



## Modelling habitat quality for arboreal marsupials in the South Coastal forests of New South Wales, Australia

Juli G. Pausas <sup>\*</sup>, L. Wayne Braithwaite, Mike P. Austin

CSIRO Division of Wildlife and Ecology, P.O. Box 84, Lyneham, Canberra ACT 2602, Australia

Accepted 22 May 1995

---

### Abstract

We present a statistical model to predict habitat quality for arboreal marsupials (possums and gliders) in the Eden district (New South Wales, Australia). The model is based on foliage and soil nutrients, the amount of decorticating bark, the susceptibility of trees to develop holes, topographic position and forest structure. The results suggest that the main factor predicting the occurrence of arboreal marsupials is the availability of food (e.g. quality of leaves, nutrients). When food is not a limiting factor, forest structure (e.g. number of large trees) determines the habitat quality. Implications for forest management are also discussed.

**Keywords:** Habitat suitability; Conservation; Forest management; Glider; Possum; *Eucalyptus* forest

---

### 1. Introduction

Harvesting eucalypt forests for both sawlogs and pulpwood is an ongoing practice in the Eden concession district, south-eastern New South Wales. Arboreal marsupials are vulnerable to disturbance by forest management techniques (Tyndale-Biscoe and Calaby, 1975). High-quality habitat for arboreal marsupials coincides with productive land most suitable for agriculture and forestry plantations (Braithwaite et al., 1988, 1993). Therefore, conflicts arise between conservation and management.

The objective of this paper is to develop a statistical model to predict the habitat quality for arboreal marsupials in the Eden region. We use the probabil-

ity of occurrence as an indicator of habitat quality. We believe that such a model will be a useful tool in the environmental decision-making process in the study area. Lindenmayer et al. (1990a, 1991b) presented several models of this kind to predict arboreal marsupials habitat in the central Highlands of Victoria, but their results cannot be directly extrapolated to different areas because they are based on a restricted environment (tall closed forest of *Eucalyptus regnans*, *Eucalyptus delegatensis* or *Eucalyptus nitens* in eastern Victoria).

Arboreal marsupials are a well-defined taxonomic as well as ecological group (guild). We use this “coarse” approach rather than the individual species approach because there is insufficient information for all individual species. This guild approach has been suggested elsewhere for modelling and management purposes (Noss, 1990; Chapin et al., 1992; Hansen et al., 1993).

---

<sup>\*</sup> Corresponding author.

Habitat quality for arboreal marsupials depends mainly on (1) the availability of food and (2) the availability of nest sites. Some arboreal marsupials are exclusively folivorous (koala and greater glider), but others may feed on gum, pollen, nectar and arthropods (Smith, 1982; Strahan, 1983). Braithwaite et al. (1983, 1984) found that the abundance of possums and gliders in the Eden area was related to forest communities with one or more species of peppermint eucalypts (*Eucalyptus radiata*, *Eucalyptus dives* and *Eucalyptus elata*). These species were shown to have high concentrations of foliage nutrients. These forests also grew mostly on high fertility soils derived from Devonian intrusive bedrock. Braithwaite's hypothesis of nutrient limitation as a controlling influence on arboreal marsupials has since been supported by additional studies (Norton, 1988; Kavanagh and Lambert, 1990; Jones et al., 1994).

Smith and Lindenmayer (1992) and Lindenmayer et al. (1990a, 1991b) showed that the abundance of *Acacia* species and the amount of decorticating bark of eucalypts are also correlated with habitat quality for some arboreal marsupials. The gum of *Acacia* is part of the diet of several marsupial species (e.g. Smith, 1982). The amount of decorticating bark has been used to estimate the availability of arthropods that live under the bark, which are also eaten by some marsupial species (Strahan, 1983; Kavanagh, 1987).

Most arboreal marsupials use natural cavities in trees to nest and are strongly dependent on the availability of these natural cavities. The relationship between natural cavities and arboreal marsupials has been shown by Smith and Lindenmayer (1988, 1992) and Lindenmayer et al. (1991c) in Victorian forests. Braithwaite et al. (1983) showed that the minimum diameter at which a tree forms a hollow suitable for an arboreal marsupial is about 60–80 cm. Inions et al. (1989) found that no trees of less than 40–50 cm diameter at breast height (DBH) contained hollows suitable for possums in Western Australia. Smith and Lindenmayer (1988, 1992) considered trees with DBH greater than 50 cm and with obvious hollows as potential nest trees. Mackowski (1984) found that trees (*Eucalyptus pilularis*) with DBH less than 1 m have very few holes (one or none), while the number of holes increases above this size. Lindenmayer et al. (1993a) showed a positive relationship between tree

diameter and the number of holes, fissures and hollow branches. Different eucalypt species have different probabilities of developing holes or different abundance of holes (Lindenmayer et al., 1991a, 1993a; Bennett et al., 1994). Lindenmayer et al. (1991c, 1993a) also provided models predicting the occupancy and the number of cavities of hollow-bearing trees for eastern Victorian forests. However, hollow-bearing trees are only a small proportion of the total trees in a stand, and therefore numbers are difficult to estimate and the application of these models is problematic. Implications for forest management of the availability of hollow-bearing trees are discussed in Lindenmayer et al. (1990b) and Smith and Lindenmayer (1992).

On the basis of these known resource requirements for arboreal marsupials and the available data, we developed a statistical model to predict the presence of arboreal marsupials (possums and gliders) in an area with a wide range of environmental conditions and high diversity of trees.

