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Foraging in a risky environment: a comparison of Bennett's wallabies *Macropus rufogriseus rufogriseus* (Marsupialia: Macropodidae) and red-bellied pademelons *Thylogale billiardierii* (Marsupialia: Macropodidae) in open habitats

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Abstract This study aimed to establish whether red-bellied pademelons (*Thylogale billiardierii*) and Bennett's wallabies (*Macropus rufogriseus rufogriseus*) alter their foraging distribution in open habitat, in response to food availability and distance to protective shelter, the latter used as a measure of predation risk. Scat counts were used as a measure of the presence or absence of these macropods over two plantations (Russell and Dunalley). These plantations differed in both their on-site food and shelter characteristics (the presence or absence of windrows). Logistic regression indicated that at Russell, which had low food availability but the presence of on-site shelter, probability of scats of both species increased with the percentage cover of both edible and inedible vegetation. The probability of both pademelon and wallaby scats decreased with increasing distance from windrows, but increased with increasing distance from forest at the plantation edge. Logistic regression indicated that at Dunalley, which had high food availability but no on-site shelter, the probability of scats of both species increased with an increase in the percentage cover of edible vegetation. In relation to predation risk, however, the two species differed in their response. Pademelons exhibited a decrease in scat probability with increasing distance from the forest at the plantation edge, while wallabies showed an increase in scat probability with distance from the forest at the plantation edge. Results indicated some differences in antipredation strategies of the two species, which may be a function of differences in body size.

Key words: feeding ecology, GIS, logistic regression, plantation, predation risk, scat counts.

INTRODUCTION

For animals prone to predation, the choice of where to feed is not straightforward. Feeding areas vary not only in foraging profitability but also in predation risk (Lima & Dill 1990). In the absence of predators, or when vulnerability is low, foragers are predicted to choose feeding sites that offer the highest net energy gain (Sih 1980; Edwards 1983). However, the absence of a predator is rare. Predators are attracted to areas where prey density is high and where habitat allows for successful capture of prey (Cowlishaw 1997), thus the best areas for foraging by prey species are often the most risky (Lima & Dill 1990; Cowlishaw 1997). Foragers must frequently trade off high quality food for safety, shift their activity to safer but less rewarding feeding patches, or heighten antipredation behaviour such as vigilance or grouping (Altendorf *et al.* 2001).

As well as making foraging decisions at higher scales, such as habitat selection (le Mar & McArthur 2005; Blumstein & Daniel 2003a), animals must therefore also make foraging decisions at a finer scale, within a habitat. One of the most common determinants in selecting where to feed within a habitat, associated with reducing predation risk, is distance from protective cover. Many species spend their non-foraging time in areas with cover that provide safety from predators (Blumstein & Daniel 2003a). To feed, however, they must leave these areas and forage in more profitable areas. In this case, increased distance from cover is often associated with increased risk of predation (Blumstein & Daniel 2003a). Many animal species trade off increased foraging benefits in order to forage closer to protective cover, for example, moose (*Alces alces*) (Edwards 1983), tits (Paridae) (Walther & Gosler 2001), and guinea pigs (*Cavia aperea*) (Cassini & Galante 1992).

Within Australia several studies have shown specifically that distance from cover is an important determinant of foraging behaviour in a wide range of

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macropod species, including eastern grey kangaroos (*Macropus giganteus*) (Banks 2001), pademelons (*Thylogale thetis*) (Wahungu *et al.* 2001) and red-necked wallabies (*Macropus rufogriseus banksianus*) (Southwell 1987). In addition, observed behaviour of several macropod species is consistent with the concept that predation risk affects other aspects of foraging behaviour, such as vigilance levels and grouping (Southwell 1987; Coulson 1999; Banks 2001; Wahungu *et al.* 2001; Blumstein *et al.* 2002a, 2003; Blumstein & Daniel 2003a).

