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Macropod habitat use and response to management interventions in an agricultural-forest mosaic in north-eastern Tasmania as inferred by scat surveys

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Abstract

Context. Native pest herbivores often require population numbers to be controlled in landscape settings where agricultural, plantation forests and native forests are juxtaposed. The Tasmanian pademelon *Thylogale billardierii* and the red-necked wallaby *Macropus rufogriseus rufogriseus* are among the most abundant native pest herbivore species in Tasmania.

Aims. We aimed to determine the habitat use of pademelons and wallabies in response to (i) environmental and seasonal variation, and (ii) two different wildlife management interventions (shooting and fencing) in an agricultural–forest mosaic in north-eastern Tasmania.

Methods. Macropod abundance before and after shooting and fencing management interventions were estimated by changes in the rate of deposition of faecal pellets (scats per unit area per time interval) on an array of permanent transects that were stratified across three habitat types (agricultural land, plantation forest, and native forest). An experiment was also conducted to determine the endurance of fresh scats in the three habitats.

Key results. More than 90% of scats remained undecomposed for over five months, and more than 50% of scats remained undecomposed for over 11 months across the study site. Decomposition rates were significantly influenced by habitat type, specifically, highest in agricultural land and lowest in native forest for both species. Scat deposition rates showed that species abundance was influenced by habitat type and season. Macropod abundance was highest in agricultural land and lowest in native forest. Compared with summer and early autumn, pademelon scat abundance significantly decreased in late autumn and spring on agricultural land but showed no change for plantation forest or native forest. Wallaby scats showed similar seasonal trends for all three habitats, lower in late autumn and spring compared with summer and early autumn. Following each of the management interventions, macropod scat deposition rates decreased predominantly on agricultural land. This effect decreased with increasing distance from intervention loci.

Conclusions. We demonstrate that scat monitoring provides a useful survey technique for the assessment of macropod habitat use, and show that macropods select for agricultural habitats. Shooting and fencing interventions reduced the use of agricultural habitats, but this effect was localised.

Implications. A whole-landscape perspective is required when assessing the impacts of management interventions on pest populations. Results highlight the formidable challenges in controlling native herbivores in habitat mosaics, given the localised effects of management interventions and the importance of environmental and seasonal factors as drivers of habitat use.

Additional keywords: habitat heterogeneity, macropod abundance, red-necked wallaby, scat deposition rate, Tasmanian pademelon, wildlife management.

Introduction

Wild mammalian herbivores, such as macropods, can achieve 'pest' status in landscape mosaics made up of productive agricultural lands embedded in native vegetation (Arnold and Steven 1988; Hill *et al.* 1988; Arnold *et al.* 1989; Statham 1994; Masters *et al.* 2004). This is because of the optimal combination of high quality food and water resources available in cleared land, the provision of shelter for rest, and low levels of predation in the

surrounding uncleared land (Rounsevell *et al.* 1991; While and McArthur 2006). Therefore, the management of pest species in such heterogeneous, resource-rich environments needs to take into account a species' resource use across the entire landscape and understand how this changes temporally. Further, management interventions designed to control herbivore populations can additionally alter habitat use, by influencing animal movement patterns across the landscape and population

demographics of the target species (Porter *et al.* 1991; Driessen 1992; Efford *et al.* 2000; Viggers and Hearn 2005; Wiggins *et al.* 2010).

An important step in managing wildlife populations is to acquire information of the target species' habitat use and how this changes in response to both temporal variation and anthropogenic influences (i.e. land management and intervention strategies). There are several ways to achieve this step, with one of the most common strategies incorporating the use of radio-telemetry (e.g. Johnson 1980; le Mar et al. 2003; Di Stefano et al. 2007). For example, Wiggins et al. (2010) tracked the movement patterns of pademelons and wallabies, using GPS technology, in response to shooting and fencing interventions in research concurrent with this study. The radio-telemetry showed that animals altered their home-range size and mean centroid locations associated with changed use of agricultural habitat in response to the interventions. Importantly, both species responded differently to each intervention type. In response to shooting, individuals that survived increased their home-range size and agricultural land use. In response to fencing, both species decreased their home-range size and their use of agricultural land (Wiggins et al. 2010).