## 2. Methods

### 2.1. Study area

The study area corresponds to the Eden concession district, on the South Coast of New South Wales (Australia), approximately 405 000 ha. All forests are dominated by eucalypt species and are harvested mainly for woodpulp. Keith and Sanders (1990) provide a description of the vegetation of the area. The altitude ranges from near sea level to about 1100 m. Bedrock types are also varied and include conglomerates, sandstones, granites, granodiorite, tonalities and hornfels. Details and a location map of the study area are given in Braithwaite (1983) and Braithwaite et al. (1984).

### 2.2. Sampling

Data on animals and their habitat were collected from clear-cut forest coupes, each between 5 and 30 ha in size and dispersed over the study area. A 0.25 ha sample plot was established around each tree in which an animal was found during logging. Additional random plots within the coupes were estab-

lished to obtain information on the forest structure in the absence of arboreal marsupials. For the present work, only plots located in coupes where no animals were found were accepted as indicative of the absence of marsupials. Because the home range of some species is greater than the plot size, and to avoid problems of negative autocorrelation, plots without arboreal marsupials but located in coupes where there were animals were not accepted for analysis. The total number of plots used was 471.

In each plot, site characteristics (topographic position, bedrock type, slope, aspect, latitude, longitude, altitude) and diameter at saw cut of the trees (60–80 cm above ground level) were measured. A total of 533 leaf samples was obtained from 46 tree (eucalypts) species over the study area. For each tree species, between three and 33 samples were obtained, depending on the abundance of the tree in the study area. These samples were from mature fully expanded leaves taken at random from the crown of the tree. The foliage concentration of nitrogen, phosphorus, potassium and magnesium was determined according to Lambert (1976).

### 2.3. Numerical analysis

For each plot, basal area and number of trees in each diameter class and for each tree species were

computed. The eight diameter classes used were (in cm): < 10, 10–19.9, 20–29.9, 30–39.9, 40–59.9, 60–79.9, 80–100, > 100.

Because of the known variation in foliage nutrient concentration due to different factors (tree age, leaf position on the crown, climate, soil type, etc.), the foliage nutrient concentration was not used directly; instead, it was transformed to a factor. The values of foliage nutrient concentration were averaged for each tree species. Then, all tree species were ranked from 1 to 5 (from low to high concentration) to obtain a species foliage nutrient index. The ranking method based on four variables (four nutrients) was done by means of principal component analysis. The significance of this index is shown in Table 1. There were significant differences in nitrogen, phosphorus and potassium values for the different levels of this index, but not for magnesium.

For each tree species, a bark decorticating (shedding) index from 0 (e.g. stringybark eucalypts) to 2 (some gum eucalypts) was assigned to indicate the amount of shedding bark of each species. Similarly, a hole index from 1 to 3 (1, low; 2, intermediate; 3, high) was assigned to indicate the proneness to produce holes suitable for arboreal marsupials, based on field experience. These indices were obtained by averaging subjective estimates from three field biologists.

Table 1

Mean and standard deviations (SD) of the foliage nutrient concentration ( $\text{mg g}^{-1}$  dry weight) for the five levels of the species foliage nutrient index (ANOVA and multiple comparison are also shown)

Species foliage index		Nitrogen	Phosphorus	Potassium	Magnesium
1	Mean	8.85 d	0.430 e	3.379 d	2.204
	SD	0.88	0.057	0.447	0.454
2	Mean	11.21 c	0.525 d	4.367 c	1.740
	SD	1.72	0.087	0.652	0.426
3	Mean	12.32 c	0.689 c	5.843 b	1.786
	SD	2.35	0.109	1.259	0.444
4	Mean	14.50 b	0.839 b	6.961 a	1.499
	SD	1.16	0.090	1.164	0.431
5	Mean	17.53 a	1.038 a	6.858 a	1.714
	SD	1.62	0.142	0.912	0.073
ANOVA		***	***	***	NS

Significance of ANOVA: \*\*\*  $P < 0.001$ ; NS, not significant. In columns, means a with different letter are significantly different at  $P < 0.05$ .

For each plot, a site foliage nutrient index (FNI) was developed as follows:

$$FNI = \frac{\sum_i BA_i FNI_i}{BA} \quad \text{for } i = 1, \dots, n$$

where  $BA_i$  is the basal area of the  $i$ th species,  $FNI_i$  is the foliage nutrient index of the  $i$ th species,  $BA$  is the total basal area of the plot, and  $n$  is the total number of tree species in the plot. In the same way, a bark shedding index (bark index) and a hole index (hole index) for each site were computed using the corresponding species indices. For the hole index, only trees with diameter greater than 60 cm were considered, because smaller eucalypts rarely produce holes (Braithwaite et al., 1983; Mackowski, 1984). For the bark index, only trees with diameter greater than 20 cm were considered. Dead trees were not considered for computing the bark index and FNI.

A soil nutrient index was estimated on the basis of soil analyses from different bedrock types and used as a five factor level (see Braithwaite et al., 1993, and Austin et al., 1995, for details of the estimation of this index).

The final data set tested included the above four site indices (foliage nutrients, bark, hole and soil nutrients), slope and topographic position of the plot, and the stand structural parameters: basal area, tree density, number of trees and basal area of trees with diameter greater than 60 cm, number of trees and basal area of trees with diameter lower than 20 cm, and the proportion of these small trees in respect to the total plot density.

