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ORIGINAL ARTICLES

Relationships between food quality and reproductive success in female red-necked wallabies *Macropus rufogriseus banksianus*

Karen Higginbottom

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This study indicates that even in the absence of overt intraspecific competition, fine-scale spatial variation in food quality can lead to individual variation in reproductive success. Life history data on individual female red-necked wallabies *Macropus rufogriseus banksianus* were obtained over a six-year period. Vegetation surveys were conducted to analyse the composition of vegetation in the feeding range of each female, from which individual food quality indices were derived. Females' rates of rearing offspring to permanent emergence from the pouch and to weaning were positively correlated with the quality of food in their feeding ranges. Time spent in the pouch by offspring and age at first parturition of daughters were negatively correlated with maternal food quality. It is proposed that quality of available food affects growth rates and survival of offspring through its effects on maternal lactation and/or forage intake by offspring.

Key words: Ideal Free Distribution, Macropodidae, nutrition, reproductive success

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Under the Ideal Free Distribution model, individuals in a population are distributed in relation to their resources so that individual resource intakes and fitnesses are equalised (Fretwell & Lucas 1970). This situation is expected to apply where individuals are able to move freely and have equal competitive abilities. The concept has been applied mostly to situations where limited resources occur as items of similar quality or in discrete patches (Kennedy & Gray 1993). In such situations it is predicted that an increased density of competitors will cause increased exploitation competition (*sensu* Krebs & Davies 1987), which in turn will lead to a corresponding reduction in individual intake or access rates.

In large polygynous mammals, the most critical resource limiting female reproductive success is ex-

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pected usually to be food (Trivers 1972, Clutton-Brock, Guiness & Albon 1982, *cf.* Forchhammer, Stenseth, Post & Langvatn 1998). A female mammal's nutritive intake can affect diverse aspects of her life history such as survival of herself and her offspring, reproductive rate, litter size, age at first breeding, milk yield, and weight and growth rate of offspring (Austin & Short 1972, Gilmore & Cook 1981, Iason, Duck & Clutton-Brock 1986, Lee 1987, Robertson, Hiraiwa-Hasegawa, Albon & Clutton-Brock 1992, McGuire, Littleton, Schulze & Rasmussen 1995). In non-territorial species that feed on diffusely distributed vegetation, and for which food quality rather than quantity affects reproductive success (Krebs & Davies 1987), the effects of exploitation competition should be much lower than in the scenario described above. In such species, heavy clumping of individuals around high-quality resources might be expected to occur and to be associated with equalised fitness.

The only research on non-territorial mammals to have examined the relationship between spatial variation in food quality and reproductive success has been on red deer *Cervus elaphus* on the Island of Rum. Iason et al. (1986) found that female deer feeding on high-quality food had higher reproductive success than those feeding elsewhere. Using a more comprehensive measure of reproductive success and a broader spatial scale (but excluding the above 'high-quality' group of females), Conradt, Clutton-Brock & Guiness (1999) found that higher densities of deer feeding in the higher quality areas led to equalising of reproductive success between areas. Further field studies are needed to test the Ideal Free Distribution model empirically.

The red-necked wallaby *Macropus rufogriseus banksianus* (Desmarest) is a polygynous and relatively solitary medium-sized macropodid marsupial lacking a tightly structured social organisation (Calaby 1966, Johnson 1989a). Unlike males, adult females occupy home ranges that are relatively stable from year to year (Johnson 1987, pers. obs.). The diet of red-necked wallabies consists of grasses, forbs and shrubs; the relative proportions of these in the diet of different populations apparently being habitat dependent (*cf.* Finlayson 1930, Kaufmann 1974, Dawson 1989, Jarman & Phillips 1989). These food resources are diffusely distributed, and so are probably not economically defendable (Krebs & Davies 1987). As in most other macropodids, territoriality or overt agonistic behaviour relating to food resources does not typically occur (Croft 1989, Jarman 1994). Thus, it might be expected that individual feeding areas would be heavily clumped into areas of optimal food quality and that individual differences in reproductive success relating to differences in food intake would be minimal.

