Habitat selection by the common wombat (*Vombatus ursinus*) in disturbed environments: Implications for the conservation of a ‘common’ species

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**ABSTRACT**

The construction of habitat models is a repeatable technique for describing and mapping species distributions, the utility of which lies in enabling management to predict where a species is likely to occur within a landscape. Typically, habitat models have been used to establish habitat requirements for threatened species; however, they have equal applicability for modelling local populations of common species. Often, few data exist on local populations of common species, and issues of abundance and habitat selection at varying scales are rarely addressed. We provide a habitat suitability model for the common wombat (*Vombatus ursinus*) in southern New South Wales. This species is currently perceived as abundant throughout its extensive range across temperate regions of eastern Australia, yet little factual survey data exist and populations appear under threat. We use wombat burrows to reflect habitat selection and as our basis for ecological modelling. We found that environmental variables representing proximity to cover, measures of vegetation and proximity to watercourses are important predictors of burrow presence. Extrapolation of habitat models identified an abundance of habitat suitable for burrows. However, burrows in many suitable areas were abandoned. Our estimate of the population size was similar to the total annual mortality associated with road-kill. Theoretically, given the availability of suitable habitat, common wombat populations in the region should be thriving. It seems likely that this area once supported a much higher number of wombats; however, limiting factors such as road mortality and disease have reduced the populations. The persistence of wombats in the study region must be supported by migration from other populations. Our findings challenge the perception that wombats are currently common and not in need of monitoring, suggesting that perceptions of abundance are often clouded by socio-political motives rather than informed by biological and ecological factors.

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1. Introduction

Human mediated disturbance represents the most profound change to landscapes around the world, yet the ecological consequences for many species are not well understood. As human disturbance continues to degrade and fragment eco-systems, conservation biology must increasingly aim to identify and preserve suitable habitat needed to sustain species (Foley et al., 2005; Wilson et al., 2005). Habitat models are often utilised to achieve this, and can provide managers with the ability to predict where a species is likely to occur within a landscape (Warren et al., 2005; Dayton and Fitzgerald, 2006;...
Rotenberry et al., 2006). Typically, habitat models have been used to establish habitat requirements for rare or threatened species (Reading et al., 1996; Ben Wu and Smeins, 2000; Gibson et al., 2004; Santos et al., 2006; Seoane et al., 2006). Threatened species warrant this attention due to the more immediate risk of loss of diversity (Soule et al., 2005); however it is also important to preserve local biodiversity, including local populations of common species, that may become threatened in the near future.

Species are generally perceived as common if they have extensive ranges and are abundant, although it is often hard to establish accurate assessments of abundance. Often, few data exist on local populations of common species, and issues of abundance at varying scales are rarely addressed. In the absence of monitoring, managers are only able to be reactive to decline, rather than proactively preventing decline. Recent evidence suggests that even common species can become susceptible to localised population extinction. Ramp and Ben-Ami (2006) found that the long term viability of a population of the common swamp wallaby (Wallabia bicolor) was in steady decline from the threat of roads, competition by rusa deer (Cervus timorensis) and predation by red foxes (Vulpes vulpes). There have been documented regional declines of once prevalent common herbs (Trillium camschatcense) and local declines of widespread vertebrate species like the ubiquitous northern dusky salamander (Desmognathus fuscus fuscus) (Bank et al., 2006), as well as more historic examples like the near extinction of the American Bison (Bison bison) and the extinction of the passenger pigeon (Ectopistes migratorius), both of which occurred virtually simultaneously (Farrow, 1995).