#### 2.4. Modelling procedure

The presence or absence of arboreal marsupials was related to site parameters using generalized linear modelling techniques (McCullagh and Nelder, 1989). Because the dependent variable was binary (presence/absence), a binomial error distribution was assumed and a logit link function was used (McCullagh and Nelder, 1989; Austin et al., 1990). A forward stepwise procedure was used to enter the site variables into the model, and only variables that accounted for a significant change in deviance with probability less than 0.05 were considered (see Austin et al., 1990, and Nicholls, 1989, for details of the procedure and tests used). In each step of the for-

ward selection, the possibility to remove any of the variables within the model was also tested, and they were removed if the loss in deviance was not significant. This combination of forward and backward selection is a flexible way to select a suitable statistical model.

Topographic position was at first a factor with six levels (ridge, upper slope, middle slope, lower slope, gully, and flat). Preliminary statistical analysis showed no significant differences in the probability of occurrence of marsupials between several categories. So, this variable was grouped to two levels: ridge or slopes, and flats or gullies. A similar effect was observed for the soil nutrient index. This index had four levels, and preliminary analysis showed that to group it into two levels (low or intermediate, and high) explained a similar amount of deviance with fewer degrees of freedom. Having grouped the soil nutrient factor in two levels, there was no significant difference in FNI between these two soil nutrient levels, mainly because of the high variance in the first level.

A residual analysis was undertaken for the model using three diagnostic measures (Pregibon, 1981): the adjusted residuals, the potential influence each cell may have to the fit, and the coefficient of sensitivity. The prediction of success was computed as described in Lindenmayer et al. (1991b) and assuming that a prediction of a presence was when the probability of occurrence was greater than 0.5.

Each variable of the final multivariable model obtained was displayed graphically assuming the mean value for the other variables (unless otherwise stated) and showing the 95% confidence intervals.

### 3. Results

From 276 plots on which marsupials were present, 52.5% were greater gliders (*Petauroides volans*). The other marsupial species found in the sampling were feathertail glider (*Acrobates pygmaeus*), sugar glider (*Petaurus breviceps*), yellow-bellied glider (*Petaurus australis*), squirrel glider (*Petaurus norfolcensis*), common brushtail possum (*Trichosurus vulpecula*), and common ringtail possum (*Pseudocheirus peregrinus*). These marsupial species were found in a wide range of forest commu-

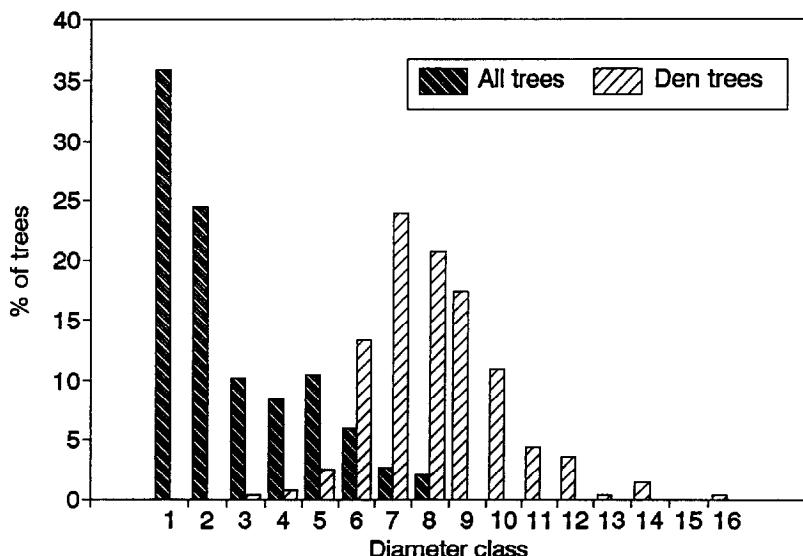


Fig. 1. Diameter class distribution of the overall trees sampled (total trees) and of the trees used by the arboreal marsupials (den trees). Labels of diameter classes: 1–4 refer to diameter classes of 10 cm (i.e. < 10 cm, 10 to 19.9, etc.); 5–16 refer to diameter classes of 20 cm (i.e. 40 to 59.9, 60 to 79.9, etc.). For "all trees", trees with diameter greater than 100 are included in the diameter class 8 (100 to 119.9 cm).

nities. They used 20 different species as den trees. The tree species most used were *Eucalyptus cypellocarpa*, *Eucalyptus fastigata* and *Eucalyptus viminalis*. Fig. 1 shows the size class distribution of all trees (darker pattern) and den trees (lighter pattern)

in all plots together; 83% of the den trees, compared with 4.8% of the total trees, were greater than 80 cm in diameter.

The most significant variable (i.e. explained most deviance) predicting the occurrence of arboreal mar-

Table 2  
Summary of the analysis of deviance for the occurrence of arboreal marsupials

Variable	Deviance	d.f.	Change in deviance
Null model	648.3	470	
<b>For FNI &lt; 2.5</b>			
null	446.5	329	
+ FNI	347.7	328	98.8 ***
+ topography	342.8	327	4.9 *
+ soil nutrients	337.6	326	5.2 *
+ hole index	328.1	325	9.5 **
+ bark index	322.0	324	6.1 *
<b>For FNI &gt; 2.5</b>			
null	103.8	140	
+ large trees	92.9	139	10.9 ***
+ DR + DR <sup>2</sup>	79.8	137	13.1 **
+ BA ratio	74.3	136	5.4 *

FNI, foliage nutrient index; DR, proportion of the number of small trees; BA ratio, proportion of the basal area of small trees. Responses curves are shown in Figs. 3–5. Significance of the change in deviance: \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ . d.f., degrees of freedom.