This study focused on the within-habitat foraging behaviour of two macropod species, the Red-bellied pademelon (*Thylogale billiardierii*) and the Bennett's wallaby (*Macropus rufogriseus rufogriseus*), in relation to predation risk. Pademelons are the smaller species, with average female mass 4 kg and male mass 7 kg compared with wallaby average female mass 14 kg and male mass 20 kg (Strahan 1983). These species occur most commonly in areas of dense forest which they use for diurnal shelter, closely adjoined to open habitat such as cleared land, where they can feed on grass and forbs during nocturnal foraging bouts (Calaby 1991; Johnson & Rose 1991; le Mar & McArthur 2005; Sprent & McArthur 2002). Despite studies on closely related mainland species, the red-necked wallaby (*Macropus rufogriseus banksianus*) and red-necked pademelon (*Thylogale thetis*) (Southwell 1987; Wahungu *et al.* 2001; Blumstein *et al.* 2002a,b), few studies have focused on antipredation behaviour in the Tasmanian (sub) species (but see Blumstein & Daniel 2003b). The Tasmanian situation is particularly interesting, however, due to its relatively intact carnivore fauna (Watts 1993; Blumstein & Daniel 2003b). There, the major extant predators of these two species are humans, through shooting (Robertshaw & Harden 1989), two dasyurid carnivores, the Tasmanian devil (*Sarcophilis harrisii*) and spotted-tailed quoll (*Dasyurus maculatus*) (Jones & Barmuta 1998), and in the recent past the Tasmanian tiger (*Thylacinus cynocephalus*) (Blumstein & Daniel 2003b). Anecdotal evidence (le Mar 2002) suggests that these two species employ differing strategies to deal with the threat of predation, pademelons relying on crypsis whereas wallabies prefer to outrun their predators.

Our aim was to determine whether the distribution of red-bellied pademelons and Bennett's wallabies foraging in open habitat in Tasmania was related to either distance from protective shelter, used as a surrogate for perceived predation risk, or variation in the abundance of edible vegetation (food quantity) within that habitat. In order to answer this question we used two forestry plantations in their establishment phase. These plantation sites differed in their vegetation and shelter characteristics.

MATERIALS AND METHODS

Study site

We used two eucalypt plantations in southern Tasmania, differing in their surrounding vegetation and the presence or absence of on-site shelter in the form of windrows. The first site, hereafter referred to as Russell, adjoined the Russell State Forest (grid reference – 55G 480 5426,11.7 ha, 200–300 m a.s.l.) and was initially planted with *Eucalyptus globulus* seedlings in early 2000. Pre-planting site preparation had included the stacking of wood into 2.5-m high windrows, ripping of plantation lines and use of herbicide to reduce cover of species considered weeds from a forestry perspective. Despite the latter, a number of plant species, most notably bracken (*Pteridium esculatum*) and fireweed (*Senecio longifolia*) had re-established at the time of this study (April–May 2002). Tree seedlings were small (<10 cm) and sparsely distributed. The plantation was surrounded by wet *Eucalyptus obliqua* forest, mixed *Eucalyptus obliqua* and *Acacia dealbata* forest and established *Eucalyptus nitens* plantation.

The second site (grid reference – 55G 561 5253, 8 ha, 110–175 m a.s.l.), hereafter referred to as Dunalley, had been pasture and had no windrows. At the time of the study (June 2002) it had not yet been planted with tree seedlings. The dominant vegetation was pasture and native grass (*Poa* spp.), with sparsely located patches of Sagg (*Lomandra longifolia*) and bracken. The site was surrounded by *Eucalyptus globulus* dry sclerophyll forest, established *Eucalyptus globulus* plantation and established *Pinus radiata* plantation.

Sampling and mapping of scats, vegetation and shelter

Scats were used as indicators of relative animal abundance within each site. In doing so we assumed that the distribution of scats was correlated with animal distribution. Although no data are available on the defecation behaviour of Bennett's wallabies and Tasmanian pademelons, studies on other macropods have shown that the frequency of defecation is strongly correlated with feeding activity (Hill 1981; Johnson *et al.* 1987). Scats have also been used successfully by other authors, as a way of measuring spatial distribution in a variety of macropod species (Caughley 1964; Woolnough & Johnson 2000; Banks 2001). Scat analysis has the advantage of providing a long-term image of behaviour of the population as a whole. One the other hand, we recognize that it does not allow us to measure the behaviour of individuals nor distinguish any potential differences in behaviour of individuals.

Scats were identified based on the literature (Triggs 1996) and previous experience. It has been suggested that scats of these two species are easily distinguishable (Johnson 1978) but some observer error in identification can occur (Bulinski & McArthur 2000). Despite this, we argue that overall estimates of distribution were reasonably accurate because of the large sample size and the reduction of density results to presence or absence of each macropod species (see later).

