Changes in the Relative Density of Swamp Wallabies (*Wallabia bicolor*) and Eastern Grey Kangaroos (*Macropus giganteus*) in Response to Timber Harvesting and Wildfire

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1. Introduction

Natural disturbances such as wildfire and storms act as major regulating forces in forest ecosystems (Attiwill, 1994; Lugo, 2000; Ryan, 2002), and in more recent times human disturbances such as urbanisation, land clearing and timber harvesting have also had a marked impact on forest extent and structure, and on the distribution and abundance of forest dwelling organisms (Abrams, 2003; Dale et al., 2000; Gaston et al., 2003; Thompson et al., 2003; Wilson and Friend, 1999). For many animals, disturbance events alter predation risk through changes to forest structure, and effect the distribution and abundance of food resources. Because both predation (Ferguson et al., 1988; Hughes et al., 1994) and food (Geffen et al., 1992; Tufto et al., 1996) can have a strong influence on movement patterns and habitat use, disturbance is predicted to alter the habitat choices of many species.

How disturbances such as fire and timber harvesting alter the habitat use of medium to large mammalian herbivores is variable and species dependant (Fisher and Wilkinson, 2005). For example, woodland caribou (*Rangifer tarandus caribou*) tended to avoid early successional stands, whether these resulted from timber harvesting (Mahoney and Virgl, 2003) or fire (Schaefer and Pruitt, 1991). In contrast, other ungulates responded positively to recently burnt (Archibald and Bond, 2004; Gasaway et al., 1989) or harvested (Cederlund and Okarma, 1988; Sullivan et al., 2007) sites, probably due to increased food resources in these areas. The response of herbivores to fire and timber harvesting also changes over time, with effects being detected across a range of temporal scales (Mahoney and Virgl, 2003; Pearson et al., 1995). Catling et al. (2001) showed that in some cases temporal responses of fauna to fire and habitat structure may be non-linear.

In mainland southeastern Australia, macropodid marsupials (kangaroos and wallabies) are the dominant native medium to large herbivorous fauna in woodland and forest ecosystems, with eastern grey kangaroos (*Macropus giganteus*) and swamp wallabies (*Wallabia bicolor*) two of the most abundant species. Eastern grey kangaroos are predominantly grazers (Taylor, 1983), preferring heterogeneous habitats that provide

relatively open, high quality foraging sites close to or interspersed with shelter vegetation (Hill, 1981; Moore et al., 2002; Southwell, 1987; Taylor, 1980). In contrast, swamp wallabies are mixed feeders (Davis et al., 2008; Di Stefano and Newell, 2008; Hollis et al., 1986) who prefer densely vegetated habitat, particularly during the day (Di Stefano et al., 2009; Lunney and O'Connell, 1988; Swan et al., 2008; Troy et al., 1992).

The response of these species to timber harvesting and fire has been rarely studied, particularly for eastern grey kangaroos. In native Eucalypt forest, swamp wallabies used recently harvested (1-5 year old) areas more than older regenerating and unharvested sites (Di Stefano et al., 2007; Di Stefano et al., 2009; Lunney and O'Connell, 1988), although factors such as topographical position (Lunney and O'Connell, 1988), sex and diel period (Di Stefano et al., 2009) were important factors influencing habitat use at finer spatial and temporal scales. In a plantation forestry environment, Floyd (1980) found that swamp wallaby density was uniformly high at two year old sites and uniformly low at one year old sites. Density in unharvested forest and ten year old sites was higher at the periphery than in the centre, an effect probably influenced by the close proximity of food resources to the edges of these more sheltered environments. Fewer data are available about the response of eastern grey kangaroos to timber harvesting. Hill (1981) found that kangaroo density was higher in partially harvested forest than in either unharvested forest or open woodland, and suggested this was related to the spatial interspersion of both food and shelter within harvested stands.

There appear to be no published data quantifying the response of swamp wallabies to fire, although Catling et al. (2001) presented an analysis for a pooled sample of swamp and red-necked wallabies (*Macropus rufogriseus*). In this case, time since fire had little effect on wallaby abundance in structurally simple habitats but there was a strong negative relationship in structurally complex habitats. The use of burnt habitat by kangaroos is likely to increase after fire (Catling et al., 2001; Southwell and Jarman, 1987), probably as a result of increased nutrient content of regenerating forage (Murphy and Bowman, 2007) and the removal of dense movement-impeding vegetation (Taylor, 1980). In a dry sclerophyll landscape, Catling et al. (2001) observed a non-linear relationship between kangaroo density and time since fire, with density increasing for about a decade before declining.

Our objective was to quantify changes in the relative density of swamp wallabies and eastern grey kangaroos in response to disturbance. Timber harvesting and wildfire in a commercially managed mixed species eucalypt forest provided four alternative habitat types, and we expected the density of both species to differ between them. On the basis of the work cited above we predicted that swamp wallabies would use densely vegetated sites more than open ones, and that wallaby density would be positively related to the abundance of lateral cover. In contrast, we expected kangaroo density to be positively related to food availability (grass) (Taylor, 1980, 1984), but for this effect to be moderated by vegetation density, as both food and shelter are likely to influence habitat choices by this species (Hill, 1981; Moore et al., 2002; Southwell, 1987).

In addition, the co-occurrence of a wildfire and one of the harvesting events provided a rare opportunity for direct comparison between harvested and burnt sites of the same age, both with respect to the structure of the regenerating forest and the response of the focal species. This comparison is important from a conservation perspective, as congruence between harvesting effects and those of natural disturbances such as fire are likely to result in better conservation outcomes in managed landscapes (Hunter, 1993; Lindenmayer et al., 2006).