However, a common drawback to the use of radio-telemetry is the overly costly nature of this technology restricting the number of animals that can be studied, and its often limited ability to provide a whole-landscape perspective of animal population responses to seasonal cycles and wildlife management interventions. An alternative approach is to assess habitat utilisation through surveying and monitoring of fecal pellets (scats). Previous research has shown that scat surveys can provide useful information on a range of ecological facets including a species' habitat use (Telfer et al. 2006; Jones and Jackson 2009), diet composition, foraging ecology in response to landscape disturbance (Murphy and Bowman 2007), behavioural ecology, and population dynamics (Caughley 1964; Putman 1984; Johnson and Jarman 1987; Southwell 1987). Thus, scats can act as powerful bio-indicators for monitoring populations at a landscape scale (Bulinski 2000; Webbon et al. 2004; Rosalino et al. 2007; Ruibal et al. 2009). Macropods are ideally suited for this type of survey because they reportedly feed and deposit scats in the same area (Johnson 1977; Johnson and Jarman 1987).

This research aimed to examine the effects of habitat heterogeneity and wildlife management strategies on localised populations of the two most abundant macropod species across the Tasmanian landscape, the Tasmanian pademelon Thylogale billardierii (Desmarest, 1822) and the red-necked wallaby Macropus rufogriseus rufogriseus (Desmarest, 1817) (Marsupialia: Macropodidae). Pademelons and wallabies reportedly cause extensive grazing and browsing damage to pasture, crops, recently established plantations, and forest regeneration areas across the Tasmanian landscape, contributing to significant losses in economic productivity (Statham 1983; Coleman et al. 1997; Bulinski and McArthur 1999). While similar instances of browsing pressure caused by localised macropod populations occur throughout Australia (e.g. Hill et al. 1988; Edwards et al. 1996; Viggers and Hearn 2005), the consistently high levels of browsing pressure experienced in Tasmania appear to be related to the relatively high densities of native herbivore populations across the state,

associated with agricultural–forest mosaics that provide reliable watering points and patches of feeding and shelter within close proximity of one another (Rounsevell *et al.* 1991; Coleman *et al.* 1997; le Mar and McArthur 2005).

A range of management strategies have been employed in attempts to control pest macropod populations across the Australian landscape, including shooting and exclusion fencing (Statham 1994; Pople and Cairns 1995; Underhill et al. 2007). To date, methods of wildlife management in Tasmania have predominantly focussed on lethal interventions, including poisoning using 1080 (sodium monofluoroacetate), and shooting (Coleman et al. 1997; le Mar and McArthur 2001). The uncertain long-term benefits of these strategies, coupled with growing social opposition to their use because of animal welfare issues and impacts on non-target species, has prompted the use of alternative methods of wildlife control, including barrier fencing and the development of less palatable tree cultivars (Statham 1994; Coleman et al. 2006; Miller et al. 2006; Day and MacGibbon 2007). There is thus a need to increase our understanding of how macropods use the landscape and how animals respond to current and new management interventions (Priddel 1987; Driessen 1992; Viggers and Hearn 2005; Wiggins et al. 2010).

We aimed to determine the habitat use of pademelons and wallabies in response to (i) environmental and seasonal variation, and (ii) two different wildlife management interventions (shooting and fencing) across the landscape. We hypothesised that macropod abundance, measured using faecal pellet density, would (a) be highest in resource-rich environments (agricultural land), especially in the summer growing season, and (b) decrease in the sites of management interventions (agricultural land) following interventions of shooting and fencing. This data provides us with the opportunity to contrast these whole-landscape surveys with the more targeted radio-telemetry approach used by Wiggins *et al.* (2010).