In Australia, an example of a common species where few data exist is the common wombat (Vombatus ursinus). Included in the suborder Vombatiformes, wombat ancestors were once a diverse and dominant group with diversity peaking during the late Pliocene and Pleistocene, with many forms larger than the current extant species (Woolnough and Steele, 2006). However, five of the seven known families within this suborder are now extinct; with only the koala (Phascolarctos cinereus) and three species of wombat surviving. Of the three species, the southern hairy-nosed wombat (Lasiorhinus latifrons) is restricted to fairly small fragmented areas, and listed as vulnerable, the northern hairy-nosed wombat (L. krefftii) is listed as critically endangered, with only the common wombat typically perceived as common and well adapted to its range. Yet, despite the perception of commonality driven by its extensive range, there is evidence that its distribution has been reduced since European arrival, particularly in western Victoria, southern Queensland, and northern South Australia (Triggs, 1988; McIlroy, 1995; Buchan and Goldney, 1998). This recognised range reduction, however, is quite broadly described, with no real data detailing where local populations exist, over what scale the decline has been observed, or what the factors of decline are.

The contraction of common wombat populations from former ranges does suggest that a number of factors may be affecting common wombat abundance at a local population level. Most evident are the numerous wombat fatalities from collisions with vehicles on highways (Ramp et al., 2005). Sarcoptic mange, caused by a parasitic mite of the skin (Sarcoptes scabiei), has been identified as the most significant infectious disease affecting the common wombat (Hartley and English, 2005). It is thought to limit the activity of mature wombat grooms, thus affecting wombat reproduction (Skerratt et al., 1999), and is in most cases fatal. Feral animals such as wild dogs and foxes have also been shown to prey on common wombats (Newsome et al., 1983; Corbett, 1995; Banks, 1997). Licenses are also issued by state agencies permitting wombat destruction on the grounds of them being nuisance animals, with claimants stating undue property damage.

In the present study we used wombat burrows to reflect habitat selection and as our basis for ecological modelling. Using burrow location data, three sets of habitat models were constructed: (a) a habitat suitability model based on the presence–absence of burrows in the landscape; (b) a habitat suitability model based on the Getis-Ord G* spatial hotspot clustering statistic; (c) a model of the likelihood of a burrow being occupied or abandoned. The central aims of this study were (1) to assess factors that were important for predicting burrow presence, clustering and occupation and (2) to evaluate the areas within the study area of prime habitat for the species. The common wombat was used as a model species because they have been positively associated with varying habitats (Mallett and Cooke, 1986; Rishworth et al., 1995; Skerratt et al., 2004), suggesting great adaptability and widespread abundance. However, given the advent of several threatening processes that reduce local population numbers, we do not have a clear idea of how large a local population needs to be sustainable, or how individuals are connected throughout the broader landscape. Importantly, we are lacking a basis as to what landscape features and at what scales of influence may be used to predict the presence of wombats, so that accurate monitoring of populations can begin. To address this, our habitat modelling approach accounts for multiple scales, by using both landscape-level and site-level variables as predictors in our modelling. Habitat modelling will assist with understanding the ecology and requirements of local populations, and indeed the population throughout its range.

In an effort to evaluate our habitat models for this species, the following hypotheses were tested: (1) high habitat suitability is not necessarily indicative of healthy local population numbers; (2) perceived benefits from living near cleared land may result in reduced annual survival and population sustainability.

2. Methods

2.1. Study area

The study was conducted on the Blowering Reservoir foreshores between the townships of Tumut (35°19’S, 148°14’E) and Talbingo (35°34’S, 148°18’E) in Kosciuszko National Park, southern New South Wales, Australia (Fig. 1). The area is bound in the west by the Blowering Reservoir while the east is characterised by grassy south-west facing slopes of remnant pasture and native forest. The Snowy Mountains Highway runs North–South through the site, fragmenting the foreshore area from the slopes. The study area is dominated by cleared land, moist and dry forest, blackberry thickets
(Rubus fruticosus), patches of bracken fern (Pteridium esculentum) and briar bushes (Rosa rubiginosa). Hill slopes are dominated by shrubs (Leptospermum spp.) and patches of trees (Eucalyptus spp.). Introduced grass species are widespread; mostly perennial ryegrass (Lolium perenne) and paspalum (Paspalum dilatatum). Native grasses such as kangaroo grass (Themeda australis) and tussock grass (Poa spp.) are also present (Jaremovic and Croft, 1991). The area has a temperate climate, with cool wet winters and warm summers, and an average yearly rainfall of 900 mm (Australian Bureau of Meteorology records for Tumut Plains). Common wombats share the open pasture grazing sites with native and introduced herbivores; namely kangaroos (Macropus giganteus), swamp wallabies (Wallabia bicolor), emus (Dromaius novaehollandiae) and rabbits (Oryctolagus cuniculus). The site is representative of many sites across the range of the common wombat, where there is a mix of native forest, human land-use areas, and a multitude of threats. Recognised threats in the region include disease, road mortality, pest shooting, and predation.