2. Methods

2.1 Study site

The Pyrenees State Forest in west central Victoria (37°05′ latitude, 143°28′ longitude) is dominated by a single range running approximately east-west and rising to 750 m above sea level (Figure 1). This dry sclerophyll landscape is dominated by two Ecological Vegetation Classes: Grassy Dry Forest on the northerly aspects and Herb Rich Foothill Forest on the southerly slopes. Messmate/blue gum (*Eucalyptus obliqua/E. globulus bicostata*) associations dominate the overstorey and constitute a forest type often referred to as Low Elevation Mixed Species. A sparse shrub layer includes silver wattle (*Acacia dealbata*), common heath (*Epacris impressa*), gorse bitter-pea (*Davisia ulicifolia*) and austral bracken (*Pteridium esculentum*). A more detailed description of vegetation and other site characteristics is given in Di Stefano et al. (2007).
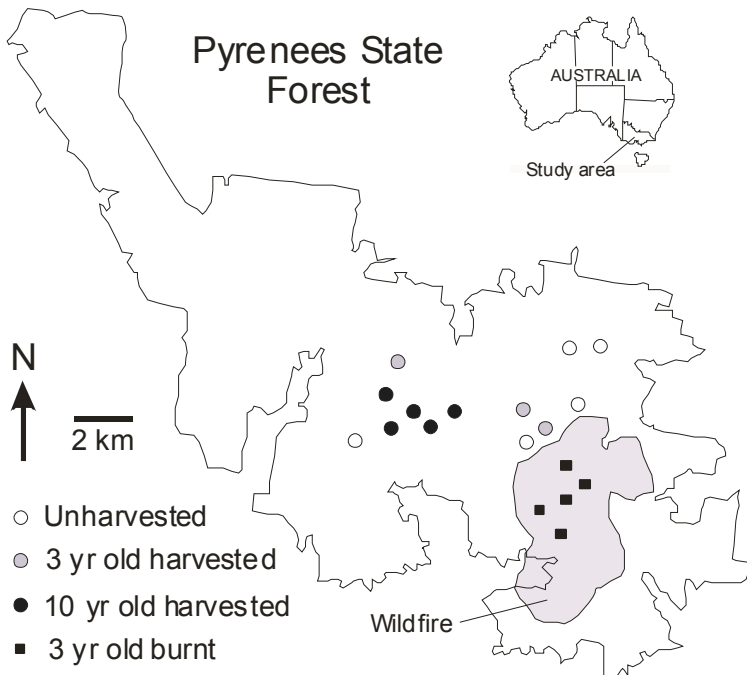

Fig. 1. Map of the Pyrenees State Forest, southeastern Australia, showing the location of the sampling plots.

Since 1990, timber harvesting in the Pyrenees has created 25 regenerating blocks (coupes), 10-30 ha in size and of various ages, surrounded by essentially unharvested forest. The harvesting technique is referred to as the seed tree system, and involves the retention of four to nine mature trees per hectare to provide seed for the next crop and habitat for arboreal animals. Harvesting generally takes place between late spring and autumn (October to April) after which logging debris is burnt to prepare a seedbed and stimulate seed fall (Lutze et al., 1999).

In addition to unharvested areas we used three year old and ten year old regenerating sites to represent three age classes within the harvested landscape. Three year old sites were dominated by relatively homogeneous stands of 1-2 m tall, densely regenerating *Eucalyptus* seedlings, and contained substantial quantities of silver wattle, austral bracken, grass and forbs. Ten year old sites supported patches of dense, closed stands of 3-6 m tall eucalypt regeneration and had variable levels of forb, grass and shrub cover. The cover of bracken, however, remained relatively high.

In March 2001 a wildfire burnt about 2000 ha of forest at the eastern end of the study area (Figure 1). The wildfire and the post-harvest burns at the three year old regenerating sites occurred within a few months of each other, thus presenting the opportunity to compare the impact of the two disturbance types within the same forest ecosystem. In contrast to three year old harvested sites, the burnt area retained many live mature trees regenerating via lignotubers at the base of the trunk and epicormic shoots. It was also relatively heterogeneous, with some sites devoid of regenerating plants, but others densely populated by regenerating eucalypt seedlings, silver wattle and austral bracken. Some patches within the burnt area supported stands of eucalypt seedlings at even higher densities than the harvested areas.

2.2 Experimental design and monitoring

We used all the available three year old sites (*n* = 3) and selected a random sample of ten year old sites (*n* = 5) from a pool of eight that were available. In the unharvested and burnt areas we used the road network as a sampling frame and randomly selected sites (*n* = 5 in each area) from a larger pool of potential areas. On most occasions sites were more than one kilometre apart, although limitations imposed by the road network and the location of harvested areas meant that a few were somewhat closer together. In addition, the location of the burnt and harvested areas prevented the spatial interspersion of sites from each of the four habitats. The locations of the sites within the study area are shown in Figure 1.

At each site, ten 15 m² circular plots (radius 2.18 m) were established in a 5 × 2 arrangement on a randomly positioned 40 m grid and within these the accumulation of kangaroo and wallaby faecal pellets were monitored over time as a surrogate for herbivore abundance (Southwell, 1989). In the interpretation of results we make the assumption that relative differences between pellet numbers in each habitat are an accurate reflection of relative differences in animal density. Plots were cleared of faecal pellets in June 2004, and then pellets were counted approximately two and four months later during late winter (July/August) and spring (September/October). Raw data were converted to pellets ha^{-1}day^{-1} prior to analysis. We were able to differentiate between wallaby and kangaroo faecal pellets relatively easily on the basis of size, shape, colour and internal texture (Triggs, 2004).

During the spring monitoring time we used the plots described above to quantify shelter and food resources at each site. For both species shelter (lateral cover) was measured as the vertically projected cover of any live or dead vegetation between 0.5-3 m. Food resources were measured as the cover of grass for kangaroos and the cover of forbs for wallabies, as eastern grey kangaroos eat mainly grass (Taylor, 1983) and swamp wallabies consume substantial quantities of forbs (Hollis et al., 1986), particularly in the Pyrenees (Di Stefano and Newell, 2008). In addition, we quantified the percentage cover of tree canopy, live or

dead vegetation <0.5 m, and a variable representing the combined cover of litter and woody debris. Cover values were estimated by a single observer (K.W.) to the nearest 5%. The cover of vegetation <0.5 m was discarded prior to analysis as it was highly correlated with the cover of grass.

