four quokka swamps were mapped (Hayward 2002) and the plants within them were identified and their abundance estimated using the Braun–Blanquet scale. Availability in food-preference studies is greatly affected by scale. Whether to use the food-plant abundance found within an individual's foraging range, its seasonal home range, its annual range or the species' range greatly affects the accuracy. Logistical constraints of adequately assessing plant abundance in 53 home ranges seasonally meant that the potential group foraging area was assessed, based on home ranges. Because of these sources of bias, a conservative preference index was selected that did not require exact availability data (see below).

These plants were then ranked in order of decreasing abundance based on the number of quadrates in each vegetation unit in which each species was recorded (Table 1). Eucalypts (*Eucalyptus* and *Corymbia* species) were excluded from this analysis because their leaves were too high for quokkas to reach in order to feed on them.

Data analysis

Dietary diversity was measured via the Shannon–Wiener diversity index (Krebs 1989),

$$H' = -\Sigma p_i(\ln(p_i))$$

where p_i is the proportional use of the ith food item. The diversity index (H') was calculated for each individual and each value is considered an independent observation, allowing the significance to be tested conventionally (Luo *et al*. 1994). ANOVA was used to compare samples with Scheffe's multiple-contrast *post hoc* test to compare means. Data were arcsine-transformed to improve normality of distribution and reduce heterogeneity of variance in the data.

Food preferences were derived using Johnson's (1980) rank preference index (t_i) where the rank of eaten food items in an individuals' diet (r_i) (from 1 (most used) to x (least used)) is subtracted from the rank of the availability of that food item (s_i) according to the equation:

$$t_i = r_i - s_i.$$

The average rank differences across all individuals were then taken to give an order of relative preferences for all the species in the diet and the smallest average rank indicates the most preferred resource (Krebs 1989). Species whose mean was below zero were considered to be relatively preferred while those whose mean was above zero were considered to be relatively avoided. This method was selected above other more precise measures of preference, such as Jacob's index (Jacobs 1974), because of the known biases in frequency-of-occurrence estimates of diet (Norbury and Sanson 1992) and the imprecision of the forage-availability data, as discussed above. It was thought that preferences highlighted by a more conservative index such as the rank preference index would hold true despite these biases.

Results

In total, 97 quokka faecal samples from 53 individuals were analysed and 29 plant species were identified in the diet of the quokka (Table 1). Overall, plant leaf and stem were the major components, accounting for over 96% of the species'

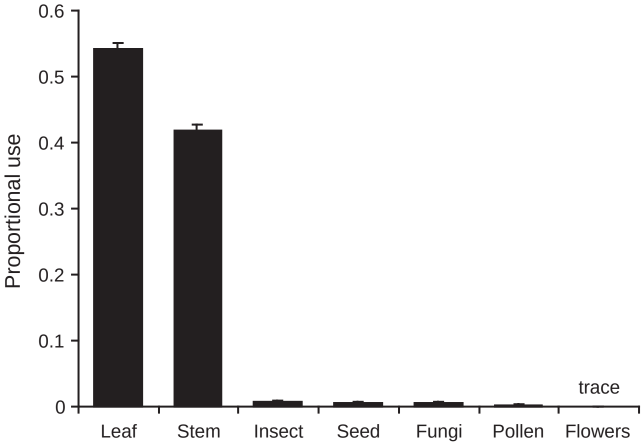

Fig. 2. Proportional use (mean ± s.d.) of broad dietary items for quokkas in the northern jarrah forest.

Table 2. Table of orthogonal factor scores arising from the principal components factor analysis of the broad dietary items in the diet of the quokka

Species	Factor 1	Factor 2	Factor 3
Insect	0.260	–0.025	0.088
Stem	**0.446**	–0.065	–0.069
Seed	–0.008	**0.516**	0.005
Leaf	**–0.467**	–0.017	–0.064
Fungi	0.067	0.012	**0.664**
Flowers	–0.052	**0.527**	0.022
Pollen	0.046	0.021	**0.645**
Variance	**32.8%**	**24.4%**	**15.9%**

diet (Fig. 2). Insect elytra, seed, fungi, pollen and flowers accounted for the remaining 4% (Fig. 2) but are likely to have been incidentally ingested while browsing on plants. There was a negative relationship between the proportion of leaf and stem in the diet ($r^2 = 0.92$, $n = 97$, $P < 0.001$) and this reflects the youngest seral stage available at each site (Victor Road, <5 years after fire; Hadfield, ~5–9 years; Chandler and Kesners, ~10–14 years) (Hayward 2002) (Fig. 3).