For the scat survey, Russell and Dunalley were divided visually into nine and six sections respectively. On each site, sections were searched in a random order to avoid any bias from additional scats produced during the data collection period. Soil mounds established for planting tree seedlings divided each section into 20–80 rows, each about 1.5 m wide, and were used as guides for even searching effort. Rows were searched for scats by walking from one end of a section to the other, at 0.5 steps s^{-1}. In areas of thick vegetation, this pace was reduced to search for scats among vegetation. Observations were made to within 1 m of windrows and the plantation edge. Due to the large number of scats at Dunalley, the site was subsampled, by recording the number of scats in a 1 × 1 m quadrat every 10 m, instead of recording the location of every scat.

For each scat (at Russell) or quadrat (at Dunalley), we recorded the species, number and location of scats using a handheld Garmin etrex Global Positioning System (GPS) (Kansas City, MO, USA). Multiple scats encountered within a 50 cm radius of one another were recorded as the same GPS waypoint at Russell. The mid-point of the quadrat was used at Dunalley. Vegetation was characterized by recording the percentage cover of each vegetation class within a 1 × 1 m area of a given scat (Russell) or quadrat (Dunalley). Vegetation characteristics were recorded every 10 m at both sites whether or not there were scats. Overall vegetation cover could be greater than 100%, due to differences in height of vegetation types. For analyses, vegetation was grouped into an edible class (Russell: grasses and forbs; Dunalley: grasses, forbs and sagg) and an inedible class (Russell: bracken and fireweed; Dunalley: bracken) based on dietary information (Johnson & Rose 1991; Sprent & McArthur 2002) and personal observations.

Waypoints, obtained from the location data recorded onto the GPS, were converted into shape-files using the Arc-View Version 3.2 GIS program. Using Arc-Info, a fishnet grid containing 10 × 10 m grid cells was created and overlaid onto the Arc-View plantation map. This grid cell size was chosen to reflect the maximum error expected from the GPS (3–10 m). The distances of each grid cell from forest at the plantation edge ('edge') and nearest windrow ('windrow') were calculated using the 'select by theme' function within Arc-View. The resulting cells, defined by vegetation characteristics, distances from edge and windrow (independent variables), and the scat density for each species (dependent variables), were used in analyses.

Statistical analysis

Correlations between independent variables were identified using the CORR procedure in SAS (SAS Institute Inc. 1989). No variables were strongly correlated (all $r < 0.7$; Tabachnick & Fidell 1989; highest absolute $r = 0.4$ and 0.2 at Russell and Dunalley respectively), therefore all were used in the overall analysis. Data from each site were randomly divided into two data sets, A and B, containing two thirds and one third of the initial data respectively. Due to the high proportion of grid cells without scats, scat densities were converted into presence/absence for logistic regression (described below). All analyses were first performed on data set A, and then tested for consistency on data set B. The two species (pademelons and wallabies) were tested separately.

Probability of the presence of a scat in relation to vegetation and shelter

We used logistic regression to model the probability of the presence of a scat, hereafter termed scat probability, in relation to percentage cover of edible and inedible vegetation, distance from forest at the plantation edge and distance from nearest windrow (Russell only), using the logit link function (Proc Logistic, SAS Institute Inc. 1989). We first tested the full model, which included all variables, for its significance by the −2 log-likelihood statistic, its explanatory power by the maximum rescaled r^2 value and its capacity successfully to discriminate presence/absence by the c-value. For the latter, values of $c > 0.70$, $c > 0.80$ and $c > 0.90$ were considered to be acceptable, excellent and outstanding respectively (Lemeshow & Le Gall 1994). The Wald statistic was used to test significance of effects of each independent variable. This statistic was considered to be reliable because the sample size for all models was large (Quinn & Keough 2002). The adequacy of the model was also examined using the Hosmer– Lemeshow (HL) goodness-of-fit statistic. Variables were then progressively excluded and the reduced models were examined as above. The difference in the log-likelihood estimates of the models was tested using the χ^2 statistic, against the appropriate degrees of freedom, further to confirm the need to retain or exclude particular variables. The final accepted model incorporated variables that optimized explanatory power (r^2), discrimination (c) and goodness of fit. Using the final model, we then illustrated the effect of each variable on the scat probability, by plotting the probability against the variable of interest within its observed range with the remaining variables fixed at their average values. We followed the same procedure using data set B.