2.3 Data analysis

Principle components analysis (PCA) and an associated vector fitting procedure were used to assess how the 18 sites differed with respect to the measured habitat variables. The routine was run in PRIMER 6 and each variable was standardised by its maximum value prior to analysis. Analysis of similarities (ANOSIM), also run in PRIMER 6 on a Euclidian resemblance matrix derived from the standardised data, was used to test for multivariate difference among habitat types.

We used repeated measures ANOVA in GenStat 13 to analyse the effects of habitat type and season (winter, spring) on relative macropod density. Differences between particular habitat types were then assessed by constructing a table of contrasts including mean differences and their associated 95% confidence intervals. Assumptions of normality and homogeneity of variance were assessed using half-normal and fitted value plots respectively. For both data sets the variance was somewhat heterogeneous but as transformations had little effect on the output we ran the analysis on the raw data.

Generalised linear mixed models were used to assess the relationship between relative density and three predictor variables: season, shelter and food. In addition to its role as a predictor, season was used as a random factor in the statistical model to account for the nesting of season within site. Assumptions of normality and homogeneity of variance were assessed for the top ranked models using half-normal and fitted value plots respectively, and no transformations were deemed necessary. Models were run in R v. 2.13 using the lme4 package (Bates and Maechler, 2009).

We developed a candidate set of eight models designed to test the consistency of the data with our a priori expectations about the relationships between relative density and resource abundance. First, we built three models examining the effect of food, shelter, and the interaction between the two. We then build three additional models examining the interaction between season and the two primary resources. Finally, we added a global model which included all three variables and their interactions, and a null model (containing only the intercept and the random factor) to provide a baseline against which potentially more informative models could be compared. Models including interactions always contained the main effects of the interacting variables. In addition, food and shelter values were centred before computing the interaction between them to avoid colinearity between the original variables and their multiplicative effect (Quinn and Keough, 2002).

Models were compared using an information theoretic approach (Burnham and Anderson, 2002). Akaike's Information Criteria (AIC) and Akaike weights were used to rank models and assess their relative fit to the data. The importance of each variable (season, shelter and food) was assessed by calculating predictor weights, the sum of the Akaike weight for each model containing the focal variable (Burnham and Anderson, 2002).

3. Results

3.1 Disturbance and resource availability

The amount of shelter vegetation, forbs and grass in each of the four habitat types is shown in Figure 2. Unharvested sites were characterised by low levels of shelter vegetation and somewhat higher levels of grass and forb cover. All three year old harvested sites contained substantial amounts of shelter while three year old burnt sites had highly variable levels of shelter and grass. Shelter at three year old harvested and burnt sites was composed mostly of regenerating eucalyptus seedlings, austral bracken (*Pteridium esculentum*) and silver wattle (*Acacia dealbata*). Grass cover at ten year old harvested sites was also highly variable, with moderate levels of shelter also appearing in this habitat.
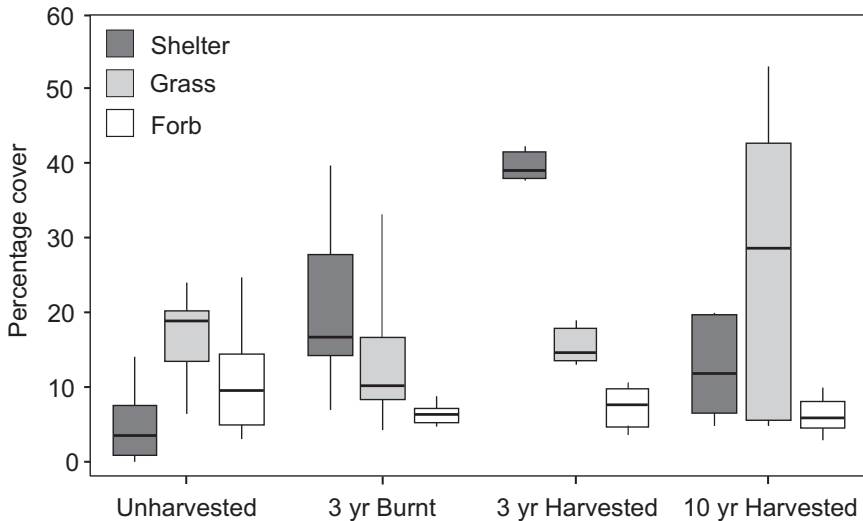

Fig. 2. The percentage cover of shelter vegetation, grass and forbs within the four habitat types. Boxes represent the interquartile range, horizontal lines represent medians and vertical lines represent minimum and maximum values.