Principal components factor analysis of these broad dietary components reduced them to three factors that explained 73.1% of the variability in the data (Bartlett's $\chi^2 = 489.01$, d.f. = 27, $P < 0.01$) (Table 2). The first two factors separated the diets of quokkas at each site and between the seasons. Quokkas at Victor Road had significantly more leaf and less stem in their faecal pellets than quokkas at Hadfield and Kesners (Table 3). In summer, quokkas ate significantly less seeds and flowers than in all other seasons while quokkas at Chandler had more of these two food items in faecal pellets than at all other sites (Table 3).

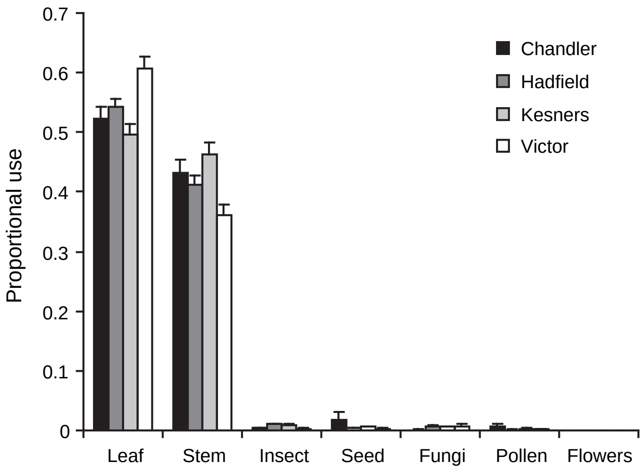

Fig. 3. Proportional use (mean ± s.d.) of broad dietary items for quokkas at each study site in the northern jarrah forest.

Twenty-nine plant species were recorded in the diet of the quokka; however, 11 species dominated the diet and occurred in over 90% of scats of individual quokkas (Table 1). Each of these were dicotyledonous shrubs, confirming that the quokka is a browsing herbivore. Of these, *Thomasia* species were found in the faeces of quokkas (36%) more than twice as frequently as the next most common food species, *Mirbelia dilatata* (15%). Three other species occurred in more than 5% of faeces: *Bossiaea aquifolia* (13%), *Agonis linearifolia* (8%) and *Dampiera hederacea* (7%) (Fig. 4). As well as forming the bulk of faecal pellets, *Thomasia* species were relatively preferred, along with *Dampiera hederacea*, while *Agonis linearifolia*, the dominant plant of the swamps, was relatively avoided (Fig. 4). Of the remaining six dominant species that account for a further 13% of the faeces, *Amphipogon turbinatus* and *Leptocarpus coangustatus* were relatively preferred and *Pteridium esculentum* was relatively avoided (Fig. 4).

Table 3. Two-factor ANOVA table of the Principal Component Factors 1 and 2, comparing each season and the four study sites

Scheffe's *post hoc* tests showed that quokkas at Victor Road had significantly less stem and more leaf in their faecal pellets than quokkas at Hadfield ($P = 0.035$) and Kesners ($P < 0.001$) for Factor 1 scores. For Factor 2 scores, Scheffe's *post hoc* test showed that quokkas ate significantly lower amounts of seed and flowers in summer than in all other seasons ($P < 0.001$ for each) and that quokkas at the Chandler site ate significantly more of these two food items than did quokkas at the other sites ($P < 0.001$)

Comparison	d.f.	s.s.	*F*	*P*
Factor 1				
Season	3	1.77	0.70	0.558
Site	3	11.84	4.64	<0.001
Season × site	9	5.93	0.77	0.641
Residual	81	68.934		
Factor 2				
Season	3	47.02	189.58	<0.001
Site	3	36.40	146.77	<0.001
Season × site	9	73.68	99.03	<0.001
Residual	81	6.70		