### 2.2. Burrow location as presence data

To address the problem of reliability of presence–absence data, we used wombat burrows as a reflection of common wombat habitat selection, rather than species sighting records. An equal number of randomly generated points were used as absences. Burrow location has been shown to represent site selection in other species such as the muskrat (Ondatra zibethicus) (Nadeau et al., 1995). Similarly, variations of wombat density have been shown to correlate with the placement of the burrow within a landscape (Downes et al., 1997), presumably because wombats strongly associate burrow construction in relation to physiographic features of the landscape. Rishworth et al. (1995) found a linear relationship existed between the number of burrows present in an area and the mean number of wombats. Wintle et al. (2005a) suggest that presence–absence models are effective, but caution that they often succumb to false negative observation errors in species surveys. The problematic nature of using random absence locations in conjunction with species’ sightings has been documented in studies by Ferrier et al. (2002), Elith et al. (2006), and Olivier and Wotherspoon (2006). Because the entire study site was surveyed to the best of our capacity, we were able to reasonably confident of non-burrow locations when assigning random absences across the area. By choosing to model a fixed location, we were able to ascertain where wombats were actively choosing to construct burrows, and where they were not.

### 2.3. Data collection

Burrow surveys were conducted daily in June and July 2005 by systematically surveying the entire study area on foot, following Rishworth et al. (1995). East–west aligned transects were traversed by four observers spaced lengthwise 15–30 m apart (depending on visibility due to terrain). Each transect ran from the border of the reservoir in an easterly direction for an average distance of 1600 m, such that the end points were all latitudinally aligned. Approximately 120 transects per observer were traversed in total, to cover an area of 30 km². Detectability of wombat burrows was shown to be accurate (1 burrow missed for every 30 detected) in subsequent burrow surveys employing a double sampling approach (Pollock et al., 2002) to determine detection probability (E. Roger, unpublished data). Burrow locations were recorded using a global positioning system (GPS) and scored as either abandoned or occupied based on the criteria for major burrows described by McIlroy (1973). Maximum height and width of burrow entrances were measured. Entrance areas greater than 2100 cm² were scored as occupied, while visible signs of occupation such as tracks and presence of scat were also used. When in doubt, small sticks were placed across burrow entrances and checked the following morning for signs of displacement.

### 2.4. Burrow location model development

#### 2.4.1. Dependent variables

Burrow locations (both occupied and abandoned) were compiled using ArcGIS (Environmental Systems Research Insti...
Potential predictor variables at each burrow location were significant at approximately the 95% level (Laffan, 2006). The sample, with values greater in magnitude than ±2 being the mean represents the strength of the spatial clustering in area. The extent to which a cluster values represent a cluster of data values below the mean, while negative cluster values represent a cluster of data values below the mean. In our case, a positive $G_i$ value represents a cluster of burrows, while a negative $G_i$ value represents a non-burrow area. The extent to which a $G_i$ value is greater or less than the mean represents the strength of the spatial clustering in the sample, with values greater in magnitude than ±2 being significant at approximately the 95% level (Laffan, 2006). The $G_i$ statistic was calculated after Laffan (2006), using circular radii from 125 m to 12,500 m at 125 m increments, aggregated into a single layer using the radius with the greatest magnitude.