Materials and methods

Study site

Research was conducted in the Scottsdale region of northeast Tasmania, Australia ($41^{\circ}06'$ S, $147^{\circ}35'$ E), within an agricultural–forest mosaic spanning ~130 km² (Fig. 1). The geological composition of the area includes the igneous rock types basalt and granite (Tasmania Geological Survey 1977). Four replicate sample sites were defined within this area; the outer boundary of each site was defined by a 6 km diameter circle (Fig. 1). At each site, a minimum of 30 line transects were randomly located following stratification by habitat type (agricultural, plantation forest, native forest) using mapping derived from Tas.VEG (2005). There were 127 transects in total. The transects were 100 m in length and randomly orientated, marked at 20 m intervals with wooden posts and plastic survey tape.

Wildlife management interventions

The following management interventions were carried out: in February 2009 (late summer) a lethal cull by shooting was undertaken over an 18 day period at sites A and D; in April 2009 (mid-autumn) a fencing intervention was undertaken at



Fig. 1. A map showing the three main habitat types (agricultural land, plantation forest, native forest), the four sample sites (indicated using circular zones), and individual line transect locations across the study site in Scottsdale, north-east Tasmania, Australia. Sites A and D were subjected to the wildlife management interventions of shooting, and site D fencing.

site D (see Wiggins *et al.* (2010) for full details); and in July 2009 (mid-winter) a second shooting intervention was undertaken over a nine day period at sites A and D. There were two replicate sites for the experimental control (sites B and C).

In brief, for the shooting interventions, a qualified marksman undertook a cross-sectional cull of macropods at site A (within the agricultural land in the centre of the plot) and site D (within the agricultural land in the south-west of the plot) (Fig. 1). Approximately 400 macropods were culled from both sites in summer, and 100 macropods were culled in winter. The fencing intervention (fence construction) involved the erection of a line of wallaby mesh fence spanning 2 km, with electrical standoffs 10–15 cm off the ground on both sides, across the boundaries of agricultural land in the south-west of the plot at site D (Fig. 1; Wiggins *et al.* 2010). The management interventions occurred over a scale and timeframe representative of typical intervention efforts occurring in this and similar landscapes.

Habitat structure and composition

Habitat classifications were guided by Tas.VEG (2005) and further defined by the environmental and vegetation differences derived from habitat surveys (Fig. 1). At the start of each transect, the slope, aspect, elevation, and dominant vegetation type were noted and the classification and abundance of canopy and midstorey cover were made using the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1932). Tree basal area of the dominant species was assessed using a Bitterlich wedge (Banfai and Bowman 2007; Šálek and Zahradník 2008). At the six points along the transects, percentage cover was estimated for ground vegetation, leaf litter, moss, rock, bare ground, and coarse woody debris within a 2 m radius (12.6 m² area) circular plot. The abundance of understorey vegetation in each circular plot was assessed using the Braun-Blanquet cover-abundance scale.

Scat surveys

Scat counts were used to assess the relative abundance of pademelons and wallabies. Sampling occurred at the six circular plots in each transect. Individual pellets were identified (Triggs 1996), counted and removed. Transects were established and initially cleared at time 0 (summer; day 0, December 2008), then surveyed and cleared at ~6 week intervals at time 1 (summer; from day 60, January 2009), time 2 (early autumn; from day 105, March 2009) and time 3 (midautumn; from day 150, April 2009), and at a six month interval for time 4 (spring; from day 316, September 2009). Sampling periods coincided with the wildlife management interventions, providing information of pre- and post-intervention activity. These surveys complemented a concurrent study being run by Wiggins et al. (2010). For each sampling period, mean scat deposition rate (scats $m^{-2} day^{-1}$) was calculated for each habitat type for each species.

To test the endurance of scats among habitats we established 15 1×1 m quadrats in January 2009 to assess the relative persistence of scats in each habitat type. Five replicate quadrats were established across the three dominant habitats (a) agricultural land; (b) plantation forest; and (c) native forest. Ten fresh scats (individual pellets), five each from pademelons

and wallabies, were placed within each quadrat and marked with a colour-coded paperclip. Scats were assessed at five-month intervals and assigned a presence–absence score. If scats could no longer be identified due to high levels of decay, they were assigned as absent.