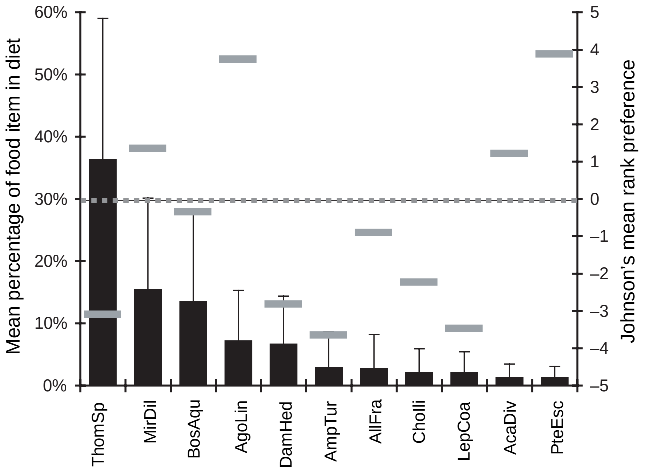

Fig. 4. Overall food use and relative preference for the 11 most common food plants in the diet of the quokka in the northern jarrah forest. Percentage usage in the diet is shown as black bars (mean ± 1 s.d.) and the horizontal lines and squares (grey shading) show Johnson's mean rank preference, with rectangles below the grey dotted line being relatively preferred. Abbreviations for the food plants on the *x*-axis are: ThomSp, *Thomasia* species; MirDil, *Mirbelia dilatata*; BosAqu, *Bossiaea aquifolium*; AgoLin, *Agonis linearifolia*; DamHed, *Dampiera hederacea*; AmpTur, *Amphipogon turbinatus*; AllFra, *Allocasuarina fraseriana*; ChoIli, *Chorizema illicifolia*; LepCoa, *Leptocarpus coangustatus*; AcaDiv, *Acacia divergens*; and PteEsc, *Pteridium esculentum.*

Thomasia species formed more than half the diet in winter and spring and were relatively preferred throughout the year (Fig. 5). *D. hederacea* was also relatively preferred throughout the year (Fig. 5). *B. aquifolia* was eaten in accordance with its relative availability, with increased occurrence in the diet in summer and autumn. Conversely, *M. dilatata* and *A. linearifolia* were avoided throughout the year despite a large increase in the former in the diet over summer (Fig. 5).

Quokkas at all sites showed similar relative preferences for the 11 most common species in the diet (Fig. 6). The most notable difference in diet at each site was the 20% increase in the amount of *Thomasia* in the diet of quokkas at Victor Road compared with the other sites (Fig. 6).

The 29 plant species recorded in the diet were separated by their location relative to the swamp into three areas: inside the swamp, along the edge of the swamp in bullich–blackbutt open forest, and outside the swamp in the jarrah forest communities (Table 1). There was no significant difference in what quokkas ate outside the swamp seasonally or between the sites; however, quokkas ate more plants from inside the swamp in spring and winter, compared with autumn and summer when they ate more plants from the edge of the swamp (Table 4). Quokkas at Chandler had more plants from inside the swamp in their faeces than did those at Kesners; and quokkas at Victor Road ate more plants from inside the swamp and fewer plants from the swamp edge than did those at Hadfield and Kesners (Table 4).

Quokkas at Victor Road had a significantly lower diversity of plants in their diet than did the quokkas at all other sites (Table 5). There was no significant seasonal difference in dietary diversity overall although quokkas at Victor Road had a more diverse diet in autumn than in the other seasons (Table 5).