2.4.2. Predictor variables

Potential predictor variables at each burrow location were based on published findings (McIlroy, 1973; Catling and Burt, 1995; Buchan and Goldney, 1998; Walker et al., 2007) but inclusion depended on availability as GIS data layers. Blackberry was chosen as a predictor variable, as a result of our field observations and those of Triggs (1988). Site-level predictor variables used included: distance to drainage lines (the Blowing Reservoir was not included in the analysis), forest cover and distance to blackberry bush, while landscape-level predictors were: slope, normalised difference vegetation index and hillshade. All environmental variables were stored as raster layers within ArcGIS with a resolution of 25 m.

A raster layer of slope (degrees) was derived from a 25 m resolution Digital Elevation Model (DEM). A hillshade raster, generated within ArcGIS, was used to provide a proxy for relative radiation load. It provides an alternative to aspect, as circular variables like aspect do not behave well in correlative studies (Beers et al., 1996). Raster layers of distance from burrow to the nearest watercourse (m) and the nearest blackberry bush (m) were generated using the Euclidian distance function in ArcGIS Spatial Analyst.

Vegetation community data (Ramp et al., 2005) were derived from 30 m LANDSAT data and used to calculate the proportion of forest cover surrounding each burrow. A circular sampling area based on the average home range of common wombat (Skerratt et al., 2004) was generated assuming the radius of a circle was equal to the diameter (320 m) of an average reported home range for wombats. The area covered by all forest communities in the study area (moist forest, disturbed forest, severely disturbed forest, moist forest tending to dry and dry forest) was aggregated into a proportion of area covered by forest (following Ramp et al., 2005). A normalised difference vegetation index (NDVI) image was calculated using an ASTER (advanced spaceborne thermal emission and reflection radiometer) image (15 m resolution, acquired 26 December 2000) to provide an index of vegetation greenness within the study area. NDVI is calculated as (NIR – VIS)/(NIR + VIS), where NIR is the near infrared light reflected by the vegetation and VIS the visible light reflected by the vegetation (Pettorelli et al., 2006). Negative NDVI values correspond to an absence of vegetation, while higher positive values are associated with greater density and greenness of the plant canopy (Justice et al., 1985). The NDVI values were then converted into a habitat complexity index (NDVI-SD) by taking the standard deviation of values within a 200 m radius. This used the focal statistics within ArcGIS, in the process resampling the ASTER 15 m cell sizes to conform to the 25 m used for the remainder of the data. In the NDVI-SD index, one will obtain higher values for mixed forest and grassland, and lower values for pure forest and grassland.

2.4.3. Burrow location

Burrow location was modelled using binary logistic regression using both occupied and abandoned burrows as presences and randomly generated locations as absences, while burrow hotspots were modelled using Gaussian logistic regression using $G_i$ values and associated predictor variables at each location. Generalised additive models (GAMs) were constructed for each possible combination of predictors in R (R Development Core Team, 2005). Model selection was conducted using bootstrapping and the .632 estimator rule which has been shown to be appropriate when the underlying parameter distributions are unknown (Hastie et al., 2001). Bootstrapping involves resampling the modelling data while the .632 rule pulls the leave-one-out bootstrap estimate down towards the training error rate and therefore reduces upward bias (Rajvong, 2005). Bootstrapping has been shown to outperform cross-validation, particularly using the .632 rule (Efron, 1983; Efron and Tibshirani, 1997), and provides a predictive performance estimate of a model without the expense of collecting a completely new model-testing set (Wintle et al., 2005a). All predictor variables were checked for collinearity. In order to evaluate model performance, two loss functions were employed: misclassification error rate and deviance (only the deviance loss function was used to evaluate model performance for the burrow hotspot model). Loss functions assess the discrimination performance of habitat models derived using regression. Use of the misclassification error rate requires a threshold value to classify the predicted probability as presence or absence. Rather than choosing an arbitrary threshold, a receiver operating characteristic (ROC) curve was used to find the threshold that best discriminates between the sensitivity (probability that a burrow is correctly predicted) and 1 minus specificity (a false positive prediction) (Ferrier et al., 2002).