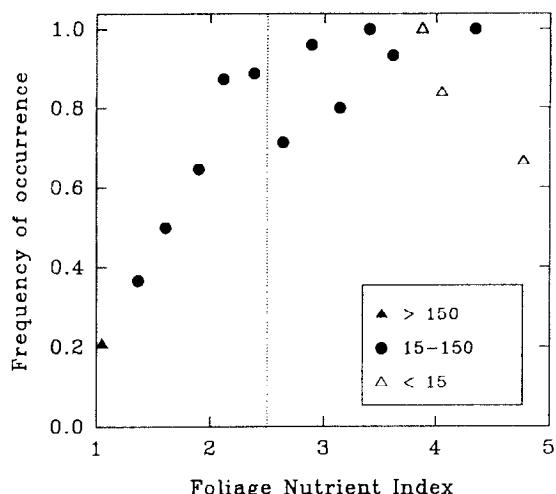


Fig. 2. Observed response of arboreal marsupials to site foliage nutrient index (FNI). Each point represents the frequency of occurrence for observations in a range of 0.25 units of FNI. The vertical line indicates the FNI value of 2.5, i.e. the level where the model was split (see text). Different symbols refer to the number of observations.

supials was site FNI. Along that nutrient gradient, there was a strong positive relationship with the probability of occurrence at low nutrient levels, until a certain level of FNI is reached ( $FNI \approx 2.5$ ; Fig. 2). This pattern suggested that the presence of arboreal marsupials along each segment of the gradient might be governed by different parameters. Therefore, the data were split in two parts ( $FNI < 2.5$  and  $FNI > 2.5$ ), and the statistical modelling was done for each part (Table 2). The split model was later compared with the model using the full data set, and a significant increase in explained deviance was obtained using the split model (Table 3).

At low values of FNI (i.e.  $FNI < 2.5$ ), the significant variables were FNI, topography, soil nutrient index, hole index and bark index. The occurrence of

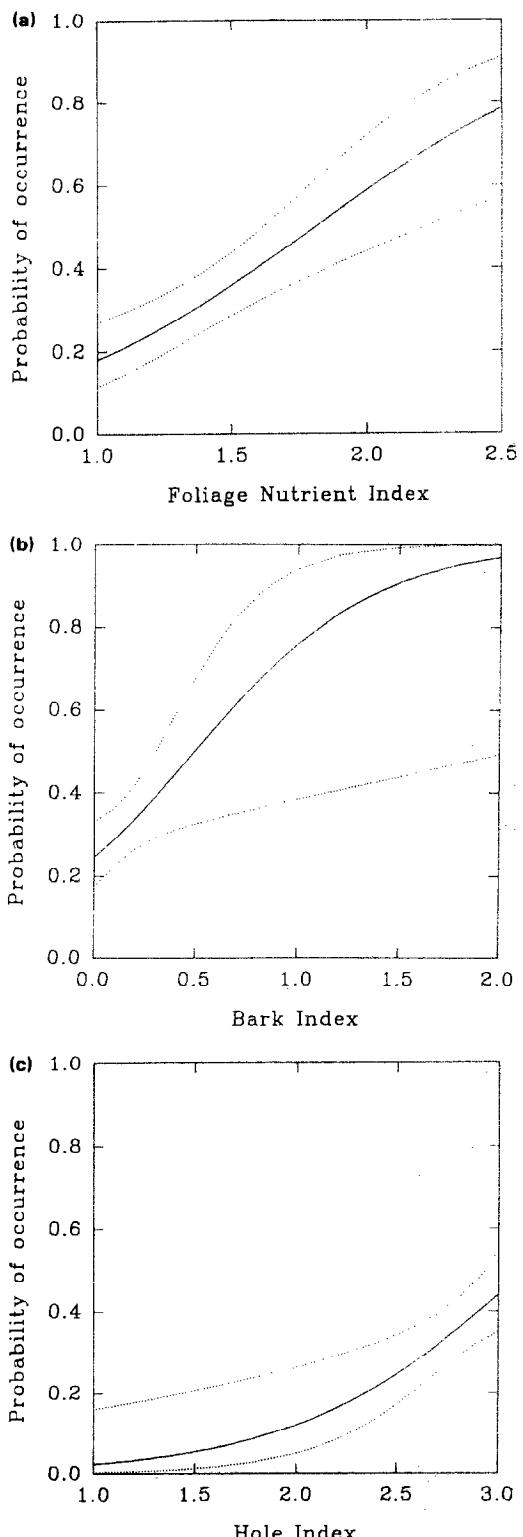


Fig. 3. Predicted probability of occurrence of arboreal marsupials in sites with FNI less than 2.5 (see Fig. 2), in relation to FNI (a), bark index (b) and hole index (c). These predictions correspond to forest on ridge or slopes with low or intermediate soil nutrient levels. Dotted lines refer to 95% confidence interval.