Statistical analysis

All statistical analyses were implemented in R version 2.10.0 (R Development Core Team 2009), with the mixed effects models using the package lme4 (Bates *et al.* 2008). Normal probability plots and plots of standardised residuals were used to examine normality of the data. A multi-model inference approach was used to select models from a candidate set developed to describe relationships between the response variable and possible explanatory variables (Burnham and Anderson 2002). The Akaike information criterion (AIC_c) was used to rank and weight the models. The AIC_c identified the model most strongly supported by the data, based on the bias-corrected, maximised log-likelihood of the fitted model, discounted by the number of parameters used (Burnham and Anderson 2002; Prior *et al.* 2006).

Relative scat endurance was analysed using a generalised linear mixed model using scat presence as the response variable; habitat, season and species as the explanatory variables; and individual transects (nested within sites) as the random effect.

Habitat use was analysed for the control (non-intervention) sites using a linear mixed model. Data were analysed separately for each species using scat deposition rate as the response variable; habitat and season as the explanatory variables; and individual transects (nested within sites) as the random effect.

Effects of shooting and fencing on macropod scat deposition rates were analysed using a generalised linear mixed model (Gaussian distribution, identity link) using scat deposition rate as the response variable; distance to agricultural land, distance to plantation forest, and distance to native forest as the fixed effects; and individual transects (nested within sites) as the random effect. Following each of three interventions (three sample periods) models were run for each of the two species and each of the three habitat types (making a total of 18 separate model sets) using scat deposition rate as the response variable; distance from the intervention sites, distance from agricultural land, and distance from plantation forest as the explanatory variables; and individual transects (nested within sites) as the random effect. For analysis of deposition rate on agricultural land, four models were run in the candidate model sets, representing all possible combinations the two fixed effects (distance to plantation forest, distance to native forest), including a null model. For analysis of deposition rate on plantation forest, the four models run represented all possible combinations of the two fixed effects (distance to agricultural land, distance to native forest), including a null model. For analysis of deposition rate on native forest, eight models were run in the candidate model sets, representing all possible combinations of the three fixed effects, including a null model. The selected models were run using a generalised linear mixed model. The candidate model sets receiving the strongest support are listed in Table 1.

Table 1. Results of AIC_c-based model selection for (1) scat endurance; (2) habitat use; and (3) scat deposition rates of Tasmanian pademelons and red-necked wallabies in response to distance from intervention sites (D_{Int}), distance from agricultural land (D_A), and distance from plantation forest (D_P) for each intervention and each habitat type surveyed

Also shown is the number of parameters in each model (K), AIC_c weights (w_i) and results of the mixed models for scat deposition rates. Only the model with the best support is shown for each intervention for each habitat for each species

	Model	K	Wi	D _{Int}	D _A	D_P
(1) Scat endurance						
Macropod scat presence	Habitat + season + species	7	0.65			
(2) Habitat use	*					
(a) Pademelon scat deposition rate	Habitat+season	7	0.99			
(b) Wallaby scat deposition rate	Habitat+season	7	0.99			
(3) Scat deposition rates						
Lethal intervention (late summer)						
(a) Pademelon scat deposition rate						
Agricultural land	D _{Int}	3	0.92	12.27 ± 2.63	_	_
Plantation forest	$D_{Int} + D_A$	4	0.60	0.33 ± 0.64	-2.00 ± 1.57	_
Native forest	D _A	3	0.33	_	-1.19 ± 0.40	_
(b) Wallaby scat deposition rate						
Agricultural land	D _{Int}	3	0.96	3.53 ± 0.67	_	_
Plantation forest	$D_{Int} + D_A$	4	0.82	2.04 ± 1.02	-0.56 ± 2.51	_
Native forest	$D_{Int} + D_A + D_P$	5	0.58	1.35 ± 0.71	-0.72 ± 0.82	1.32 ± 1.44
Fencing intervention (mid-autumn)						
(a) Pademelon scat deposition rate						
Agricultural land	D _{Int}	3	0.94	3.49 ± 0.79	_	_
Plantation forest	$D_{Int} + D_A$	4	0.41	0.24 ± 0.26	-0.55 ± 0.63	_
Native forest	$D_A + D_P$	4	0.78	_	0.87 ± 0.54	-0.31 ± 0.24
(b) Wallaby scat deposition rate						
Agricultural land	D _{Int}	3	0.88	0.92 ± 0.25	_	_
Plantation forest	$D_{Int} + D_A$	4	0.55	0.53 ± 0.37	0.26 ± 0.93	_
Native forest	$D_{Int} + D_A + D_P$	5	0.45	0.42 ± 0.26	0.81 ± 0.54	-0.63 ± 0.30
Lethal intervention (mid-winter)						
(a) Pademelon scat deposition rate						
Agricultural land	D _{Int}	3	0.85	4.69 ± 1.24	_	_
Plantation forest	$D_{Int} + D_A$	4	0.81	1.22 ± 0.79	-3.72 ± 1.97	_
Native forest	$D_A + D_P$	4	0.44	_	-0.35 ± 0.22	-0.24 ± 0.09
(b) Wallaby scat deposition rate						
Agricultural land	D_{P}	3	0.71	_	_	3.24 ± 2.95
Plantation forest	$D_{Int} + D_A$	4	0.63	0.24 ± 0.66	3.86 ± 1.64	_
Native forest	$D_{Int} + D_A + D_P$	5	0.57	-1.25 ± 1.04	1.01 ± 2.12	-0.59 ± 1.20