Like most macropodids, female red-necked wallabies display embryonic diapause associated with lactational quiescence and post-partum oestrus, the latter occurring less than two hours after parturition (Merchant & Calaby 1981, Tyndale-Biscoe & Renfree 1987). In captivity, the oestrus cycle averages 33.4 days and pouch-life averages 284.9 days (Merchant & Calaby 1981), but there are no published figures for age at weaning. The only published estimates of survivorship have been obtained from an earlier study on the present population, and showed that only 50% of young that emerge permanently from the pouch survive till weaning (Johnson 1989b). Dingoes *Canis familiaris dingo* occur commonly in the study area (Jarman & Wright 1993) and are thought to be the main proximate cause of mortality of macropodids, while foxes *Vulpes vulpes* are very rare (Jarman, Johnson, Southwell & Stuart-Dick 1987).

The present study of a population of red-necked wallabies investigates whether spatial variation in the quality of food available to individual females (as a consequence of the females' spatial distribution) is related to several aspects of their life-histories that are expected to contribute to their reproductive success. It then briefly examines the implications of these findings with regard to theoretical predictions on the spacing of individuals within populations. This is the first published field study to have investigated these relationships at the intra-population level in marsupials.

Methods

General

The 144-ha study area (the western portion of the area described by Jarman et al. 1987) is situated in a valley called 'Wallaby Creek' (152°45'E, 28°45'S) in subtropical northeast New South Wales, Australia, consisting mostly of semi-cleared cattle grazing properties. The study area was inhabited by a median of 61 adults and subadult red-necked wallabies, including 40 adult females. Females occupied overlapping home ranges of a median 11.8 ha (Johnson 1986, pers. obs.).

Data were collected during monthly field trips of

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about 10 days' duration. All adults were individually recognisable based on their natural features (Jarman, Jones, Johnson, Southwell, Stuart-Dick, Higginbottom & Clarke 1989) and well habituated to human observers. Observations were carried out on foot with the aid of binoculars.

Wallaby locations and activity

The study area was marked with a rectangular grid, which divided it into 50 x 50 m grid squares, and allowed the location of each sighted wallaby to be described within a radius of 10 m.

Between November 1984 and October 1987 inclusive, I carried out monthly systematic censuses of the study area designed to provide even coverage of the whole area during all seasons of the year. Each census followed a standard route planned to allow all parts of the area to be thoroughly scanned for any wallabies present. Each time I sighted a wallaby, I recorded its activity when first seen. I recorded a wallaby as feeding if it was in a feeding posture or if vegetation could be seen in its mouth.

Female life history variables

Life history data for each known female were recorded during monthly visits from March 1981 to July 1984 by C. Johnson, and in more detail from August 1984 to October 1987 by myself, including a continuous period from July 1986 to February 1987. We made specific efforts to find and observe females and their offspring during key parts of their life-history cycles. We inferred the timing of oestrus from the behaviour of courting males (Johnson 1989a), and of parturition from the timing of oestrus and the absence of another oestrus event about 33 days later (the average length of an oestrous cycle). The maximal set of life history data for each female included timing of each successive parturition, timing of permanent emergence from the pouch (PEP) of each offspring, timing of weaning of each offspring, timing of death (disappearance) of each immature offspring, and timing of first parturition of each female offspring. From these data I determined the following for each offspring: whether or not it survived to weaning, pouch-life duration, young-at-foot (YAF) duration (interval between PEP and weaning); and for female offspring, their age at first parturition. In total, we obtained records on one or more of these variables for 240 offspring, produced by 28 females.

I then calculated the following life-history variables for each adult female (number of females given in brackets) over the entire study period:

- PEP Rate: rate (per year) of producing offspring to permanent emergence from the pouch (N = 20)
- Weaning Rate: rate (per year) of producing offspring to weaning (N = 20);
- Parturition Age of Daughters: mean age of daughters giving birth to their first offspring (N = 15).
- Pouch Life: mean duration of offsprings' pouch lives (N = 21);
- YAF Duration: mean young-at-foot duration of offspring (N = 19);

For the first three of these variables, only females with at least five years of records were used. Pouch Life and YAF Duration were based on 2-6 records per female.

Diet, vegetation and food quality indices

According to faecal analyses, red-necked wallabies at Wallaby Creek are predominantly grazers, feeding mostly on the leaves of introduced short grasses (Jarman & Phillips 1989). My observations indicated that they fed almost exclusively on green plant parts.