RESULTS

Scat and vegetation characteristics at the two study sites

At Russell, wallaby and pademelon scats occurred in 30% and 66% of the 1452 grid cells respectively. The mean scat density for wallabies was lower than for pademelons (Table 1). Vegetation occurred in 72% of the grid cells, but cover of both edible and inedible vegetation was low (Table 1). Distance of the grid cells from forest at the plantation edge ranged from 0 m to 105 m (mean of 25.9 m), and distance from nearest windrow ranged from 0 m to 70 m (mean 12.4 m) (Table 1). At Dunalley, wallaby and pademelon scats occurred in 51% and 57% of the 907 grid cells respectively. On average scat density was less for wallabies than pademelons (Table 1). Vegetation occurred in 65% of the grid cells. Edible vegetation cover was high, whereas inedible vegetation cover was low (Table 1). Distance from forest at the plantation edge ranged from 0 m to 90 m (mean 28.2 m) (Table 1). At both sites there was a significant positive correlation between numbers of wallaby and pademelon scats (Russell $r = 0.56$, $P = 0.0001$, $n = 987$; Dunalley $r = 0.30$, $P = 0.0001$, $n = 608$).

Table 1. Mean (standard deviation) of scat densities (units in count m^{-2}), vegetation classes (units in percentage cover) and distance (m) from 'edge' (forest at plantation edge) and 'windrow' (nearest windrow) for the two study sites, Russell and Dunalley

Site	Russell	Dunalley
Wallaby scats	0.01 (0.03)	2.7 (4.2)
Pademelon scats	0.10 (0.15)	4.4 (5.6)
Edible vegetation	1.7 (3.7)	63.2 (43.8)
Inedible vegetation	6.8 (8.9)	1.3 (6.4)
Distance from edge	25.9 (24.8)	28.2 (22.7)
Distance from windrow	12.4 (11.7)	–

Probability of scats at Russell

Using data set A all four variables were included in the final model for both species (Table 2). The model explained 17% of the variation for wallaby scats (–2 log likelihood = 125.85, d.f. = 4, $P = 0.0001$, max-rescaled $r^2 = 0.17$) and 34% of the variation for pademelon scats (–2 log likelihood = 270.712, d.f. = 4, $P = 0.0001$, max-rescaled $r^2 = 0.34$). Model discrimination was acceptable ($c = 0.733$) for wallabies and excellent ($c = 0.831$) for pademelons. The HL goodness-of-fit statistic was significant for both wallabies (HL = 17.66, d.f. = 8, $P = 0.0240$) and pademelons (HL = 96.333, d.f. = 8, $P = 0.0001$). However, examination of observed and expected results indicated that for wallabies estimates were accurate when the probability of scats was high. Overestimation only occurred when the probability was very low (data not shown). For wallaby scats, removing the variable with the weakest effect (distance from windrow) reduced the goodness of fit unacceptably (HL = 35.508,

Table 2. Results from the logistic regression analysis at Russell using data set A for (a) wallaby and (b) pademelon scat probability

Variable	d.f.	Parameter estimate	95% Confidence Interval –	95% Confidence Interval +	Wald χ^2 statistic	*P*-Value
(a) Wallaby						
Intercept	1	−1.683	−2.042	−1.334	86.77	0.0001
Edge	1	0.022	0.016	0.029	46.97	0.0001
Windrow	1	−0.015	−0.030	0.000	3.57	0.0588
Edible	1	0.110	0.066	0.156	23.12	0.0001
Inedible	1	0.022	0.006	0.038	7.51	0.0061
(b) Pademelon						
Intercept	1	−0.199	−0.548	0.148	1.26	0.0001
Edge	1	0.020	0.012	0.028	23.30	0.0001
Windrow	1	−0.031	−0.045	−0.017	18.54	0.0001
Edible	1	0.303	0.210	0.406	36.67	0.0001
Inedible	1	0.089	0.065	0.116	46.82	0.0001

'Edge' and 'windrow' refer to distance (m) from forest at plantation edge and from nearest windrow respectively. 'Edible' and 'Inedible' refer to percentage cover of vegetation classes.

d.f. = 7, $P = 0.0001$) and so it was retained in the final model.

The probability of wallaby scats steadily increased with distance from plantation edge (Fig. 1a), decreased slightly with distance from windrow (Fig. 1b) and increased with percentage cover of inedible vegetation (Fig. 1d). The probability of wallaby scats increased rapidly as the percentage cover of edible vegetation increased from 0% to 30% and was almost certain above approximately 40% (Fig. 1c).