Table 3

Summary of the analysis of deviance comparing the model split by the FNI (Table 2 and Figs. 2–5) with the model using the full data set (not shown)

Model	Deviance	d.f.	Change in deviance
Null model	648.3	470	
Full model	440.9	465	207.3 ***
Split model	396.3	460	44.7 ***

The change in deviance is significant at  $P < 0.001$ . d.f., degrees of freedom.

arboreal marsupials showed a positive relationship with FNI, hole index and bark index (Fig. 3). The bark index showed large variation in predicting the occurrence of arboreal marsupials at intermediate and high levels (Fig. 3(b)). Forest on flat areas or gullies showed a higher probability of occurrence for arboreals than forest on slopes or ridges (Fig. 4). Forest located on high fertile soils also showed higher occurrence of arboreal marsupials. The influence of soil nutrients is more important on slopes and ridges than on flats and gullies.

At high values of FNI, the occurrence of marsupials is usually high, but some variation was found (Fig. 2). The main variables to explain that variation were the number of trees with diameter greater than 60 cm, and the proportion of the number and basal area of small trees (diameter  $< 20$  cm). None of

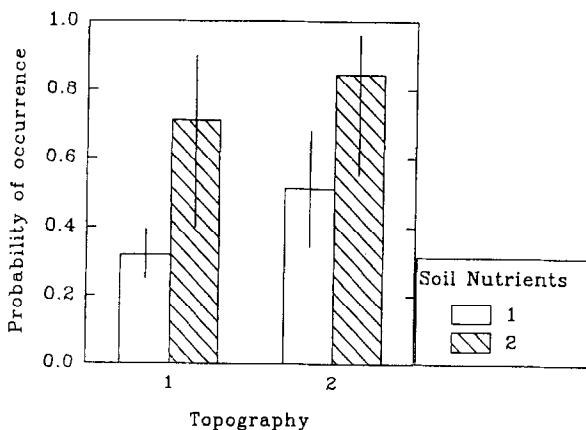


Fig. 4. Predicted probability of occurrence of arboreal marsupials in sites with FNI less than 2.5 (see Fig. 2) in different topographic positions (1, ridges or slopes; 2, flats or gullies) and different soil nutrient levels (1, low or intermediate; 2, high). All other significant variables in the model were set at mean values. Vertical lines refer to 95% confidence interval.

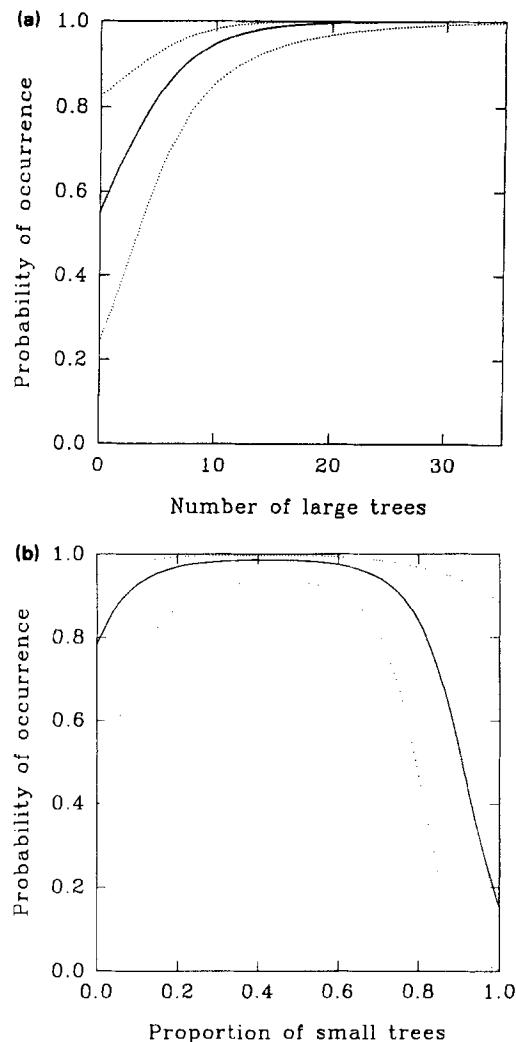


Fig. 5. Predicted probability of occurrence of arboreal marsupials in sites with FNI greater than 2.5 (see Fig. 2) in relation to (a) the number of large trees (trees with diameter greater than 60 cm), and (b) the proportion of small trees (trees with diameter less than 20 cm). Dotted lines refer to 95% confidence interval.

these variables were correlated with FNI. The number of large trees and the proportion of basal area of small trees showed a positive relationship with the presence of arboreal marsupials (Fig. 5(a)). The proportion of small trees with respect to the total trees showed a curve with a maximum at intermediate values (Fig. 5(b)). The occurrence of fauna declines when there are few small trees in the forest. It also declines, and more strongly, when there is a very high proportion of small trees with respect to the total, although the variation is relatively high at this

end of the gradient. At intermediate values, the occurrence remains high.

When the residuals of the overall model were inspected, a possible outlier was observed. One site had a very large adjusted residual, but the coefficient of sensitivity and the potential influence were not very large. In this site a common brushtail possum was observed, while the prediction was an absence of marsupials. This could be because we only have ten observations of this species in the data set, and probably the model cannot predict this species accurately as it typically inhabits open woodlands rather than forests (Strahan, 1983). The model was fitted again without this site, and the coefficients obtained were very similar to the previous model. So, the original model was accepted.

Although the model presented here is statistically significant, a measure of success is needed. The error rate of the split model (overall error for presence or absence) was 18.47%. The percentage of presences predicted correctly was 83.96 and the percentage of absences predicted correctly was 79.54. The model provides an adequate method to predict the habitat quality for arboreal marsupials in the study area.