Differences in farm management regimes and topography gave rise to considerable spatial variation in vegetation composition across the study area. This involved, firstly, variation in the predominance of introduced short pasture species; the most common being carpet grass *Axonopus affinis*, paspalum *Paspalum dilatatum* and kikuyu *Pennisetum clandestinum*, which constitute the understorey herbaceous layer. Secondly, it involved variation in overstorey herbaceous species such as snow grass *Poa labillardieri* and blady grass *Imperata cylindrica*. In particular, the part of the study area consisting of the most 'improved pasture', the southern flats, consisted of a much higher cover of introduced short pasture species than the north/upslope areas (pers. obs.). There were also large seasonal differences in vegetation composition, with total green herbaceous biomass being much greater in summer than in winter (Southwell 1987).

I conducted herbaceous vegetation surveys in winter (August) 1985 and 1986 and in summer (February) 1986 and 1987. These excluded the western portion of the study area that was all heavily forested, since analysis of faecal contents (Jarman & Phillips 1989) and my observations indicated that the amount of feeding in these areas was negligible. The biomass of live vegetation is highest in summer and lowest in winter, and the relative abundance of the common plant species differs substantially between these seasons (J. Clarke, unpubl. data; pers. obs.).

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Top-cover (*sensu* Grieg-Smith 1983) percentages of each defined component of the ground cover, summing to 100%, were estimated in 60 x 60 cm quadrats located at 10 m intervals throughout most of the study area, using a modified step point technique. These included the green component of each of the common understorey plant species (carpet grass, kikuyu, paspalum and clover *Trifolium repens*), the green component of categories of all less common understorey species (e.g. 'Other leafy forbs' included all leafy forbs other than clover), the brown component of all understorey species, all overstorey species, bare ground, and other non-herbaceous vegetation components, e.g. trees, human-made objects. In addition to these components of the ground cover (that summed to 100%), the percent area that was overlain by overstorey herbaceous species was estimated. I refer henceforth to all the above as 'cover components'. The percent cover of each of these components was calculated for each 50 x 50 m grid square as the mean across quadrats for that grid square.

Given time limitations, it was not possible to survey the entire study area in any one survey. The first winter and summer surveys covered 78.25 ha and 63.75 ha, respectively. Areas not included in the first survey were included in the second survey in the same season (total areas of 50.75 ha and 53.75 ha, including repetition of 72 and 65% of the first survey's area, for winter and summer, respectively). For each cover component, the ratio between the mean percent cover over all repeated grid squares for the first survey and that for the second survey in the same season was calculated. Then percent cover values of each component for each grid square that was measured only in the second survey were multiplied by the relevant ratio to provide an estimate of the value applying at the time of the first survey. Thus measures of each cover component were available for all grid squares as expected to apply in winter 1985 and summer 1986. These were the survey years with climatic conditions that were most similar to the long term average patterns, and thus assumed to offer 'typical' food quality for winter and summer, respectively.

A female's feeding range for a specified season (summer or winter) was defined as the complete set of 50 x 50 m grid squares where she had been recorded feeding during population censuses in that season over the period July 1985 to June 1987 inclusive. Only females with at least 10 records were included, but most had at least 20 records. The food composition (percent cover of the different cover components) of each female's feeding range was calculated as the mean across all quadrats within her range. This yielded data on feeding ranges of 33 females in winter, and 34 in summer. However, feeding range data were not available for all females for which values of life history variables were obtained, nor vice versa.

Food quality indices for individual females were calculated from data on the composition of individual females' feeding ranges, with separate indices derived for winter and summer (based respectively on the winter and summer vegetation survey data). Each index was based on that aspect of the vegetation considered to be most critical to wallabies' nutrient intake, as follows:

- Ground: percent area not overlain by overstorey herbaceous vegetation, which is expected to be positively correlated with the time and energy required to access the understorey vegetation. (However, this overstorey vegetation also provides concealment to wallabies, which may assist in predator avoidance);
- Green: percent cover of green vegetation of all species;
- Selected: percent cover of all species for which wallabies showed positive dietary selection (kikuyu, paspalum and clover). Selected species were defined as those that were significantly more abundant in patches where wallabies were seen feeding than in the grid square as a whole (pers. obs.). These also tended to be the species highest in nitrogen and lowest in fibre (J. Clarke, unpubl. data), and therefore expected to be of the highest nutritive quality (*cf.* Hume 1982, Jones & Wilson 1987);
- Clover: percent cover of clover. This was the food species most heavily selected by wallabies; it had the highest nitrogen content and lowest fibre content (J. Clarke, unpubl. data).