Following Ramp et al. (2005), final models were obtained by comparing all model subsets for the six predictors and employing the “one standard error rule” to select the best model set. The one standard error rule is often used to find a more parsimonious model than the one with the smallest error rate (Hastie et al., 2001). For the deviance loss function, the deviance per observation was calculated rather than devi-
ance so that it was comparable across different methods. Final model selection was based on comparing the best models (within both loss function groups) that contained the fewest numbers of predictor variables without compromising the predictive capability of the model.

Hierarchical Partitioning was used to lend additional support to the model selection process (Mac Nally, 2000; Brambilla et al., 2006). A goodness of fit measure for the entire hierarchy of models using all combinations of predictor variables was calculated using maximum likelihood. The contribution of each predictor to variability in the full model was identified and compared to results from the bootstrapping process.

The relationship between each predictor and the dependent variable was assessed to choose the appropriate degrees of freedom in the model based on ecological validity. Plausibility of response shapes was used to discern the relationship between variables and relationships were either retained as linear or splined with 2, 3, or 4 degrees of freedom.

Prediction values (one for every 100 × 100 m grid cell in the study area) were generated in R. The prediction values with the matching GIS coordinates were then imported into ArcGIS to create a habitat map.

2.5. Burrow occupation

Burrow occupation was modelled using occupied burrows as presences and abandoned burrows as absences. The predictor variables used in the burrow location models were used as well as the site-specific variable, distance to road (m) generated using the Euclidian distance function in ArcGIS Spatial Analyst. Distance to road was chosen as a discriminating variable important for predicting occupied burrows, rather than habitat suitability. Model selection was conducted as described for burrow location.

3. Results

3.1. Burrow location

A total of 81 occupied and 297 abandoned burrows were identified in the burrow surveys. Strong variation of wombat burrow density was found. Burrows were not evenly distributed throughout the landscape, but were clearly clumped. Based on 95% confidence intervals, occupied burrows were located a mean distance of 409 m from the road (±55), while abandoned burrows were on average, slightly closer, at a distance of 373 m (±29) from the road.

The misclassification error rate and deviance loss functions identified 27 and 57 models respectively within one standard error of the best model (Table 1). Discrimination among predictors using the deviance loss function was relatively poor compared to misclassification error. NDVI-SD was selected in 90% of models in the best model set using misclassification error, while hillshade was the least frequent selected predictor at 52%. Although slope was selected in 66% of models using misclassification error, the inclusion of slope contributed very little to the explained variance (Table 2). Aside from slope, there was good agreement among the three methods of model selection on the final model of NDVI-SD, distance to blackberries, the proportion of forest cover and distance to the nearest watercourse.

The final model explained 28.7% of the deviance (Table 3). The probability of a burrow being located in a 25 m cell was negatively associated with distance from blackberries and watercourses (Fig. 2). The probability of burrow presence was greatest when percent forest cover was around 50%, with probabilities declining either side of this mark. For NDVI-SD, the probability of a burrow increased in a linear fashion until NDVI-SD was around 0.1 and then levelled and declined slightly. Hierarchical partitioning indicated that distance to blackberries and NDVI-SD provided the most explanation. Areas scored as most likely to have a burrow were centred in patches of remnant pasture in the foreshore area in close proximity to the highway, while areas least likely to contain a burrow were at the extreme boundaries of the study region in dense native forest.

A habitat map is provided (Fig. 3) for predicted probability of burrow presence throughout the study area.

3.2. G-star statistic

The \( G_i \) results indicate that there are distinct areas of strongly positive burrow clusters, as well as areas with strongly negative burrow absences. Approximately 15% of all cells occur in strong positive (presence) clusters (\( G_i > 2 \)), while approximately half of all cells occur in strong negative (absence) clusters (\( G_i < -2 \)) (Fig. 4). There are also many spatially distinct, weakly positive (\( 0 < G_i < 2 \)) and weakly negative clusters (\( 0 > G_i > -2 \)). Generally, burrow clusters occurred within close proximity to the eastern study boundary and the Snowy Mountains Highway, while large absence clusters occupied the westerly extremes of the study area.