Sample sizes at some sites were not large enough to allow a three-factor ANOVA to compare sex, site and season but, generally, where two-factor ANOVA compared sex and the other two variables there was no significant difference for broad diet, location of food plants and specific diet. The

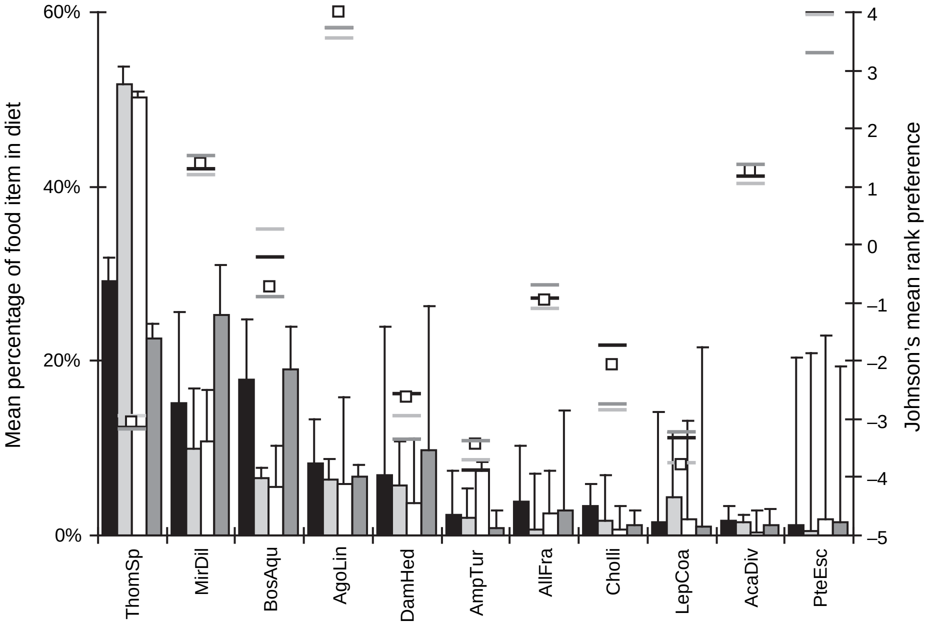

Fig. 5. Seasonal food use and relative preference for the 11 most common food plants in the diet of the quokka in the northern jarrah forest. Percentage usage in the diet is shown as bars (mean ± 1 s.d.) and the horizontal lines and squares show Johnson's mean rank preference: autumn (black, *n* = 38), winter (light grey, *n* = 20), spring (white, *n* = 18), summer (dark grey, *n* = 21). Abbreviations for the food plants on the *x*-axis are as for Fig. 4.

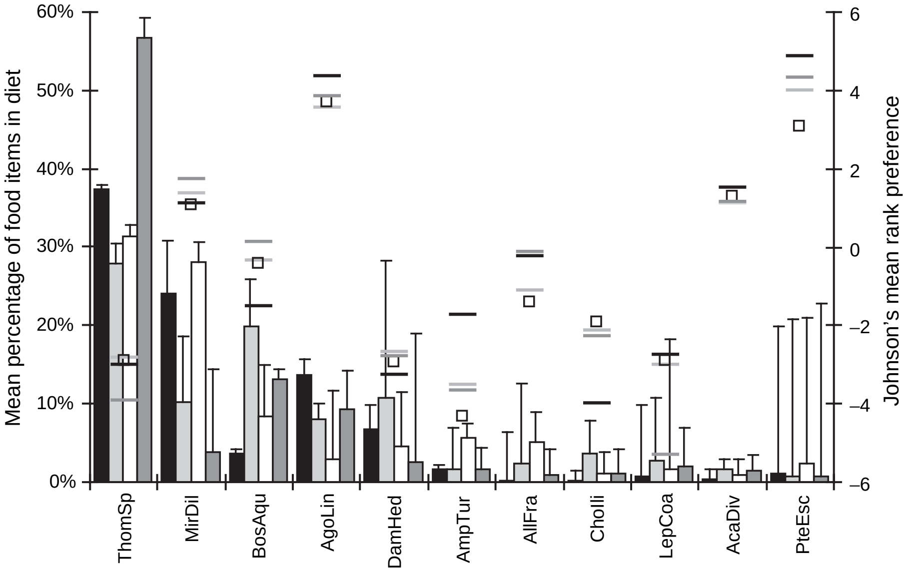

Fig. 6. Food use and relative preference for the 11 most common food plants in the diet of the quokka at the four study sites in the northern jarrah forest. Percentage usage in the diet is shown as bars (mean ± 1 s.d.) and the horizontal lines and squares show Johnson's mean rank preference: Chandler (black), Hadfield (light grey), Kesners (white), Victor Road (dark grey). Abbreviations for the food plants on the *x*-axis are as for Fig. 4.

exception was dietary diversity: males had significantly greater dietary diversity than females (Table 5; Fig. 7).