Statistical analyses

Relationships between food quality indices applying to females' feeding ranges, and between those food quality indices and life history variables, were tested using Spearman's rank correlations, as some of these variables displayed significant deviations from normality. In the absence of a suitable non-parametric equivalent, backward stepwise multiple linear regression analyses were conducted to test which combina-

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Table 1. Variability in life-history variables for female red-necked wallabies at Wallaby Creek.

Life history variable	Median	SD	Min.	Max.	N
PEP Rate (offspring/year)	1.18	0.08	1.00	1.26	20 adult females
Weaning Rate (offspring/year)	0.60	0.21	0.32	1.01	20 adult females
Parturition Age (months)	25	4.9	17	34	25 daughters
Pouch Life (months)	9.5	0.9	7.0	11.5	115 offspring
YAF Duration (months)	4.8	0.7	3.5	5.5	31 offspring

Table 3. Correlations (Spearman rank) between food quality indices applying to females' feeding ranges. All correlations were significant at $P < 0.05$. See text for definitions of quality indices.

	Green	Clover	Selected
Summer feeding ranges (N = 34 females)			
Ground	0.47	0.56	0.88
Green		0.29	0.51
Clover			0.67
Winter feeding ranges (N = 33 females)			
Ground	0.62	0.57	0.62
Green		0.93	0.95
Clover			0.97

tion of food quality indices best predicted the numbers of sightings of feeding wallabies within grid squares (Zar 1996). They were also used to test whether any combination of food quality indices provided a better predictor of each life history variable than did a single index. The food quality of feeding ranges in different parts of the study area was compared using Mann-Whitney tests. An F_{max}-test was used to test for differences in variability of food quality indices between seasons.

Results

There was substantial variation between individual female wallabies at Wallaby Creek in PEP Rates and Weaning Rates, and between individual offspring in duration of the various life-history stages (Table 1). Females usually bred continuously, but in an estimated 13% of 223 cycles an interruption occurred in reproduction, apparently through a combination of losses of pouch young, failure to produce or maintain viable blastocysts, and anoestrus (Higginbottom & Johnson 2000). High mortality (41%) occurred during the young-at-foot stage (N = 212 young-at-foot). There was also substantial variation between females in composition of feeding ranges, and in associated food quality indices (Table 2).

There were significant correlations between all food quality indices, although these were smaller in summer than in winter, and lower for Ground than for the other indices during winter (Table 3).

There were significant correlations with one or more food quality indices for all life-history variables except YAF Duration (Table 4). The higher the quality of food available to a female, the higher her rate of raising offspring to weaning and to permanent emergence from the pouch, the earlier her offspring emerged from the pouch, and the earlier her daughters gave birth to their own first offspring. There was also a trend for high availability of clover in the summer feeding range to be associated with relatively long young-at-foot durations.

Mean duration of pouch life, mean age of daughters at first parturition, and PEP rate were all more strongly correlated with the percent cover of all green

Table 2. Percentages of each cover component in feeding ranges of adult female wallabies. Measures for the vegetation refer to green components only unless otherwise indicated. Whether a plant species is defined as 'leafy' or 'stemmy' depends on whether >50% of its biomass typically comprises leaf or stem; the former are of higher nitrogen and lower fibre content than the latter (J. Clarke, unpubl. data). The last three measures listed, as well as clover, are food quality indices (see definition in text).

	Summer feeding range (N = 34)			Winter feeding range (N = 33)		
Cover component	Mean (%)	SD	Range (%)	Mean (%)	SD	Range (%)
Overstorey species	20	8	31	14	7	33
Carpet grass	34	7	26	15	4	14
Kikuyu	8	7	23	4	4	13
Paspalum	12	6	27	3	2	7
Clover	2	1	4	10	8	28
Other leafy forbs	2	0.7	3	4	1	5
Other leafy grasses	8	3	11	3	2	12
Stemmy grasses	0.5	0.5	1	0.2	0.3	1
Brown vegetation	14	4	13	43	7	30
Bare ground	5	2	11	10	6	22
Other	7	4	17	5	2	11
Ground	80	8	31	87	6	28
Green	76	6	28	44	11	43
Selected	23	10	36	17	12	40

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Table 4. Correlations (Spearman rank) between life history variables and food quality indices in winter and summer feeding ranges of individual female wallabies. One-tailed significance levels (P) are *** P < 0.01, ** P < 0.05, * P < 0.1.