The probability of pademelon scats gradually increased with distance from plantation edge (Fig. 2a) and decreased greatly with distance from windrow (Fig. 2b). Pademelon scat probability increased rapidly as both the percentage cover of edible and inedible vegetation increased (Fig. 2c,d).

As with data set A, all four variables were included in the final model for both wallabies (–2 log likelihood = 74.075, d.f. = 4, $P = 0.0001$, max-rescaled $r^2 = 0.20$) and pademelons (–2 log likelihood = 140.078, d.f. = 4, $P = 0.0001$, max-rescaled $r^2 = 0.35$) when data set B was used. Model discrimination was acceptable ($c = 0.754$) for wallabies and excellent ($c = 0.831$) for pademelons. The direction of effects of variables were the same as those developed from data set A for both species, however, for wallabies distance to windrow and percentage cover of edible vegetation were not significant (data not shown). The HL goodness-of-fit statistic was significant for both species with overestimation at the highest and lowest probabilities and for padmelons underestimation at intermediate levels (data not shown).

Probability of scats at Dunalley

Using data set A, two variables, distance from edge and percent cover of edible vegetation, were included in the final model for each species (Table 3). The model explained 63% of the variation for wallaby scats (–2 log likelihood = 389.97, d.f. = 2, $P = 0.0001$, max-rescaled $r^2 = 0.63$) and 68% of the variation for pademelon scats (–2 log likelihood = 427.82, d.f. = 2, $P = 0.0001$, max-rescaled $r^2 = 0.68$). Model discrimination was excellent for both wallabies ($c = 0.88$) and pademelons ($c = 0.89$). The HL goodness-of-fit statistic was not significant for either wallabies (HL = 13.03, d.f. = 8, $P = 0.1108$) or pademelons (HL = 14.297, d.f. = 8, $P = 0.0743$) indicating a good fit, and examination of observed and expected results confirmed accurate estimates across all probabilities (data not shown).

Scat probability increased steadily with distance from forest at the plantation edge for wallabies but decreased steadily for pademelons (Figs 3a,4a). Scat probability increased for both pademelons and wall-

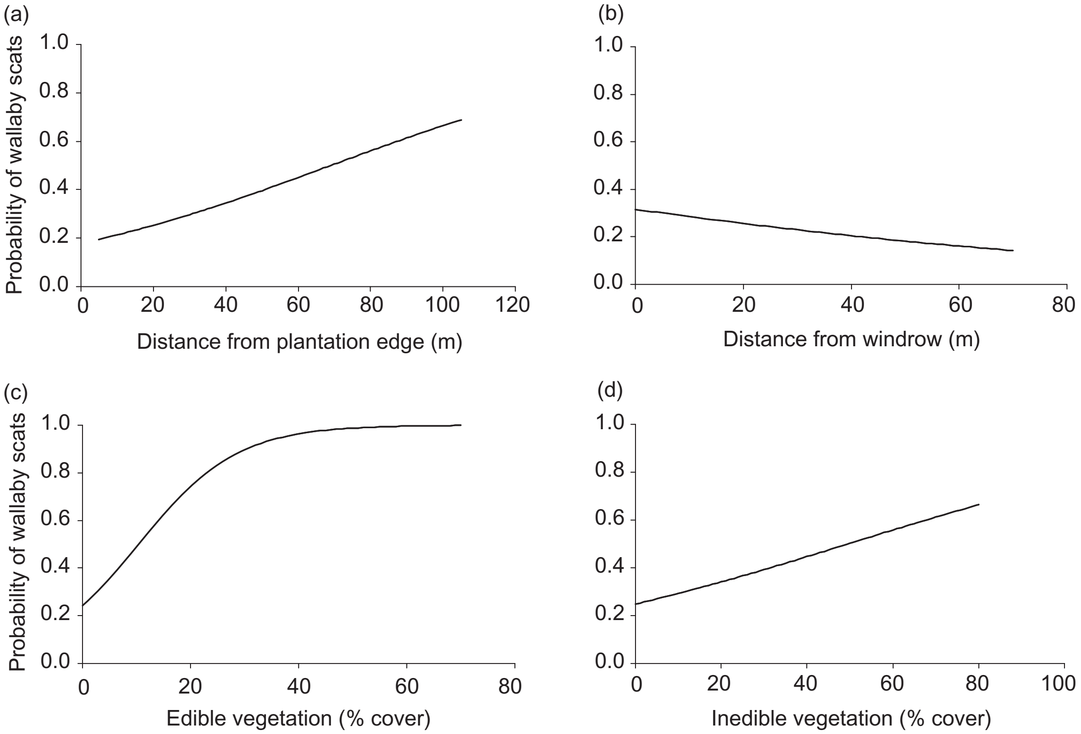

Fig. 1. Probability of wallaby scats in relation to (a) distance from plantation edge; (b) distance from nearest windrow; (c) percentage cover of edible vegetation and (d) percentage cover of inedible vegetation, using the final model developed from data set A, at the Russell site.