Discussion

As elsewhere, quokkas are browsing herbivores; however, in the northern jarrah forest they have a distinct preference for leaf and stem of more succulent, trichome-bearing, dicotyledonous species such as the two *Thomasia* species (*T. pauciflora* and *T. paniculata*) and *Dampiera hederacea.* Eleven plant species made up 90% of the quokka's diet and five of these accounted for 79% of the diet. Despite a preference for these species, the 29 species recorded in the quokka's diet here and the range of habitats that the quokka occurs in throughout its distribution (Hayward 2002) suggests that its tastes are broad and that dietary deficiencies are not the cause of its threatened status. Indeed, two of the five individuals that died, and were not preyed upon, possessed large fat stores in the body cavity when autopsied (Hayward 2002).

While diet does not appear to be a limiting factor to the quokkas at the sites studied here, the relationship between several of the most important food plants and post-fire seral

Table 4. ANOVA table of the location of food plants found in the quokka diet, comparing each season and the four study sites

Scheffe's *post hoc* tests showed that quokkas ate more plants inside the swamp in spring and winter than in autumn and summer ($P < 0.001$ for each) and that quokkas at the Chandler site ate more plants inside the swamp than did quokkas at Kesners ($P = 0.024$), and Victor Road quokkas ate more swamp plants than did quokkas at Hadfield and Kesners ($P < 0.001$ for each). Similarly, quokkas ate more plants at the edge of the swamp in summer and autumn than in spring and winter (Scheffe's *post hoc* test, $P < 0.001$ for each) while quokkas at Victor Road ate fewer plants from the edge of the swamp than did quokkas at Hadfield and Kesners ($P < 0.001$ for each)

Comparison	d.f.	s.s.	*F*	*P*
Inside				
Season	3	0.58	10.19	<0.001
Site	3	0.57	10.08	<0.001
Season × site	9	0.37	2.14	0.035
Residual	81	1.54		
Edge				
Season	3	0.60	11.21	<0.001
Site	3	0.32	5.96	0.001
Season × site	9	0.364	2.26	0.026
Residual	81	1.45		
Outside				
Season	3	0.01	0.31	0.818
Site	3	0.05	1.89	0.137
Season × site	9	0.06	0.90	0.529
Residual	81	0.64		

Table 5. Three two-factor ANOVA results of dietary diversity (H′) comparing each season, sex and the four study sites

Scheffe's *post hoc* tests showed that quokkas at Victor Road had significantly lower dietary diversity (H′) scores than did those at all other sites (Chandler, $P = 0.004$; Hadfield and Kesners, both $P < 0.001$), and the autumn diet there was more diverse than in other seasons ($P < 0.001$)

Comparison	d.f.	s.s.	*F*	*P*
H′ – Season	3	2.76	1.73	0.168
Site	3	14.95	9.36	<0.001
Season × site	9	11.69	2.44	0.017
Residual	81	43.15		
H′ – Sex	1	0.92	1.50	0.225
Site	3	16.58	9.01	<0.001
Sex × site	3	0.54	0.29	0.830
Residual	89	54.57		
H′ – Sex	1	4.96	6.69	0.011
Season	3	4.20	1.89	0.137
Sex × season	3	3.61	1.62	0.190
Residual	89	65.94		

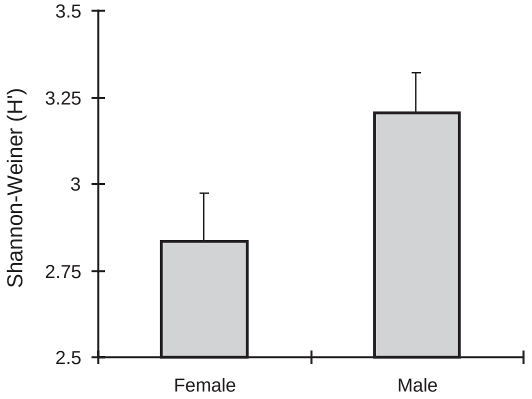

Fig. 7. Mean (± 1 s.d.) Shannon–Weiner dietary diversity (H′) of male and female quokkas in the northern jarrah forest.