Life history variable	Feeding range	Food quality index				Number of females
		Ground	Green	Selected	Clover	
Pouch Life (months)	Winter	-0.15	-0.56***	-0.50**	-0.53**	18
	Summer	-0.32*	-0.30	-0.43**	-0.54***	19
YAF Duration (months)	Winter	-0.18	0.01	0.11	0.17	19
	Summer	0.007	0.11	0.20	0.38*	19
Parturition Age of Daughters (months)	Winter	0.03	-0.59**	-0.58**	-0.55**	15
	Summer	-0.39*	0.11	-0.43*	-0.33	15
PEP Rate (offspring/year)	Winter	0.05	0.44**	0.32*	0.33*	20
	Summer	0.22	0.25	0.21	0.12	20
Weaning Rate (offspring/year)	Winter	-0.18	0.20	0.23	0.36*	20
	Summer	0.46**	-0.26	0.30	0.27	20

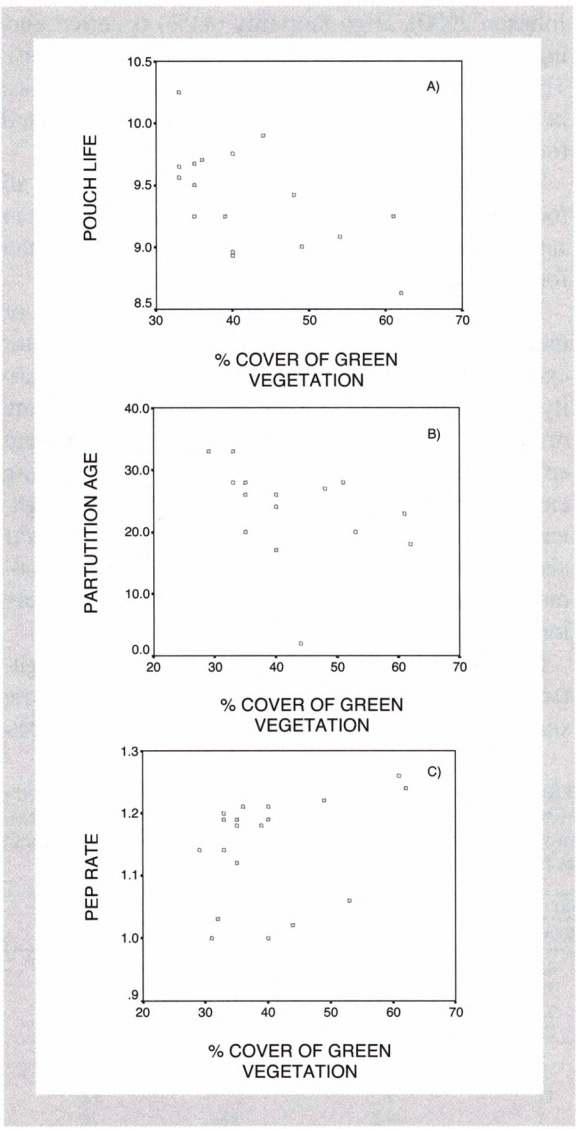


Figure 1. Relationships between the life history variables Pouch Life (A: in months), Parturition Age of Daughters (B: in months) and PEP Rate (C: number of offspring/year) and percent cover of green vegetation in winter.

vegetation in winter (Green) than with any other quality index (Fig. 1). Weaning rate was significantly correlated only with the percent area not overlain by overstorey vegetation (Ground; Fig. 2).

In all cases where there was a significant correlation of a food quality index with Pouch Life, PEP Rate, or Parturition Age of Daughters, the correlation coefficient was greater for winter than for summer (see Table 4). For the single significant correlation with Weaning Rate, the correlation coefficient was greater in summer.

Further examination of the association between PEP rates and food quality indicated that it was due to females with high food quality not only having offspring with short pouch-life durations, but also having low rates of reproductive interruptions (sample sizes were insufficient to test the latter separately).