Results

Habitat structure and composition

There were clear environmental and vegetation differences between agricultural land (predominately for stock grazing), plantation forest and native forest habitats (Table 2). Agricultural land was on lower valley slopes, plantation forest on flat plateaus and native forest on intervening slopes (Table 2). Canopy cover was dominated by black peppermint (Myrtaceae: Eucalyptus amygdalina) in agricultural land and native forest, with either shining gum (E. nitens) or radiata pine (Pinaceae: Pinus radiata) growing in plantation forest (Table 2). Basal area was highest in plantation forest and lowest in agricultural land (Table 2). The dominant midstorey vegetation was tall grasses in agricultural land, bracken fern (Dennstaedtiaceae: Pteridium) in plantation forest, and a well developed mid-layer of tea tree (Myrtaceae: Leptospermum) in native forest. The dominant understorey vegetation consisted of sedges and thistles in agricultural land, grasses in plantation forest, and bracken ferns in native forest (Table 2). Ground

vegetation cover was highest in agricultural land compared with plantation forest and native forest. Levels of leaf litter cover were lowest in agricultural land and highest in native forest (Table 2). Plantation forest contained higher levels of bare ground and coarse woody debris than agricultural land and native forest (Table 2).

Relative scat endurance

Macropod scat endurance was influenced by habitat, season and species (Tables 1 and 3). In total, $70.0 \pm 9.5\%$ (mean \pm s.e.) of pademelon scats and $80.0 \pm 4.5\%$ (mean \pm s.e.) of wallaby scats remained identifiable and in the quadrats over 11 months. Scat endurance was highest in native forest and lowest in agricultural land for both species (Table 3; Fig. 2). Scat endurance decreased over time, with the biggest difference occurring between summer (January 2009) and spring (November 2009) (Table 3; Fig. 2). However, 92% of scats endured over a five month period between summer and winter in all three habitats (Fig. 2). This indicates that the rate of scat

	Agricultural land $(n=10)$	Plantation forest $(n=25)$	Native forest $(n=92)$
Environment			
Slope (°)	4.7 ± 2.4	1.6 ± 1.5	6.3 ± 3.9
Elevation (m)	58.6 ± 11.2	101.0 ± 2.5	118.5 ± 3.1
Vegetation			
CBA^{A} (m ² ha ⁻¹)	8.0 ± 9.0	32.0 ± 8.0	22.0 ± 10.0
Dominant species	E. amygdalina	E. nitens	E. amygdalina
Mid-storey cover ^B	Grasses $(50.0 \pm 0.0\%)$	<i>P. esculentum</i> $(26.0 \pm 0.2\%)$	L. scoparium $(28.0 \pm 0.1\%)$
Ground cover			* ` ` ` `
Ground vegetation (%)	62.6 ± 4.3	30.1 ± 1.9	33.8 ± 1.0
Leaf litter (%)	19.8 ± 3.1	31.1 ± 2.2	42.5 ± 1.0
Bare ground (%)	13.3 ± 2.1	26.0 ± 1.6	13.6 ± 0.7
CWD ^C (%)	3.2 ± 1.0	9.8 ± 0.8	8.1 ± 0.4
Understorey cover ^B	Sedges, thistles $(7.5 \pm 0.3\%)$	Grasses (28.0 ± 0.5)	<i>P. esculentum</i> (10.0 ± 0.4)