stage helps to explain the habitat requirements of the quokka (Christensen and Kimber 1975; Hayward 2002). Quokkas require a mosaic of seral stages at a site to persist (Hayward 2002). The requirement for young (<10 years after fire) stages is likely to be for food while long-unburnt areas (>25 years) are thought to provide refuge from predation and also food immediately after a fire (Hayward 2002). The results of this study support the theory that the dietary requirements of the quokka may be met only during these early post-fire seral stages, and therefore explain why sites become unsuitable for quokkas 10 years after a fire (Hayward 2002). Such short-term requirements would originally have driven a regular cycle of localised extinction and colonisation of isolated habitat patches as part of a functioning metapopulation (Hayward *et al*. 2003, 2004).

The lack of seeds recorded in the quokka's diet by Storr (1964*b*) was intimated as being due to inappropriate techniques (Jarman 1994). While seeds now have been recorded in the diet of the quokka with this technique, seeds and the other 4% of the diet made up of insects, fungi, pollen and flowers are considered to have been incidentally injested during browsing on leaves and stems.

It has also been suggested that quokkas consume a large amount of fungi in their diet (Christensen 1980; Chapman 1999). Despite detailed specific searches and assistance from experts using different stains and preparation methods (E. A. Jefferys, personal communication; Luo *et al*. 1994), only a very small number of fungal spores were found. This is supported by the dearth of sand or soil particles in the faecal pellets, which indicates that quokkas were not digging for the fungi they ingested.

The increase in the proportion of some plant species in the diet in different seasons may relate to the annual period of growth of these plants. Increases in the proportion of *Thomasia* species in the diet in winter and spring, *B. aquifolia* in summer and autumn, and *M. dilatata* in summer probably reflect increases in nutrients (particularly nitrogen) available in the fresh growth of the plants (Storr 1961*b*). Seasonal variation in the diet has also been observed in quokkas on Rottnest Island. At the end of the long, dry summer period the quokka selects succulent plants such as *Carpobrotus* and *Rhagodia*, which are high in water content but low in nutrients; however, at the start of the winter rains it selects relatively nutrient-rich but water-deficient shrubs (Storr 1964*b*).

Similarly, the higher proportion of *Thomasia* species in the diet of quokkas at Victor Road than at the other sites probably relates to the rapid growth following the fire that occurred less than five years before this study. The relationship between fire and plant growth in each swamp (Hayward 2002) probably also explains the significant relationship found between the proportion of leaf and stem in the diet and the fire history of a site. The higher proportion of foliage in the diet of quokkas at Victor Road than at the other sites may explain the reduced dietary diversity of this site where nutrient requirements may be satisfied by the increased amount of nutrient-rich leaf and fresh growth of the *Thomasia*. There may be a succession of food plants in the diet with vegetation succession following fire, from the more succulent species such as *Thomasia* to the more scleric species such as *M. dilatata* (Fig. 6). Nonetheless, the impact of predation pressure on this unbaited site (compared with monthly baiting to control European red fox (*Vulpes vulpes*) numbers at the other sites) (Hayward *et al*. 2003) cannot be discounted, as quokkas from the Victor Road site do eat more plants from inside the swamp than do those at the more heavily baited sites.

The seasonal variation in the location of plants eaten probably also reflects the growth period of those plants. During the wetter months of spring and winter, more plants are eaten from inside the swamps, although this is likely to be from the inside edge of the swamp vegetation because of the inundation of the swamp and the relocation of quokkas to its edge at this time (Hayward *et al*. 2004). The drying of the swamp in summer and autumn leads to an increase of plants eaten from the edge of the swamp as the search for sufficient nutrients and water leads to a corresponding increase in home-range size (Hayward *et al*. 2004). The high water requirements of the quokka may also be satisfied at this time by its foraging behaviour by seeking dew on the leaves of plants to increase water uptake, as occurs on Rottnest Island (Main and Bakker 1981).

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