For each life history variable, multiple linear regression analyses revealed that a single food quality index was as good a predictor of that variable as were the various combinations of indices. The variation between grid squares in total number of sightings of

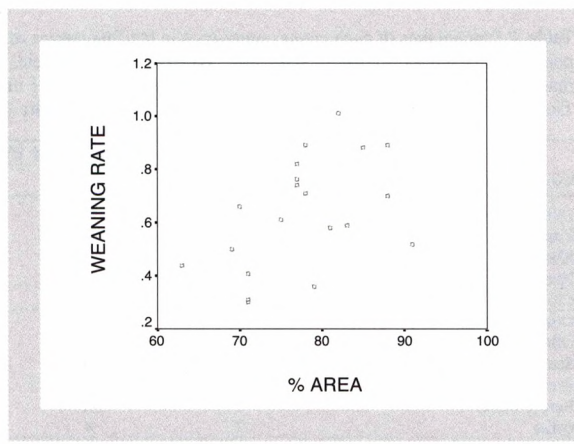


Figure 2. Relationship between Weaning Rate and percent area not overlain by overstorey herbaceous vegetation in summer

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Table 5. Best-fit multiple linear regressions of numbers of sightings of feeding wallabies on food quality indices.

Food quality index	Coefficient (B)	SE	Partial r	F for coefficient	Significance of F
Summer[1]					
Selected	0.69	0.12	0.31	35.8	0.0000
Ground	0.43	0.10	0.23	19.3	0.0000
Constant	-0.97				
Winter[2]					
Selected	0.56	0.11	0.26	26.2	0.0000
Ground	0.46	0.11	0.21	16.8	0.0001
Constant	-0.97				

[1] Test of significance of regression equation: F (df = 2) = 47.3, P = 0.0000. Adjusted multiple $R^2 = 0.21$

[2] Test of significance of regression equation: F (df = 2) = 35.1, P = 0.0000. Adjusted multiple $R^2 = 0.159$

Table 6. Comparisons of food quality of feeding ranges between the southern flats and north/upslope areas. Mann-Whitney U tests were used to compare food quality indices applying in summer and winter feeding ranges between females with the majority of their feeding ranges in the southern flats (N = 17) and those with the majority of their feeding ranges in the north/upslope area (N = 13). In all cases where the difference was statistically significant, food quality was higher in the southern flats than north/upslope. Significance levels (P) are *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$, NS non-significant.

	Summer		Winter	
Food quality index	Z	P	Z	P
Ground	4.3	***	2.3	**
Green	1.4	NS	4.1	***
Selected	4.5	***	4.4	***
Clover	3.2	***	4.2	***

all feeding wallabies, however, was best predicted from the independent and positive contributions of Selected and Ground indices (Table 5). This applied to both summer and winter.

Food quality according to all indices except Green in summer was higher on the southern flats than north/upslope in both summer and winter feeding ranges (Table 6). There was much greater variability between female feeding ranges in winter than in summer for Green and Clover indices, and slightly more variability in Ground during summer than during winter (Table 7).

Discussion

In this study, I found that food quality available to individual female red-necked wallabies was related to several aspects of their life histories. If these relationships were causal, then access to high-quality food enables a female to have a high rate of reproduction and of weaning of young, offspring with short pouch lives and possibly long young-at-foot durations, and daughters that give birth to their own first offspring relatively early.

However, inferring a causal effect first requires elimination of other variables with a spatial distribution related to that of food quality which could influence life history variables. Weaning rate, which is influenced principally by juvenile survivorship, is the aspect of life history most likely to be influenced by variables other than those relating to nutrition.

First, survivorship of offspring might be positively influenced by the availability of areas providing effective concealment and/or escape routes from predators. This explanation can be excluded since (i) the smaller the area overlain by overstorey vegetation (which usually conceals wallabies), the higher the Weaning Rate, and (ii) forested areas, which provide excellent concealment and escape routes for wallabies (pers. obs.), were associated with relatively poor food quality.

Second, it is possible that spatial variation in the intensity of predation pressure led to spatial variation in survivorship of young wallabies. Consistent with this explanation was the finding that dingoes were most frequently seen on the middle and upper slopes of the study area (Southwell 1987), where food quality was on average lower than on the southern flats. However, weaning rates of females with core areas including the northern flats were significantly lower than those of females with core areas including the southern flats (MWU $Z = 2.75$; $P < 0.01$; $N_1 = 7$, $N_2 = 7$), despite no significant differences in dingo

Table 7. Test for differences in variability of the four food quality indices between females' summer and winter feeding ranges. The F_{max}-test was conducted based on records derived from 34 females in summer and 33 in winter.