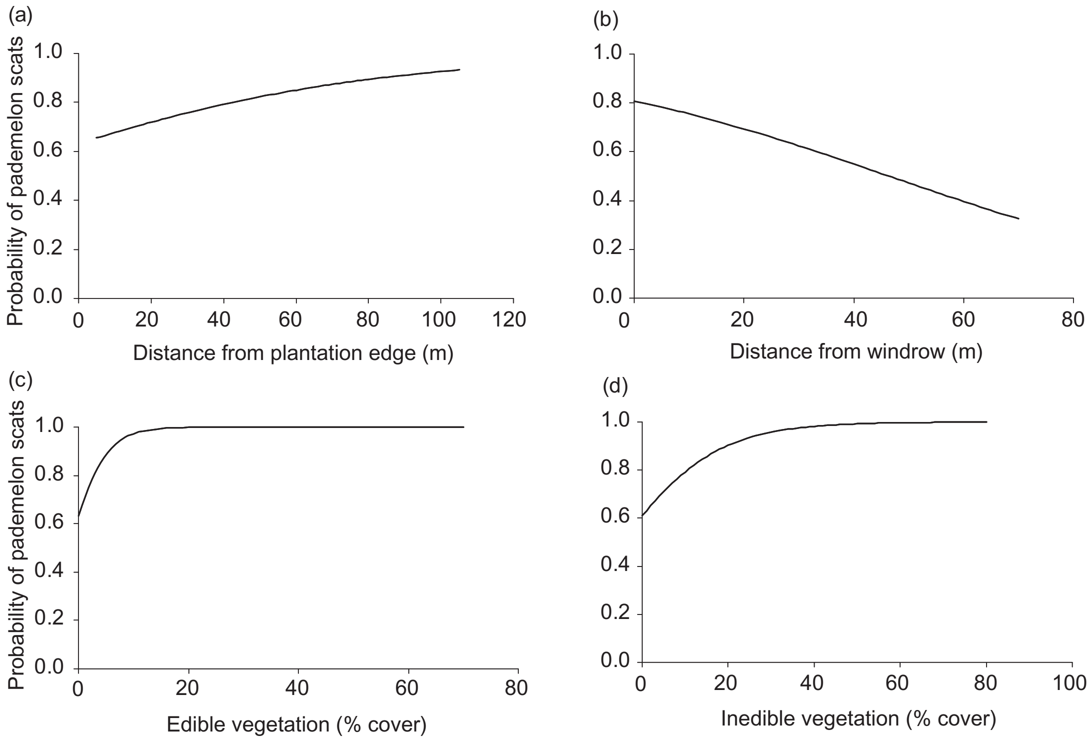

Fig. 2. Probability of pademelon scats in relation to (a) distance from plantation edge; (b) distance from nearest windrow; (c) percentage cover of edible vegetation and (d) percentage cover of inedible vegetation, using the final model developed from data set A, at the Russell site.

Table 3. Results from the logistic regression analysis at Dunalley using data set A for (a) wallaby and (b) pademelon scat probability

Variable	d.f.	Parameter estimate	95% Confidence Interval –	95% Confidence Interval +	Wald χ^2 statistic	*P*-Value
(a) Wallaby						
Intercept	1	–4.233	–5.169	–3.434	92.34	0.0001
Edge	1	0.053	0.045	0.063	134.48	0.0006
Edible	1	0.020	0.009	0.032	11.69	0.0001
(b) Pademelon						
Intercept	1	–3.375	–4.223	–2.659	72.50	0.0001
Edge	1	–0.011	–0.023	0.000	3.67	0.0555
Edible	1	0.058	0.049	0.067	155.43	0.0001

'Edge' refers to distance (m) from forest at plantation edge. 'Edible' refers to percentage cover of edible vegetation.

abies in relation to edible vegetation: when less than 40%, scat probability was very low, but it increased rapidly from 40 to 100% cover (Figs 3b,4b).