#### 4. Discussion

These results are consistent with the hypothesis that leaf quality is a major determinant of the distribution of arboreal marsupials in eucalypt forests (Braithwaite et al., 1983, 1984; Cork, 1992). A similar trend was observed by Majer et al. (1992) studying foliage arthropods in eucalypt forests. Cork (1992) has shown that the concentration of nutrients in eucalypts leaves is inversely related to phenols (e.g. tannins), which are toxic for folivorous mammals. With our data, we cannot distinguish whether the arboreal marsupials respond directly to concentration of nutrients, or to the concentration of these secondary compounds. Our results also suggest that there are other factors than leaf quality which are important in predicting the occurrence of arboreal marsupials. The model shows that there is a threshold of foliage nutrients below which the most important factors are related to availability of food (i.e. nutrients, bark index). In this range of foliage nutrients, topography and hole index are also significant,

but the effect is less than for foliage nutrients, bark index and soil nutrients (Figs. 3 and 4). Above the threshold, the factors that control the habitat quality are exclusively related to forest structure (Fig. 5). A similar threshold effect has been found in a study of the greater glider in the north coastal forest of New South Wales (Cork et al., 1994).

The importance of topography for the occurrence of arboreal marsupials has been suggested previously (Lunney, 1987; Lindenmayer et al., 1990c, 1991b). We found more arboreal animals in forest on flats or gullies than on slopes or ridges as Lunney (1987) and Lindenmayer et al. (1990c) found. Lindenmayer et al. (1991b) found a negative relationship with slope. The effect of topography can be interpreted in different ways. Gullies are more protected from fire, and this allows more stable populations of arboreal fauna. In the study area, gullies offer greater floristic diversity (Austin et al., 1996) and, furthermore, greater diversity of foraging resources are available (Kavanagh, 1984). The energetic cost that an animal needs for foraging in flat forest or gullies is lower than in forest located on slopes. We cannot distinguish between these hypotheses.

Another parameter that we found to be important for predicting the occurrence of arboreal mammals was the bark decorticating index. Lindenmayer et al. (1990a, 1991b, 1993a) showed that the amount of decorticating bark was an important factor to predict the occurrence of arboreal marsupials, the occurrence and abundance of sugar glider, and the abundance of Leadbeater's possum, in *Eucalyptus regnans* forests. In all these cases, as well as in the present study, bark index is assumed to be a surrogate measure of the availability of arthropods that live underneath the bark.

The importance of the availability of potential nest trees (PNT, i.e. trees large enough to develop a hole suitable for nesting arboreal mammals) to predict marsupial distribution has been shown by Smith and Lindenmayer (1988, 1992). Bennett et al. (1994) and Lindenmayer et al. (1991a) also showed that different eucalypt species have different susceptibility to hole formation. Our results are consistent with these studies; i.e. the occurrence of arboreal marsupials increases with the number of PNT. Our measure of PNT includes the number of large trees (Fig. 3) and the hole index (based on large trees, and assum-

ing a different tendency to develop holes for different species; see Methods section).

Some authors (Lindenmayer et al., 1990c; Smith and Lindenmayer, 1992) have shown that understory density, particularly the density (or basal area) of *Acacia* species, is an important factor in predicting the occurrence of marsupial species. High understory density allows easier movement within the forest and easier access to nests for non-gliding species. The gum of *Acacia* species is also a food resource for some species (e.g. sugar glider). We did not have available data for the amount of *Acacia* in the studied plots, and so this was not tested. Some evidence of the importance of small trees is shown in Fig. 4. A low number of small trees with a high number of large trees predicts a decrease in habitat quality. However, for forest with a very high proportion of small trees, the habitat quality decreases drastically.

The percentage of cases correctly predicted is relatively high (80–84%) and allows us to predict the arboreal marsupial distribution with some accuracy. This supports the initial assumption that arboreal marsupials are a well-defined ecological group, although part of the unexplained variation found (Figs. 3–5) might be explained if smaller groups or individual species, rather than the overall arboreal marsupials guild, were considered. Availability of food is an important factor in determining the occurrence of arboreal marsupial species; a subdivision of these species into strictly folivorous and omnivorous species may improve the habitat quality modelling for the arboreal marsupials.

Another factor to take into account when interpreting the results is the sampling methodology. The analysis presented here is mainly related to the den sites rather than to the foraging sites, and we assume that denning and foraging tend to occur close together. This is true for some of the arboreal marsupials (e.g. greater glider) for which the most data were available, but it is not necessarily true for some others with large home range (e.g. yellow-bellied glider). This problem was partially avoided by rejecting sites with absence of arboreal marsupials but located in coups with presences (see Methods section). However, some of the unexplained variability of the models could still be due to this problem.

We used the probability of occurrence as an

indicator of habitat quality for the arboreal marsupials, and we did not consider the abundance of these animals. Lindenmayer et al. (1993b) provide some statistical models, for both the presence and the abundance, for some of the arboreal marsupials in eastern Victoria. They found only slight differences between sets of predictor variables in the two cases. The relation between presence, abundance and habitat quality in animal populations is poorly understood. Winker et al. (1995) have recently suggested that the abundance of animals can be related to the stability of populations, but not to the habitat quality.