Fable 2.	Environmental variables, vegetation and ground cover structure and composition, presented as mean ± s.e., for the
	habitat types surveyed for macropod scat abundance (<i>n</i> is the number of transects in each class of habitat)

^ACBA (compartment basal area) calculated as Basal Area=(total number of trees counted divided by the number of points sampled) *Basal Area Factor (10).

^BAbundance calculated using mean ± s.e. generated from the % midpoints from the assigned Braun-Blanquet abundance score across each transect per habitat type.

^CCWD – coarse woody debris.

Table 3. Results of the mixed model testing relative scat endurance (% of scats remaining) (±s.e.) of macropod scats in response to habitat type, season and species during the 11 month trial

The mixed model was chosen based on AIC_c-based model selection presented in Table 2. The intercept applies to agricultural land, summer and pademelons; other coefficients are relative to these factors

	Macropod scat endurance (% of scats remaining \pm s.e.)		
Habitat type			
Plantation forest	0.06 ± 0.04		
Native forest	0.13 ± 0.05		
Season			
Winter	-0.06 ± 0.03		
Spring	-0.27 ± 0.03		
Species			
Wallaby	0.06 ± 0.02		

decomposition should not have influenced findings from the scat surveys.

Habitat use

For both species, habitat type and season best explained macropod habitat use (Table 1). Macropod scat deposition rates were higher on agricultural land than plantation forest and native forest habitats (Table 4; Fig. 3). Pademelon deposition rates were highest in early autumn and decreased in late autumn and spring (Table 4; Fig. 3), and wallaby deposition rates were lower in late autumn and spring compared with summer and early autumn (Table 4; Fig. 3).

Effects of shooting and fencing

For both species, distance from the intervention sites best explained scat deposition rates on agricultural land after the intervention (Table 1). Scat deposition rates on agricultural land decreased with increasing proximity to the intervention



Fig. 2. Scat endurance (percentage of scats remaining) after 303 days in the field for (*a*) the Tasmanian pademelon, and (*b*) the red-necked wallaby across time (season) broken down by the habitat types surveyed for macropod scat abundance. Values are mean \pm s.e. bars for each habitat type across each season category. Scat placement occurred in summer (day 0, January 2009) where 100% of scats were present at this time; scats were then sampled in winter (day 150, June 2009) and spring (day 303, November 2009).

Table 4. Results of the mixed model testing macropod habitat use for the control (non-intervention) sites examining scat deposition rates (scats km²) (\pm s.e.) in response to habitat type and season

The mixed model was chosen using the AIC_c-based model selection presented in Table 2. The intercept applies to native forest and early autumn; other coefficients are relative to these factors

	Scat deposition rate (scats $\text{km}^{-2} \pm \text{s.e.}$)		
	Pademelon	Wallaby	
Habitat type			
Agricultural land	26565.8 ± 3174.7	2667.7 ± 3949.1	
Plantation forest	609.8 ± 1143.2	-414.9 ± 2186.4	
Season			
Summer	-116.0 ± 521.0	784.7 ± 1360.2	
Late autumn	-492.7 ± 791.5	-5439.8 ± 1258.2	
Spring	-102.8 ± 521.8	-2685.9 ± 1350.6	

sites following the summer shooting intervention $(r^2 > 0.87)$, for pademelons in the winter shooting intervention $(r^2 = 0.79)$, and for both species following the fencing intervention $(r^2 > 0.47)$. There were no clear trends apparent for either species in scat deposition rates in plantation forest $(r^2 < 0.16)$ or native forest $(r^2 < 0.04)$ habitats post-intervention, as indicated by lower model support (Table 1).