	Summer		Winter		F_{max}-test	
Food quality index	Mean	SD	Mean	SD	F	P
Ground	80.4	7.8	86.6	5.9	4.19	0.045
Green	75.6	5.7	43.6	10.8	17.53	0.000
Selected	22.5	10.4	16.9	12.2	1.43	0.236
Clover	2.4	1.0	9.8	7.7	76.77	0.000

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sightings between these areas. Nevertheless, this explanation cannot be totally dismissed given lack of direct information on spatial variation in predation risk.

The net result of the relationships found in my study was that adult females with access to relatively high amounts of good quality food could be expected to experience relatively high reproductive success. As in other mammals studied in this context (Clutton-Brock 1988), the primary contributor to a female red-necked wallaby's reproductive success is her own survival to weaning, and of secondary importance is the rate at which she weans offspring. Weaning rate is in turn maximised by short pouch-life durations, continuous reproductive cycles, and high survival of offspring. It is also possible that by beginning to breed at a relatively early age, daughters of females with high food quality may enhance their reproductive success.

The validity of any suggested mechanisms to explain the relationships between food quality and life-history indices is hindered by a paucity of studies that elucidate the relationships between food intake, lactation and life history variables of macropodids. However, the following proposed explanations are most consistent with available information.

I propose that the shorter pouch lives of offspring of females with high food quality were due to these females having relatively high milk outputs, reflected in relatively high growth rates of pouch young, so that they reached critical size for permanent emergence from the pouch relatively early (*cf.* Janssens & Rogers 1989). This is consistent with the finding of Green, Merchant & Newgrain (1988) that captive tammar wallabies *Macropus eugenii* varied greatly in milk consumption during late pouch life, which was directly reflected in variation in their growth rates.

The relationship between food quality and PEP rates indicates that in addition to affecting growth rates, good nutrition may be important in maintaining continuous reproductive cycles. Such an effect has not been recorded for red-necked wallabies before. However, the lack of ability to statistically separate the effect of nutrition on incidence of reproductive interruptions means that this conclusion remains tentative.

I suggest that daughters of females with high food quality reached sexual maturity relatively early mainly because they had access to good quality forage (in the home range they shared with their mothers), perhaps enhanced by good nutrition during pouch life. Typically in mammals, sexual maturity is related to attaining a certain critical weight (e.g. Sadleir 1969, Albon, Mitchell & Staines 1983). In other macropodid species, females reached sexual maturity earlier if they came from populations with relatively abundant food supplies (Shield 1964, Frith & Sharman 1964, Bolton, Newsome & Merchant 1982), and if they were from captive rather than wild populations (Shield 1964, Maynes 1977). Under certain conditions (especially expanding populations), females that begin to breed relatively early may have enhanced lifetime reproductive success (Woolfenden & Fitz-patrick 1984, Harvey & Zammuto 1985, Stearns 1972).

The relationship between weaning rates and food quality was due partly to higher PEP rates of offspring whose mothers had access to good food, but mainly to their higher survival as young-at-foot. The latter could reflect variation in milk and/or forage intake by the young-at-foot. Milk intake of captive tammar wallabies decreases sharply after permanent emergence from the pouch (Dove & Cork 1989), while forage intake increases sharply (pers. obs.). This change-over occurs at a stage when the wallaby's ability to digest plant matter is poorly developed (Dawson 1989) and when, by virtue of its small body size, food quality is particularly important (Clutton-Brock & Harvey 1978).

If a relationship indeed exists between young-at-foot duration and food quality, then this could be explained by mothers with access to good food being able to suckle their offspring for a relatively long period. Further data are required to confirm this result and to determine whether offspring that are suckled for longer have enhanced growth rates or reproductive success.

It is not possible to be sure which aspect of food quality is most important in influencing life history variables due to the high intercorrelations between food quality indices. However, it seems that relatively gross measures of food quality that indicate total availability or accessibility of palatable food (which might better be termed 'quantity' measures) are more important than measures relating to the relative nutritional value of available food species. This is despite the finding that the number of wallabies feeding in an area is apparently affected by the abundance of plant species of relatively high nutritional value (see Table 5), and the fact that wallabies do select strongly among potential food species (J. Clarke, unpubl. data; pers. obs.). Experimental studies are required to

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determine how the different vegetation attributes interact to influence wallabies' nutritional status and hence life history variables.