#### 4.1. Implications for forest management

Integrated harvesting (sawlog production in association with woodchipping) is the main method used for timber harvesting in the Eden area. This potentially produces a significant reduction of habitat quality for arboreal marsupials. The majority of the trees in the logging areas will not reach a size useful for arboreal marsupials before the area is re-logged (Fig. 1). To ameliorate this impact, harvesting practices in the Eden area include the retention of some large trees (known as "seed trees" and "habitat trees") and areas of unlogged forest in gullies ("wildlife corridors"). Our results show that the retention of such large trees is an important factor for arboreal marsupials (e.g. nest sites; Figs. 1 and 5(a)) and should be encouraged (Smith, 1985; Recher et al., 1987), but that the availability of food is a more important factor. The "habitat trees" to be retained should preferentially be tree species with high foliage nutrients, with shedding bark and with holes available for arboreal marsupials (e.g. *Eucalyptus elata*, *Eucalyptus viminalis*, *Eucalyptus dalmatica*, *Eucalyptus fastigata*, *Eucalyptus dives*, *Eucalyptus fraxinoides*, *Eucalyptus badjensis*). To preserve unlogged gullies or flat areas is also an important factor for protecting arboreal marsupials, but more important is the soil fertility (Fig. 4). The retention of unlogged areas in high fertility country is desirable for conservation purposes. Thus, forest management needs to preferentially protect high nutrient sites to maximise the value of forest wildlife management prescriptions, but, for this to be effective, it is also necessary to retain the other forest attributes the model suggests are important for fauna

(e.g. high number of large trees for den sites). A conflict arises because forests with high fertility are also those preferred for harvesting due to their higher productivity. Therefore, the high-quality areas for arboreal marsupials are the same as those identified as of maximum utility for timber production. In this context, Braithwaite et al. (1993) found a poor representation of forest with highly fertile soils in preserved forests (e.g. national parks, flora reserves) in contrast with its representation in timber production forests.

## 5. Conclusions

The main factor predicting the occurrence of arboreal marsupials is the availability of food. The availability of food is estimated by the quality of leaves (foliage nutrients and its correlates), the amount of decorticating bark (availability of arthropods) and the soil nutrients. When the food is not a limiting factor, forest structure determines habitat quality for arboreal marsupials. In this case, the number of large trees (potential nest trees) and the proportion of small trees to the total are the most important parameters.

## Acknowledgements

This work has been partially financed by the Ministerio de Educación y Ciencia (The Spanish Government) with a postdoctoral fellowship to the first author. We thank S.J. Cork and A.O. Nicholls for their valuable comments as the work progressed, and M. Clayton and E.M. Cawsey for their help in sampling and data base management (respectively). Useful comments on the manuscript were provided by S.J. Cork, D.B. Lindenmayer, A.O. Nicholls and two anonymous reviewers.

## References

- Austin, M.P., Nicholls, A.O. and Margules, C.R., 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.*, 60: 161–177.
- Austin, M.P., Pausas, J.G. and Nicholls, A.O., 1996. Patterns of species richness in relation to environment in south-eastern New South Wales. *Aust. J. Ecol.*, in press.
- Bennett, A.F., Lumsden, L.F. and Nicholls, A.O., 1994. Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Pac. Conserv. Biol.*, 1: 222–235.
- Braithwaite, L.W., 1983. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood pulp at Eden, New South Wales. I. The species distribution of animals. *Aust. Wildl. Res.*, 10: 219–229.
- Braithwaite, L.W., Dudzinski, M.L. and Turner, J., 1983. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood pulp at Eden, New South Wales. II. Relationships between the faunal density richness and diversity, and measured variables of habitat. *Aust. Wildl. Res.*, 10: 231–247.
- Braithwaite, L.W., Turner, J. and Kelly, J., 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood pulp at Eden, New South Wales. III. Relationships between faunal densities, eucalypt occurrence and foliage nutrients, and soil parent materials. *Aust. Wildl. Res.*, 11: 41–48.
- Braithwaite, L.W., Binns, D.L. and Nowlan, R.D., 1988. The distribution of arboreal marsupials in relation to eucalypt forest type in the Eden (N.S.W.) Woodchip Concession Area. *Aust. Wildl. Res.*, 15: 363–373.
- Braithwaite, L.W., Belbin, L., Ive, J. and Austin, M., 1993. Land use allocation and biological conservation in the Batesman's Bay forests of New South Wales. *Aust. For.*, 56: 4–21.
- Chapin, III, F.S., Schulze, E.-D. and Mooney, H.A., 1992. Biodiversity and ecosystem process. *Trends Ecol. Evol.*, 7: 107–108.
- Cork, S.J., 1992. Polyphenols and the distribution of arboreal folivorous marsupials in *Eucalyptus* forests of Australia. In: R.W. Hemingway and P.E. Laks (Editors), *Plant Polyphenols*. Plenum Press, New York, pp. 653–663.
- Cork, S.J., Catling, P.C., Braithwaite, L.W. and Spratt, D.M., 1994. Modelling distributions of arboreal and ground-living mammals in relation to climate, nutrients, plant chemical defences and vegetation structure in the eucalypt forests of southeastern Australia. *Proceedings International Forest Biodiversity Conference*, 4–9 December 1994, Canberra, Australia, p. 51.
- Hansen, A.J., Garman, S.L., Marks, B. and Urban, D.L., 1993. An approach for managing vertebrates diversity across multiple-use landscapes. *Ecol. Appl.*, 3: 481–496.
- Inions, G.B., Tanton, M.T. and Davey, S.M., 1989. Effect of fire on the availability of hollows in trees used by the Common Brushtail Possum, *Trichosurus vulpecula* Kerr, 1772, and the Ringtail Possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Aust. Wildl. Res.*, 16: 449–458.
- Jones, B.A., How, R.A. and Kitchener, D.J., 1994. A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildl. Res.*, 21: 175–187.
- Kavanagh, R.P., 1984. Seasonal changes in habitat use by gliders and possums in southeastern New South Wales. In: A.P. Smith