Discussion

The Tasmanian pademelon and the red-necked wallaby occurred in the three main habitat types year round but both species showed preference for agricultural habitats. Differences in environmental, vegetation and ground cover structure and composition among habitat types were evident - factors that can influence macropod habitat use across the landscape (e.g. le Mar and McArthur 2005; While and McArthur 2005). Macropod scats remained largely undecomposed for over five months across all habitat types, and for over 11 months across native forest and plantation forest habitat types, giving us confidence in the use of scats as a proxy for animal abundance, given that the rate of decomposition was slower than the sampling intervals adopted in this study. The density levels of pademelon and wallaby scats generally matched the density levels measured in other studies for these species in similar habitat types (le Mar and McArthur 2005: While and McArthur 2005). Scat deposition rates varied seasonally, while distance from the intervention sites following intervention activity additionally influenced deposition rates. This information allows us to describe the habitat preferences of pademelons and wallabies and the potential effects of season and management interventions on their habitat use as outlined below.

Habitat use

Year round, pademelons displayed a greater preference for agricultural land than plantation forest and native forest habitats. In contrast, wallaby preference for agricultural land appeared greatest in summer. These results likely reflect the importance of vegetation composition as a driver of macropod habitat selection (Sanson 1989; McArthur *et al.* 1991; Sprent and McArthur 2002; le Mar and McArthur 2005). The stronger preferences of pademelons for agricultural land may be linked to their high physiological demands for high resource

availability year round, while wallabies appear to be able to exploit lower quality resources in plantation and native forest. Pademelons are the smaller of the two species and thus have higher energetic demands (basal metabolic rate) than wallabies (Hume 1989), explaining the importance of high quality resource availability for this species. Predator avoidance may also contribute to the mix of habitat use observed. Previous research has shown that pademelons rely on crypsis for predator avoidance by selecting dense native forest for diurnal shelter (le Mar and McArthur 2005), and thus favour dense under and midstorey vegetation adjacent to agricultural habitat (Sprent and McArthur 2002; Blumstein and Daniel 2003; le Mar and McArthur 2005; While and McArthur 2005; Coulson 2009). However, the open forest structure of the native forests that dominate the landscape in our study site appears to provide unsuitable habitat for pademelons, and established plantation forests were generally not close to agricultural land. Wallabies are the larger of the two species and correspondingly have a larger home-range area than pademelons (Hume 1989; Wiggins et al. 2010), enabling them to utilise a greater range of habitats with varying resource availabilities. The open eucalypt forest structure in our study site may provide a suitable flight-medium (escape paths) for wallables for predator avoidance, while the high density tree cover provided by plantation forest provides suitable diurnal shelter (le Mar and McArthur 2005).

There were also strong seasonal influences on the scat deposition rates of both species. The higher rates of scat deposition measured in summer, particularly on agricultural land, may have been influenced by high levels of resource availability coupled with seasonally driven reproductive activity (joey emergence from the pouch and seasonal breeding opportunities would have begun in spring and continued into summer) (Catt 1977; Rose and McCatney 1982; Driessen 1992). Reduced deposition rates in late autumn and spring may reflect seasonal changes in resource availability and/or thermal conditions, which may cause animals to search larger areas for food, thereby diluting scat depositions rates (Bacigalupe et al. 2003). Changes in predator abundances on a seasonal basis may have additionally influenced macropod behaviour and subsequently deposition rates (While and McArthur 2005, 2006). The influence of season on vegetation growth may also have altered the visibility of scats across the survey periods (Bulinski and McArthur 2000).

Management interventions

Results from this study demonstrate that after shooting and fencing, distance from the intervention sites appeared to influence pademelon and wallaby activity levels in agricultural land. Following each of the management interventions, pademelon scat deposition rates decreased on agricultural land with increasing proximity to the intervention sites, with a decline of 50% at around 3 km. Wallaby deposition rates followed a similar pattern in response to the first shooting and fencing interventions, but remained unchanged following the second shooting intervention, perhaps because activity levels were notably lower across the whole landscape. Given that limited data were obtained between the distances of 1.5 and 3 km from each management intervention, some caution is required with



Fig. 3. Scat deposition rates for (*a*) the Tasmanian pademelon, and (*b*) the red-necked wallaby in the three habitat types and four time periods surveyed for macropod scat abundance at the control (non-intervention) sites. Values are mean \pm s.e. bars for each habitat type from each scat survey (excluding time 0 (day 0, December 2008) when transects were initially cleared).

data interpretation. Additional data between these distance classes would be required to support (or negate) interpretations of strong positive relationships between scat deposition rates and management interventions.