There was some indication that winter food quality is more important in influencing growth rates of offspring (and thus in influencing Pouch Life, PEP Rate and Parturition Age of Daughters) than that in summer. This may be associated with inter-individual differences in important aspects of food quality being much greater during winter than during summer and/or quality being generally lower in winter, and thus more limiting (see Table 7).

The spatial variation in reproductive success found in my study runs counter to expectations based on the Ideal Free Distribution model. Natural selection is expected to have created mechanisms leading to individuals staying in or dispersing to the 'best' areas to the extent that exploitation competition from increased densities of feeding wallabies does not counteract the benefits by reducing individual food intake. To some extent females did congregate in areas of highest food quality, as reflected by the relationship between food quality and sightings of feeding wallabies (see Table 5). Nevertheless, some female wallabies fed in areas that were apparently suboptimal in terms of consequences for reproductive success. Theoretically this could be due to either (i) constraints on individuals' abilities to find and travel to the best feeding areas; or (ii) unequal competitive abilities of individuals (*cf.* Fretwell & Lucas 1970, Ken-nedy & Gray 1993).

The costs of dispersing to an unfamiliar area may provide a proximate explanation for some females living in suboptimal areas. Female red-necked wallabies display an intimate knowledge of their home ranges, apparently developed through a prolonged period of learning (Higginbottom & Croft 1999). There may be substantial costs in terms of energy expenditure and increased predation risk in searching for better areas. Conradt et al. (1999) and Coulson, Albon, Guinness, Pemberton & Clutton-Brock (1997) proposed the costs of dispersal to be at least part of the explanation for spatial variation in reproductive success in red deer and Soay sheep *Ovis aries* populations, respectively. However this does not seem to provide an adequate ultimate explanation for a dispersion pattern which results in some individuals having substantially higher reproductive success than others.

Similarly there are no obvious constraints on the abilities of female wallabies to find and travel to better feeding areas. Red-necked wallabies have well developed exploratory and locomotory abilities, and the distance from the lowest to the highest quality feeding ranges was less than one kilometre.

Thus, it seems likely that dominant individuals exclude subordinates from the best areas, but in ways which are not readily detectable by the human observer. This has been suggested as an explanation for higher fecundity of large red kangaroo *Macropus rufus* females than their smaller counterparts during drought (Newsome 1977). Despite intensive observations of the study population over a six-year period, there was no evidence of females actively displacing others from anything other than localised patches of food (usually over a distance of less than 10 metres), and even this was rare. However, populations in which individuals have equal competitive abilities are thought to be rare (Krebs & Davies 1987). Interactions between macropodids tend to be much subtler than in comparable eutherians, and may often be detected only once relative orientations and movements are analysed (Jarman 1994). Further, evidence of female dominance hierarchies has been found in both field and captive populations of a number of macropodid species (Ganloßßer 1989). Indeed, although research so far has failed to demonstrate this, Croft (1989: 515) has suggested that in macropodoids "there is probably a degree of feeding interference which is expressed in the female population by their dispersion".

Whatever its ultimate cause, the dispersion pattern recorded in this study appears to be a 'sources and sinks' situation (Pulliam 1988, Dias 1996). In 'sink' habitats, local reproduction is not sufficient to compensate for mortality, so that their occupation is maintained only by immigration from 'source' areas. There was no evidence of an overall change in population size over the 6.5 years that my study lasted (pers. obs.). Thus, assuming equal immigration and emigration, a demographic excess must have occurred in the more fertile southern flats, and a deficit in the north/upslope area. A flow of wallabies is expected to be occurring from the higher to the poorer quality feeding areas. Further research is required to establish whether and how this might be occurring.

The findings of my study are of interest because they indicate that even in the absence of overt intraspecific competition, fine-scale spatial variation in food quality can lead to differences in individual reproductive success. This has important implications for understanding the population dynamics, natural

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selection processes, life history strategies and foraging strategies of macropodids. It also means that in managing macropodid populations for harvesting, pest mitigation or conservation, one cannot assume spatial homogeneity in population dynamics.

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