- and I.D. Hume (Editors), *Possoms and Gliders*. Australian Mammal Society, Sydney.
- Kavanagh, R.P., 1987. Forest phenology and its effect on foraging behaviour and selection of habitat by the Yellow-Bellied Glider, *Petaurus australis* Shaw. Aust. Wildl. Res., 14: 371–384.
- Kavanagh, R.P. and Lambert, M.J., 1990. Food selection by the greater glider, *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? Aust. Wildl. Res., 17: 285–299.
- Keith, D.A. and Sanders, J.M., 1990. Vegetation of the Eden region, south-eastern Australia: species composition, diversity and structure. J. Veg. Sci., 1: 203–232.
- Lambert, M.J., 1976. Methods of chemical analysis. Forestry Commission N.S.W. Technical Paper No. 25.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. and Nix, H.A., 1990a. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia: I. Factors influencing the occupancy of trees with hollows. Biol. Conserv., 54: 111–131.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T. and Smith, A.P., 1990b. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia: II. The loss of trees with hollows and its implications for the conservation of Leadbeater's possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). Biol. Conserv., 54: 133–145.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. and Nix, H.A., 1990c. Habitat requirements of the Mountain Brushtail Possum and the Greater Glider in the montane ash-type eucalypt forests of the Central Highlands of Victoria. Aust. Wildl. Res., 17: 467–478.
- Lindenmayer, D.B., Cunningham, R.B., Nix, H.A., Tanton, M.T. and Smith, A.P., 1991a. Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. Aust. J. Ecol., 16: 91–98.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Nix, H.A. and Smith, A.P., 1991b. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia: III. The habitat requirements of Leadbeater's possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. Biol. Conserv., 56: 295–315.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. and Nix, H.A., 1991c. Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. For. Ecol. Manage., 40: 289–308.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Tanton, M.T. and Nix, H.A., 1993a. The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. For. Ecol. Manage., 60: 77–104.
- Lindenmayer, D.B., Cunningham, R.B. and Donnelly, C.F., 1993b. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia: IV. The presence and abundance of arboreal marsupials in retained linear habitats (wildlife corridors) within logged forest. Biol. Conserv., 66: 207–221.
- Lunney, D., 1987. Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, NSW. Aust. Wildl. Res., 14: 263–274.
- Mackowski, C.M., 1984. The ontogeny of hollows in blackbutt (*Eucalyptus pilularis*) and its relevance to the management of forests for possums, gliders and timber. In: A.P. Smith and I.D. Hume (Editors), *Possoms and Gliders*. Australian Mammal Society, Sydney, pp. 553–567.
- Majer, J.D., Recher, H.F. and Ganeshanandam, S., 1992. Variation in foliar nutrients in *Eucalyptus* trees in eastern and Western Australia. Aust. J. Ecol., 17: 383–393.
- McCullagh, P. and Nelder, J.A., 1989. *Generalized Linear Models*, 2nd edn. Chapman&Hall, London, 511 pp.
- Nicholls, A.O., 1989. How to make biological surveys go further with generalized linear models. Biol. Conserv., 50: 51–75.
- Norton, T.W., 1988. Ecology of the greater glider in different eucalypt forests in south-eastern New South Wales. Ph.D. Thesis, Department of Forestry, Australian National University, Canberra, 238 pp.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol., 4: 355–364.
- Pregibon, D., 1981. Logistic regression diagnostics. Ann. Statist., 9: 705–724.
- Recher, H.F., Shields, J., Kavanagh, R. and Webb, G., 1987. Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. In: D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins (Editors), *Nature Conservation: The Role of Remnants of Native Vegetation*. Surrey Beatty, Sydney, pp. 177–194.
- Smith, A.P., 1982. Diet and feeding strategies of the marsupial sugar glider in temperate Australia. J. Anim. Ecol., 51: 149–166.
- Smith, P., 1985. Effects of intensive logging on birds in eucalypt forest near Bega, New South Wales. Emu, 85: 200–210.
- Smith, A.P. and Lindenmayer, D., 1988. Tree hollow requirements of Leadbeater's Possum and other possums and gliders in timber production ash forests of the Victorian Central Highlands. Aust. Wildl. Res., 15: 347–362.
- Smith, A.P. and Lindenmayer, D.B., 1992. Forest succession and habitat management for Leadbeater's possum in the State of Victoria, Australia. For. Ecol. Manage., 49: 311–332.
- Strahan, R. (Editor), 1983. *Complete Book of Australian Mammals*. Angus and Robertson, North Ryde, Australia, 530 pp.
- Tyndale-Biscoe, C.H. and Calaby, J.H., 1975. Eucalypt forest as refuge for wildlife. Aust. For., 38: 117–133.
- Winker, K., Rappole, J.H. and Ramos, M.A., 1995. The use of movement data as an assay of habitat quality. Oecologia, 101: 211–216.