The ordination plot from the principle components analysis (Figure 3) shows how the 18 sites differ with respect to the cover of forbs, grass, shelter, tree canopy and litter and woody debris. The X- and Y-axes in the figure (PC1 and PC2) represent 55.6% and 27.5% of the variance in the data respectively. As shown by the vectors, sites separated along PC1 differed predominantly with respect to shelter vegetation and canopy cover while sites separated along PC2 differed with respect to grass and litter and woody debris. The degree to which sites of the same habitat type are clustered in the same section of Figure 3 represents the variance within each of the habitat groupings. By this measure, three year old harvested sites and, to a lesser extent, unharvested forest sites were relatively similar to others in the same group. In contrast, sites within the ten year old harvested and three year old burnt habitats were highly variable with respect to at least some of the measured variables. Analysis of similarities (ANOSIM) indicated that there were strong to moderate differences between all habitat types except for ten year old harvested and three year old burnt sites, which were very similar (Table 1).
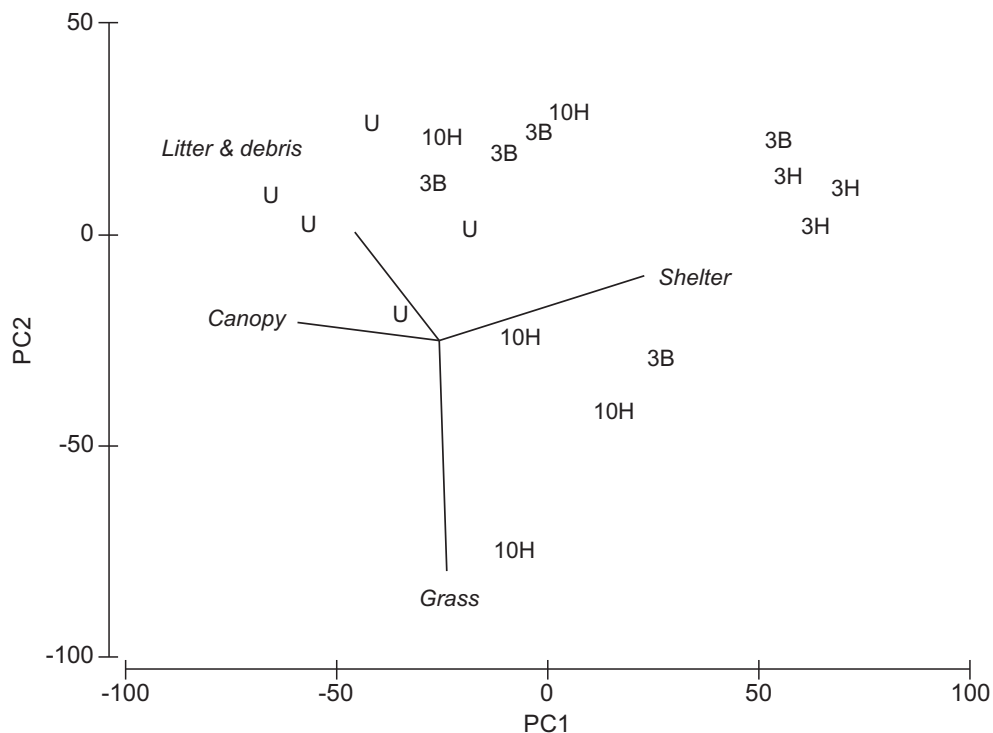
Fig. 3. Ordination plot from the principle components analysis showing how the 18 sites differed with respect to forbs, grass, shelter, canopy and litter and woody debris. The vectors (lines) on the diagram represent the strength and direction of the correlations between the original variables and the first two principle components, PC1 and PC2. U, unharvested forest; 3H, three year old harvested forest; 10H, ten year old harvested forest; 3B, three year old burnt forest.

Contrast	R	P-value
3 yr Harvested vs Unharvested	0.97	0.02
10 yr Harvested vs Unharvested	0.27	0.06
3 yr Burnt vs Unharvested	0.34	0.02
3 yr Harvested vs 10 yr Harvested	0.62	0.02
3 yr Harvested vs 3 yr Burnt	0.42	0.07
3 yr Burnt vs 10 yr Harvested	0	0.43

Table 1. Results of the Analysis of similarities (ANOSIM) procedure testing for multivariate differences between habitat types. R ranges between 0 and 1 and is a measure of effect size.

Contrast	Mean difference (pellets/ha/d)	LCL	UCL	P-value
Swamp wallaby				
3 yr Harv. vs Unharvested	268.7	187.2	350.2	<0.001
10 yr Harv. vs Unharvested	68.7	-1.9	139.3	0.06[1]
3 yr Burnt vs Unharvested	90.9	20.3	161.5	0.02
3 yr Harv. vs 10 yr Harv.	200.0	118.5	281.5	<0.001
3 yr Harv. vs 3 yr Burnt	177.8	96.3	259.3	<0.001
3 yr Burnt vs 10 yr Harv.	22.2	-48.4	92.8	0.51
Eastern grey kangaroo				
3 yr Harv. vs Unharvested	-40.2	-137.6	57.2	0.39
10 yr Harv. vs Unharvested	-43.0	-127.4	41.4	0.29
3 yr Burnt vs Unharvested	-27.3	-108.1	60.7	0.56
3 yr Harv. vs 10 yr Harv.	2.8	-94.6	100.2	0.95
3 yr Harv. vs 3 yr Burnt	-16.5	-113.9	80.9	0.72
3 yr Burnt vs 10 yr Harv.	19.3	-65.1	103.7	0.63

Table 2. Contrasts between habitat types for swamp wallabies and eastern grey kangaroos. A positive mean difference indicates that the value of the first listed habitat is larger than the second. LCL and UCL are lower and upper 95% confidence limits respectively. [1] Interpreted as evidence that 10 yr old harvested sites are used more than unharvested sites.

3.2 Relative density

The relative density of swamp wallabies was influenced by both habitat type and season (P< 0.001 in both cases; Figure 4a). The P-value associated with the habitat type by season interaction was also small (0.03), although this effect was primarily driven by very low density at unharvested sites during spring (Figure 4a), with patterns of use during the two seasons similar overall. Consequently, we consider it reasonable to interpret the main effects of habitat type and season. The ANOVA r^2 (SS_{Factor} / SS_{Total}) showed that habitat type explained 52.9% of the variance in the data, relative to 16.2% and 7.9% for the effects of season and the interaction respectively. Contrasts between the four habitat types (Table 2) demonstrate the following habitat ranks: 3H > 3B = 10H > UH, where 3H is three year old harvested, 3B is three year old burnt, 10H is ten year old harvested and UH is unharvested forest. Relative density was greater in winter (mean ± 95% CI: 164.0 ± 28.7) than in spring (66.8 ± 28.7).