As with data set A, both distance from edge and percent cover of edible vegetation were significant for both wallabies (–2 log likelihood = 146.78, d.f. = 2, $P = 0.0001$, max-rescaled $r^2 = 0.52$) and pademelons (–2 log likelihood = 199.20, d.f. = 2, $P = 0.0001$, max-rescaled $r^2 = 0.66$) when using data set B. Model discrimination was excellent for both wallabies ($c = 0.816$) and pademelons ($c = 0.894$), and the directions of effects of variables were the same as those developed for data set A for both species (data not shown). The HL goodness-of-fit statistic was not significant for wallabies although the model appeared to overestimate at the highest and lowest probabilities and underestimate at intermediate levels (data not shown), but was significant (HL = 21.47, d.f. = 7, $P = 0.0031$) for pademelons, with underestimation occurring at most levels (data not shown).

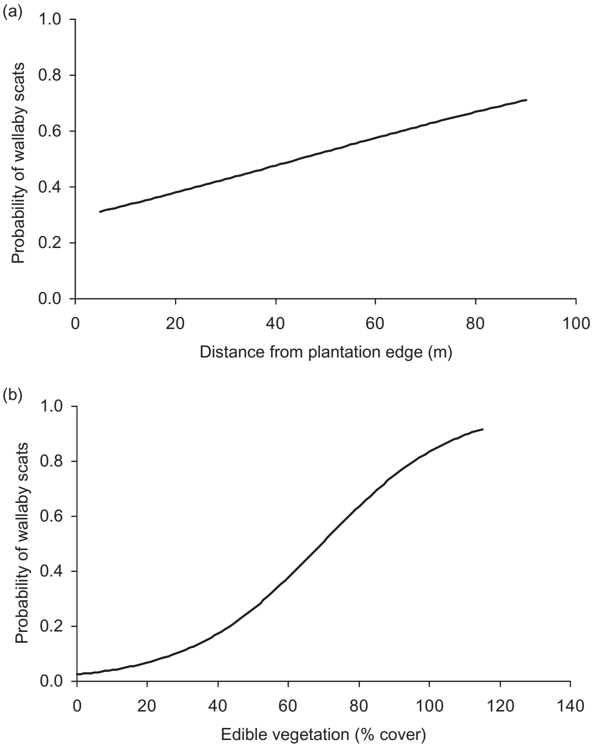

Fig. 3. Probability of wallaby scats in relation to (a) distance from plantation edge and (b) percentage cover of edible vegetation, using the final model developed from data set A, at the Dunalley site.

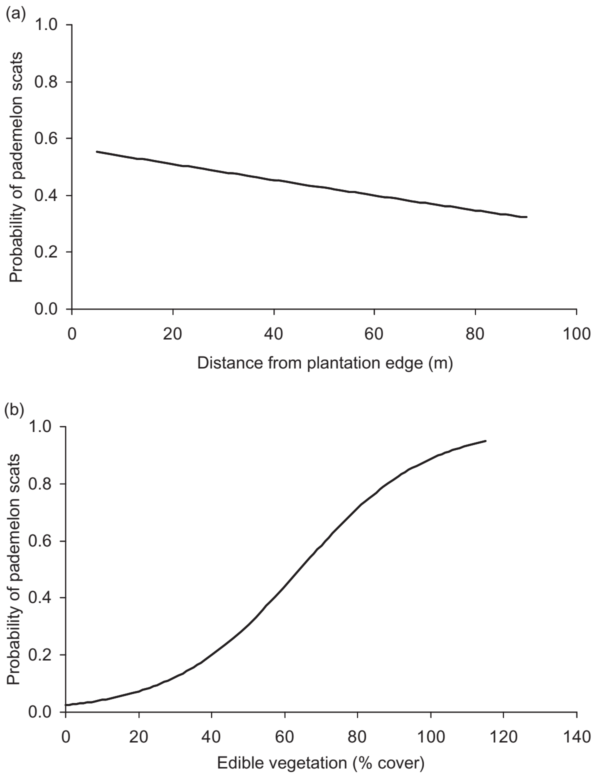

Fig. 4. Probability of pademelon scats in relation to (a) distance from plantation edge and (b) percentage cover of edible vegetation, using the final model developed from data set A, at the Dunalley site.