Lethal culling by shooting can result in an immediate reduction in population densities, with short to longer term reductions dependent on the scale of the cull and timing of subsequent interventions (McNulty *et al.* 1997; Efford *et al.* 2000). In a concurrent study, Wiggins *et al.* (2010) found that these shooting interventions resulted in reduced levels of scat abundance in the immediate areas of intervention. The movement patterns of GPS-collared pademelons and wallabies indicated that surviving individuals remained in the areas of shooting intervention, while increasing their home-range area and agricultural land utilisation, but animals from surrounding areas did not appear to move into the intervention areas at any significant rate within the following five month period (Wiggins *et al.* 2010). The reduced deposition rates with increasing proximity to intervention sites on agricultural land recorded in this study may provide support for the predictions of Wiggins *et al.* (2010), that shooting can reduce animal numbers in the immediate intervention areas. This pattern was evident following the first shooting intervention in summer for pademelons and wallabies, and was observed again following the second shooting intervention in winter for pademelons only.

Following the fencing intervention, mean scat deposition rates of pademelons and wallabies decreased in agricultural land with increasing proximity to the intervention site, although this result was supported by a weakly positive relationship for both species. This result, coupled with the behavioural observations made by Wiggins *et al.* (2010) – that pademelons moved to neighbouring properties and wallabies moved away from the site of fencing – potentially highlights the impacts that barrier fencing may have on macropod habitat use surrounding the areas of barrier placement, and the benefits of fencing to protect specific loci in the landscape from macropod herbivory (Statham and Statham 2009).

The combination of individual behavioural observations from Wiggins et al. (2010) and the landscape-scale perspective measured in this study support the theory that management interventions can have important impacts on both the movement patterns and subsequent habitat use of target populations of pest herbivores: pademelon and wallaby scat deposition rates were substantially lower on agricultural land following the three intervention activities compared with deposition rates before intervention activity. However, results from this study also highlight the importance of environmental and seasonal influences on animal habitat use, which are not always observed when focussing on individual behavioural observations. Given the complex interactions that can occur between environmental and seasonal factors in influencing animal behaviour and habitat use, the timing of management interventions may additionally contribute to changes in macropod habitat use and movement patterns across the landscape. Results also highlight the potential localised effect that management interventions can have on macropod populations.

Management implications

Macropod scat deposition reportedly occurs most frequently during feeding (Johnson *et al.* 1987), and we have demonstrated that scats can reliably persist in the landscape for up to a year. Scats can therefore provide a quick and cost effective survey technique for the assessment of macropod habitat use and abundance levels in monitoring or managing pest populations, which can be used in combination with, or in place of, other survey techniques such as radio-telemetry (Wiggins *et al.* 2010).

Results highlight the importance of heterogeneous, resourcerich environments for pademelons and wallabies, and the influences that spatial, temporal and anthropogenic activities can have on their habitat use. The combined effects of shooting and fencing interventions, along with the seasonal changes that occurred, altered macropod habitat use in an agricultural–forest mosaic. This type of information can be fed directly into wildlife management strategies and is likely to have important implications for the effectiveness and sustainability of management interventions across the landscape.

Conclusions

Faecal pellet (scat) counts provided important information on macropod abundances in responses to habitat, season and wildlife management interventions and are a useful survey technique for assessing macropod population movements. Macropod abundance was highest in agricultural land and lowest in native forest. Shooting and fencing management interventions affected macropod deposition rates, and coupled with seasonal influences, contributed to changes in habitat use and movement patterns across the landscape. Results highlight the challenges associated with managing generalist native herbivore populations in habitat mosaics given the localised effect of intervention strategies and the complex interactions that can occur between spatial, temporal and anthropogenic influences on these populations.

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