In contrast to swamp wallabies, there was no evidence that the relative density of eastern grey kangaroos differed between habitat types (P = 0.71; Figure 4b), or of a season by habitat type interaction (P = 0.18), although a statistically significant seasonal effect was again detected (mean ± 95% CI: winter 129.0 ± 28.7 compared to spring 75.6 ± 28.7; P = 0.01). The ANOVA r^2 indicated that in sum, habitat type, season and their interaction only explained 26.3% of the variance in the data. Contrasts between the four habitat types (Table 2) show substantial overlap in relative density for every habitat contrast.
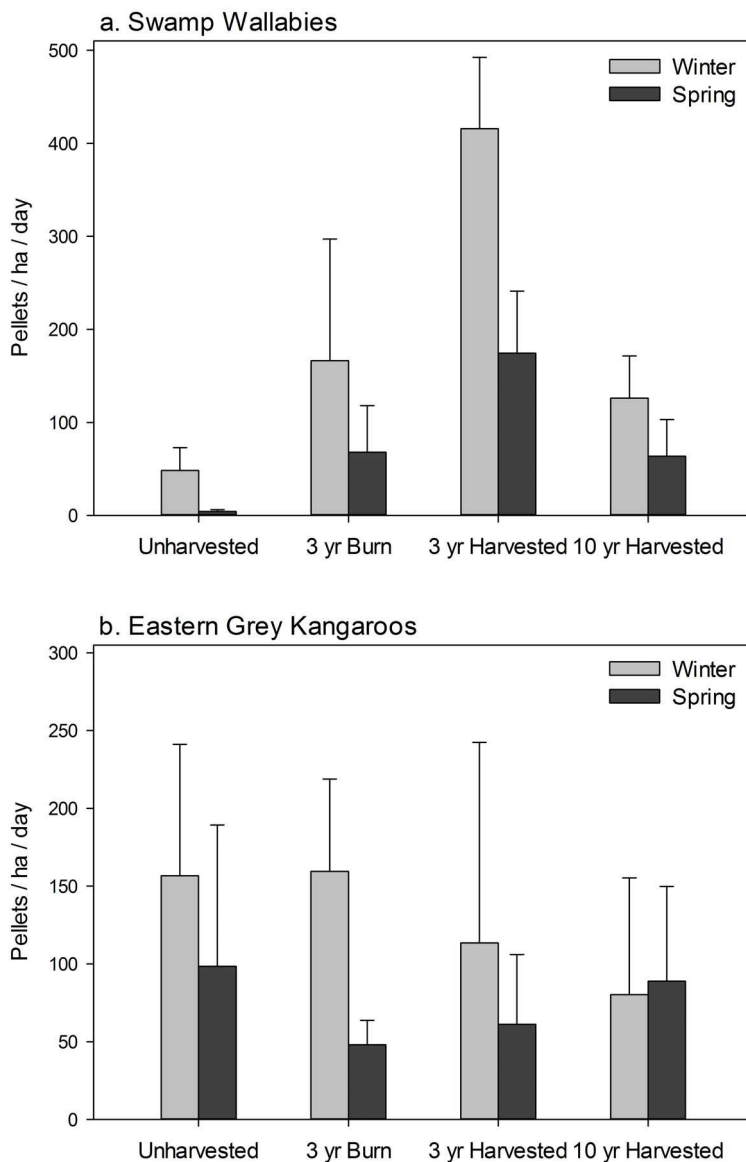
Fig. 4. Relative density of (a) swamp wallabies and (b) eastern grey kangaroos in the four habitat types during winter and spring. Errors bars represent the upper 95% confidence limit.

3.3 Relationships between relative density and resources

The model best describing patterns of swamp wallaby density across the 18 sites included the effects of season, shelter and their interaction, with a probability of 0.72 that it was the best in the set (Table 3, top). The high adjusted r^2 value (80.5%) associated with this model indicates a good fit to the data. A plot of the model (Figure 5a) shows that wallaby density was strongly and positively correlated with shelter during both winter and spring, but with a steeper rate of increase during winter. Predictor weights for season, shelter and food (forbs) were 1, 1 and 0 respectively, indicating the importance of season and shelter as predictors of wallaby density, and the negligible effect of food.

The model best predicting the relative density of eastern grey kangaroos included the effects of season, food (grass), and their interaction with a probability of 0.49 that it was the best in the set (Table 3, bottom). This relatively low Akaike weight indicates substantial model selection uncertainty, and the adjusted r^2 value of 21.9% demonstrates only a poor to moderate fit to the data. A plot of the model (Figure 5b) shows that grass cover was a better predictor of kangaroo density in spring than in winter. Predictor weights for season, food and shelter were 0.81, 0.77 and 0.37 respectively, indicating that season and grass cover were

Models	Δ AIC	Akaike weight	Adj. r^2 (%)
Swamp wallabies			
Season × shelter	0	0.72	80.5
Season × food + season × shelter	3.0	0.16	79.8
Season × food × shelter	3.5	0.12	80.4
Shelter	54.3	0.00	55.1
Food × shelter	21.3	0.00	53.1
Null	54.2	0.00	0
Season × food	55.2	0.00	9.8
Food	55.7	0.00	0
Eastern grey kangaroos			
Season × food	0	0.49	21.9
Season × food + season × shelter	2.6	0.13	19.7
Season × shelter	3.2	0.10	14.1
Season × food × shelter	3.4	0.09	21.2
Null	3.4	0.09	0
Food	4.7	0.05	0
Shelter	5.1	0.04	0
Food × shelter	7.1	0.01	0