DISCUSSION

Foraging patterns in relation to vegetation

Our results show that abundance of edible vegetation consistently influenced the within-habitat foraging patterns of both wallabies and pademelons, as determined by the presence of scats. At both sites the probability of scats increased with the percentage cover of edible vegetation (mainly grasses and forbs). By spending more time foraging in areas with a higher quantity of edible vegetation, an individual is more likely to maximize the energy gained in relation to the energetic costs of foraging. These results are consistent with previous research showing macropods choose where they forage based on food quality (Southwell 1987; Carter & Goldizen 2003).

Both pademelons and wallabies have been observed to use suitable on-site vegetation as shelter in response to predation risk (Southwell 1987; le Mar 2002). However, on an ex-pasture *Pinus radiata* plantation, tree seedlings were browsed less by pademelons and wallabies amongst tall than short bracken, which was thought to be due to reduced foraging time in those areas (Pietrzykowski *et al*. 2003). We therefore did not expect the quantity of inedible vegetation to be positively associated with the presence of either macropod. Despite this, there was a strong positive relationship between inedible vegetation, predominantly bracken and fireweed, and scat probability at Russell. We suggest that these plants were used as shelter on Russell, particularly by pademelons, which showed the stronger relationship (Table 2 comparison of Wald χ^2 statistics for wallabies and pademelons). This conclusion is supported by filmed observations of captive pademelons (A. Miller pers. obs. 2004). In individual enclosures with no or low vegetation cover (grass) pademelons flush to shade cloth shelters when disturbed, whereas in enclosures with tall vegetation (lupins, *Lupinus albus*) they simply hide amongst the vegetation. Lack of effect of inedible vegetation at Dunalley is likely to be due to the low overall cover of inedible vegetation (average 1.3%), or differences in the structure of the vegetation.

Foraging patterns in relation to predation risk

Our results suggest that both wallabies and pademelons alter their behaviour in response to predation risk. At Russell, wallaby scat probability increased substantially with distance from the forest at the plantation edge but decreased (weakly) with distance from the nearest windrow. Where windrows were absent (Dunalley), wallabies were still more likely to forage further from the forest edge. At Russell, pademelons showed a similar pattern of response to wallabies. However, the effect of windrows was greater for pademelons and similar in magnitude to the forest edge effect (but in the opposite direction). This indicates that windrows were important as on-site shelter. When present, pademelons prefer to remain close to them, but to use them at some distance from the forest edge. In contrast to wallabies, however, when windrows were absent (Dunalley), the relationship with distance from edge was reversed (now negative), indicating that pademelons then preferred to remain close to the forest edge.

Our results are supported by anecdotal evidence that these two herbivores differ in their antipredation behaviour (le Mar 2002). Wallabies have been suggested to deal with predation risk by out-running their predators (Jarman 1991; le Mar 2002). If so, early detection of a predator is important and may be best achieved by avoiding forest adjacent to open habitat when foraging, because it may conceal a potential predator (Southwell 1987). In contrast, pademelons, which are smaller, appear to avoid predators by crypsis (le March 2002), a strategy best achieved by staying close to shelter (Southwell 1987). In open areas such as pasture, this means foraging close to the forest edge (Johnson 1980; Wahungu *et al.* 2001; this study) or using tall vegetation or windrows within foraging areas (this study).

Results from our study are also similar to those found in other macropod species. Strategies to reduce predation risk in tammar wallabies (*Macropus eugenii*) and western grey kangaroos (*Macropus fuliginosus*) (Blumstein & Daniel 2002) show similar patterns to pademelons and wallabies respectively. The smaller tammars shift to forage closer to shelter when predation risk increases, while the larger kangaroos forage further away from shelter. Results from both studies support the hypothesis that specific antipredation behaviour depends on body size, as suggested by Blumstein and Daniel (2002).

Finally, Southwell (1987) suggested that the partitioning of species across an area could be caused by interspecific competition rather than predation. If two species have identical antipredation responses, in this case foraging close to cover, they would compete for the safer areas leading to the subordinate species suffering the greater predation risk. Anecdotal evidence suggests that pademelons are dominant to wallabies (le Mar 2002), therefore on a site with both species, any difference in antipredation risk may be a result of competition rather than predation risk. However, correlation results between the two species indicate that there was no negative correlation between the two species, rather a weak positive relationship. Therefore, we do not believe that competition was a strong factor in influencing where these species foraged.

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