Table 3. Model selection results for swamp wallabies (top) and eastern grey kangaroos (bottom). The model with a Δ AIC value of 0 fits the data best and Akaike weights are interpreted approximately as the probability that their associated model is the best in the set. Season: winter or spring; shelter: percentage shrub cover; food: percentage forb cover for wallabies and percentage grass cover for kangaroos. Models with interactions also contain the main effects of the interacting variables.
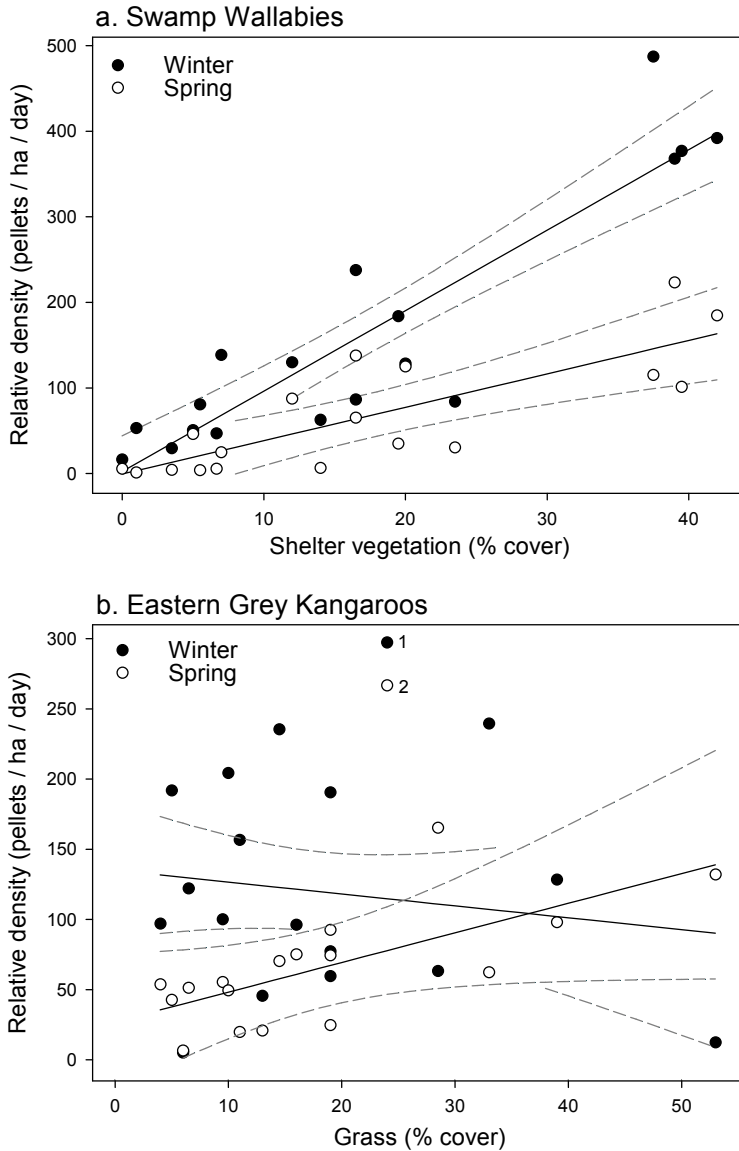
Fig. 5. Predicted relationship between (a) swamp wallaby density and the cover of shelter
vegetation and (b) kangaroo density and the cover of grass. Open and closed circles
represent the raw data for winter and spring respectively. Dashed lines are 95% confidence
limits. The predicted relationship and confidence limits in (b) were calculated after
removing the points labelled 1 and 2.

about twice as important as shelter for predicting kangaroo density. All results for eastern grey kangaroos were generated after removing data from an unharvested forest site with very high numbers of faecal pellets in both winter and spring (points labelled 1 and 2 in Figure 5b). Including these data in the analysis did not change the overall result, but further weakened the fit of the model.

4. Discussion

We have quantified the relative density of swamp wallabies and eastern grey kangaroos in a landscape where the distribution and abundance of food and shelter resources had been altered by both timber harvesting and fire. We defined four broad habitat types on the basis of time since disturbance and predicted differential use of at least some of these habitats by both species. We also predicted that density would be correlated with important resources, expecting a positive association between wallaby density and shelter vegetation, and a combined (interactive) effect of food and shelter on kangaroo density. Our finding indicated that the two species responded to the disturbances differently, but not always in the way we expected.

4.1 Resource availability

On the basis of several variables quantifying forest structure and food resources, moderate to large differences were detected between all of the habitat types except for ten year old harvested and three year old burnt sites. Three year old harvested sites had the most distinctive and consistent characteristics, with very high levels of shelter vegetation resulting from densely regenerating eucalyptus seedlings. The similarity between these sites was probably due to their location on the south side of a major ridgeline, and exposure to a consistent harvesting and seedbed preparation treatment during the same season.

In contrast, there were large differences between sites within the three year old burnt and ten year old harvested habitat types, indicating the spatially variable nature of disturbance-habitat relationships. Differences between sites burned by the same fire may be due to spatial variance in fire severity resulting from changes in weather conditions, topography, fuel load or fuel moisture (Bradstock et al., 2010). Although timber harvesting is a more uniform disturbance than fire, post-harvesting tree regeneration may also be influenced by a number of factors (Squire et al., 1991). For example, differences in seedbed conditions are known to affect the germination and establishment of eucalyptus seedlings (Dignan, 2002), and the ten year old sites used in this study did differ in this respect, with harvesting debris burnt on some sites but not on others (Merv Flett, personal communication). More generally, the development of vegetation communities after disturbance, and subsequent differences in resource availability and habitat structure, may be influenced by factors unrelated to the disturbance event, such density dependent competition, post-fire climatic conditions or site specific environmental factors (Bond and van Wilgen, 1996; Keeley et al., 2005). Factors such as these may have contributed to the high variance we observed between sites in the three year old burnt and ten year old harvested habitat classifications.

4.2 Relative density in different habitat types

We detected marked differences in swamp wallaby density among habitat types, with three year old harvested sites containing more than twice the number of faecal pellets then other

habitats. Wallaby density was also higher in three year old burnt sites and ten year old harvested sites compared to unharvested forest, but no difference between burnt and ten year old harvested sites could be detected. Our results are consistent with previous work linking high wallaby density to recently harvested areas (Di Stefano et al., 2007; Di Stefano et al., 2009; Lunney and O'Connell, 1988), and more generally with the finding that a range of medium to large herbivorous mammals are attracted to early successional environments (Cederlund and Okarma, 1988; Côté et al., 2004; Fisher and Wilkinson, 2005; Fuller and DeStefano, 2003; Sullivan et al., 2007). For swamp wallabies, density appears to be positively correlated with shelter vegetation which was often high in early successional stands. We discuss this relationship further in section 4.3.

In contrast to swamp wallabies, and contrary to our prediction, we found no differences in the relative density of eastern grey kangaroos among habitat types. This was somewhat surprising given that marked differences in resource availability between some of the habitats, and previous work in a variety of ecosystems showing that eastern grey kangaroos use broadly defined habitat associations selectively (Hill, 1981; Moore et al., 2002; Taylor, 1980). Several studies (e.g. Hill, 1981; Moore et al., 2002; Southwell, 1987) suggest that both food and shelter influence the density of eastern grey kangaroos. In particular, Hill (1981) showed that kangaroo density was high at sites with (a) high levels of both food and shelter, (b) high food and moderate shelter and (c) moderate food and high shelter. Arguably, all four habitat types included in the present study contained at least some sites conforming to one of these three classifications, possibly explaining the similar density profile we observed.

We included season in the statistical model to account for temporal variation in abundance between sampling times, and not because seasonal effects were of particular interest. For both species, density was lower in spring than in winter, and we interpret this change as part of normal temporal fluctuations experienced by many herbivorous mammals (e.g. Ager et al., 2003). Due to the short time span of our study (only one sample in winter and spring, respectively), we are unable to make any reliable inference about seasonal effects.

4.3 Relationships between relative density and resources

Using our simple set of predictor variables we were able to model swamp wallaby density with a high degree of precision. The best model included the effect of season, shelter and their interaction, as was consistent with our original prediction that wallaby density would be positively correlated with the abundance of lateral cover. Although swamp wallabies may prefer sites containing both food and shelter in close proximity (Floyd, 1980; Hill and Phinn, 1993), shelter vegetation alone appears to be a reliable predictor of relative density (Lunney and O'Connell, 1988; Di Stefano, unpublished data).

Swamp wallabies are a cryptic species and probably use sheltered sites to avoid predators such as red foxes (*Vulpes vulpes*) and wedge tailed eagles (*Aquila audax*), both of which were present at our study site. Predation is a process known to influence habitat use by medium to large herbivorous mammals (Ferguson et al., 1988; Rachlow and Bowyer, 1998), and in many cases results in a trade off between the acquisition of shelter and food (Lima and Dill, 1990; Verdolin, 2006). Some species select sites with high shelter and lower food resources when predation risk is high (Ferguson et al., 1988), but others are able to select sites that contain adequate amounts of both shelter and food (Pierce et al., 2004). At our study location, forbs, an

important food resource for swamp wallabies (Davis et al., 2008; Di Stefano and Newell, 2008; Hollis et al., 1986), were present in similar abundance regardless of shelter quantity. We have hypothesised elsewhere (Di Stefano et al., 2009) that this enabled swamp wallabies to reduce predation risk by selecting sheltered sites containing adequate food resources, and thus reduce the trade off between shelter and food that often results from predator avoidance behaviour.

We were unable to model the density of eastern grey kangaroos with a high degree of precision. The best model included the effect of season, food (grass), and their interaction, but did not fit the data particularly well, and was associated with substantial model selection uncertainty. The model showed that kangaroo density in spring was positively associated with grass cover, but density in winter was not, an effect that may have been related to increased protein concentrations during the spring sampling period (Taylor, 1984). Overall, these findings were partially consistent with the predicted positive relationship between kangaroo density and grass abundance, but not with our expectation that this effect would be moderated by shelter availability.

Although the density of eastern grey kangaroos is widely believed to be influenced by the co-occurrence of food and shelter (Hill, 1981; Moore et al., 2002; Southwell, 1987), published results are somewhat inconsistent. In some cases forage abundance or quality has been the primary driver of kangaroo density (Taylor, 1980, 1984), while in others the importance of both food and shelter has been clearly shown (Hill, 1981). Further, the relationship between shelter vegetation and kangaroo density remains unclear, with published data identifying positive, negative, and no relationship (Catling and Burt, 1995; Catling et al., 2001; Hill, 1981). In addition, results are probably influenced by the size of the sampling unit used in different studies (Ramp and Coulson, 2004). For example, the multiplicative effect of food and shelter detected by Hill (1981) was derived from estimates of density and resource availability within replicate 25 ha blocks, while we quantified variables within 0.64 ha sampling units. Smaller plots may fail to detect the influence of important resource features occurring outside the plot boundary, while larger plots may miss smaller scale patterns. Unlike swamp wallabies, the density of eastern grey kangaroos appears to be influenced by an interacting array of factors including food abundance, food quality and shelter availability. The influence of these factors are likely to depend on the scale at which they are measured, and to vary throughout the wide range of this species. Additional, multi-scale studies are required to determine how resources influence habitat use across the species' range.

As a caveat, we note that faecal pellet counts have their limitations as an index of relative abundance. One problem with this technique is the inability to detect fine-scale demographic or temporal influences on the relationship between habitat use and resources. Several studies, including some on swamp wallabies and other medium-sized macropods, have found important effects of demography and time of day on patterns of habitat use (Ager et al., 2003; Beyer and Haufler, 1994; Di Stefano et al., 2009; le Mar and McArthur, 2005; Moe et al., 2007; Swan et al., 2008). As such, analyses based on faecal pellet data provide information about broad patterns of habitat use that may hide important demographic or temporal effects.

4.4 Comparison between harvested and burnt sites

Better conservation outcomes may be achieved in managed landscapes if the impacts of human disturbances, such as timber harvesting, are similar to those of natural disturbances, such as fire (Hunter, 1993; Lindenmayer et al., 2006). The existence of three year old

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harvested and burnt sites in this study enabled us to compare these areas with respect to habitat characteristics, and the density of swamp wallabies and eastern grey kangaroos.

We found that three year old harvested and burnt sites were structurally dissimilar, and that burnt sites had a much more variable array of structural characteristics. This is consistent with previous work identifying increased structural heterogeneity within burnt plots as a major difference between early successional burnt and harvested stands (Lindenmayer and McCarthy, 2002; Schulte and Niemi, 1998).

In relation to macropods we found that three year old harvested and burnt habitats supported very different densities of swamp wallabies, but similar densities of kangaroos. This also reflects other findings, with faunal responses differing between harvested and burnt areas in some instances (Schulte and Niemi, 1998; Simon et al., 2002a) but not in others (Baker et al., 2004; Simon et al., 2002b). Differences between harvesting and wildfire, both in terms of structural characteristics and faunal responses, are likely to be greatest shortly after disturbance and converge over time (Simon et al., 2002b). Findings will also be influenced by forest ecosystem type, characteristics of the disturbance event, disturbance history, focal taxa or species, and spatial context. We did not consider spatial context in our study, but harvested and burnt sites clearly differed with respect to the nature of the surrounding habitat. Quantifying landscape characteristics around each site and assessing their influence on macropod density may be a useful extension of our current work.

An unexpected finding was the similarity between ten year old harvested three year old burnt habitats, both in terms of habitat characteristics and faunal responses. There are two likely reasons for this result. First, the extra regeneration time at ten year old sites enabled the re-development of structural attributes (e.g. tree canopy) that were present in the younger burnt sites but virtually absent from three year old harvested stands. Second, as we have already mentioned, the ten year old sites were subject to variable treatment of post-harvest debris, with burns occurring at some sites but not others. We argue that this variation in operational practice lead to differences in the post-disturbance recovery, resulting in a heterogeneous set of sites closely mimicking the structural heterogeneity found in the burnt landscape.

5. Conclusions

Using faecal pellet counts, we quantified the relative density of swamp wallabies, *Wallabia bicolor*, and eastern grey kangaroos, *Macropus giganteus*, to wildfire and timber harvesting in a native eucalyptus forest in southeastern Australia. We defined four broad habitat types on the basis of time since disturbance (unharvested, three year old harvested, ten year old harvested and three year old burnt) and predicted differential use of these habitats by both species. Multivariate analysis was used to compare sites within habitat types with regard to several habitat attributes including food and shelter resources for our two focal species. We modelled density as a function of these two resources, and predicted a positive correlation between wallabies and shelter vegetation. In contrast, we expected kangaroo density would be influenced by the interaction between food and shelter. In addition, the occurrence of harvesting operations and a fire during the same season provided an opportunity to compare harvested and burnt sites of the same age.

Structural differences were observed between all habitat types except for the three year old burnt and ten year old harvested classifications. Three year old harvested sites differed markedly from most others with respect to shelter vegetation (high) and canopy cover (low).

Swamp wallaby density was highest in three year old harvested sites and lowest in the unharvested forest, and, as predicted, showed a strong positive association with shelter vegetation. In contrast, we could not detect any influence of habitat type on kangaroo density. A statistical model that fit the data relatively poorly indicated that density was positively correlated with food resources (grass) in spring, but not in winter, a finding only partially consistent with our expectations.

Finally, we conclude that fire and timber harvesting at our study location are likely to result in very different early successional landscapes. Three year old harvested sites were structurally simple and spatially homogeneous compared to the more heterogeneous nature of the habitat both within and between similarly aged burnt sites. Kangaroo density did not change in response to these differences, but wallaby density was substantially higher in the harvested areas. The fact that our focal species responded differently demonstrates that the relationship between landscape change and fauna is species specific, depending on both the nature of the change and the requirements of particular species. Nevertheless, it has been shown elsewhere that spatially homogenous and structurally simple patches resulting from timber harvesting will, in general, be less able to support a range of species than more complex and variable landscapes resulting from fire (Lindenmayer and Franklin, 2002; Lindenmayer and McCarthy, 2002; Lindenmayer and Noss, 2006). Consequently, we suggest that forest managers should foster structural and spatial heterogeneity by varying operational harvesting practices, and incorporating fire as a major component of the disturbance regime.

6. Acknowledgements

7. References

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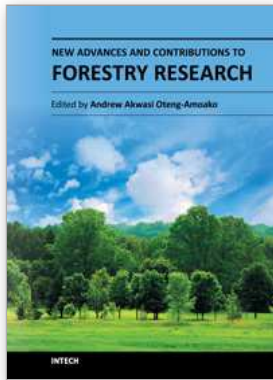
New Advances and Contributions to Forestry Research

Edited by Dr. Dr. Andrew A. Oteng-Amoako

New Advances and Contributions to Forestry Research consists of 14 chapters divided into three sections and is authored by 48 researchers from 16 countries and all five continents. Section Whither the Use of Forest Resources, authored by 16 researchers, describes negative and positive practices in forestry. Forest is a complex habitat for man, animals, insects and micro-organisms and their activities may impact positively or negatively on the forest. This complex relationship is explained in the section Forest and Organisms Interactions, consisting of contributions made by six researchers. Development of tree plantations has been man's response to forest degradation and deforestation caused by human, animals and natural disasters. Plantations of beech, spruce, Eucalyptus and other species are described in the last section, Amelioration of Dwindling Forest Resources Through Plantation Development, a section consisting of five papers authored by 20 researchers. New Advances and Contributions to Forestry Research will appeal to forest scientists, researchers and allied professionals. It will be of interest to those who care about forest and who subscribe to the adage that the last tree dies with the last man on our planet. I recommend it to you; enjoy reading it, save the forest and save life!

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