The deviance loss function identified 15 models within one standard error of the best model (Table 1). NDVI-SD and disc-

<table>
<thead>
<tr>
<th>Table 1 – Model results for habitat suitability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
</tr>
<tr>
<td>Presence–absence</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Getis-Ord</td>
</tr>
</tbody>
</table>

Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion. Symbols for predictor variables occurring in model set are distance to blackberry (B), percent forest cover (F), slope (S), distance to river (RIV), normalised difference vegetation index (N), and hillshade (H).
distance to blackberry bush were selected in 100% of models in the best model set, while the remaining four variables occurred at equal frequencies of 53%. The inclusion of distance to watercourse contributed significantly to the variance explained (Table 2). Aside from distance to watercourse, there was good agreement among methods of model selection on the final model of NDVI-SD, distance to blackberries, the proportion of forest cover and distance to the nearest watercourse.

The final model explained 37% of the deviance (Table 3). The probability of a positive burrow cluster being located in a 25 m cell was negatively associated with distance from watercourses (Fig. 5). The probability of a burrow cluster decreased with increasing distance from blackberry until a value of approximately 12 m was met, and then increased sharply, suggesting a positive relationship after a fixed distance. The probability of a burrow cluster was greatest when percent forest cover was around 50%, with probabilities declining either side of this mark. For NDVI-SD, the probability of a burrow increased linearly until the value was around 0.1 and then levelled and declined slightly.

3.3. Burrow occupation

The misclassification error rate identified 51 models within 1 standard error of the best model (Table 4). Discrimination using the deviance loss function was ineffective. Proportion of forest cover was selected in 78% of models and distance to road in 76% of models, while distance to creek was the least frequently selected predictor at 51%. The final model chosen contained the proportion of forest cover, distance to road, distance to blackberry, and NDVI-SD, explaining 15% of the deviance (Table 3). The likelihood of a burrow being occupied was negatively associated with NDVI-SD, while the probability of an occupied burrow increased with increasing percent forest cover, with probabilities declining slightly at around 60%. The probability of an occupied burrow increased linearly with increasing distance from road, as did distance from blackberry (Fig. 6). Hierarchical partitioning indicated that distance from blackberry and distance to road were the most important explanatory variables (Table 2).

4. Discussion

4.1. Burrow distribution and location

The final model included both landscape-level and site-specific variables. Using presence–absence data, burrow probability was highest near blackberry bushes and watercourses (blackberry bushes occur throughout the study area, and are not confined solely to creek areas). This result is supported by previous studies which have observed the association of common wombats with blackberry bushes (Triggs, 1988) and Boxthorn shrubs (Lycium spp.) (Taylor, 1993) and associated burrow presence with riverbanks and gullies (McIlroy, 1973; Lunney and O’Connell, 1988; Buchan and Goldney, 1998).

Table 2 – Variable coefficients and Z-scores for the three models

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>Coefficient</th>
<th>Independent contribution</th>
<th>Chi-squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence-absence</td>
<td>Intercept</td>
<td>−0.6815</td>
<td>30.52</td>
<td>−4.67</td>
</tr>
<tr>
<td></td>
<td>Blackberry</td>
<td>−0.00001</td>
<td>21.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>River</td>
<td>−0.3413</td>
<td>45.26</td>
<td>70.848</td>
</tr>
<tr>
<td></td>
<td>NDVI</td>
<td>9.3662</td>
<td>12.84</td>
<td>38.724</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>7.4922</td>
<td>56.88</td>
<td>105.296</td>
</tr>
<tr>
<td></td>
<td>Getis-Ord</td>
<td></td>
<td></td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td>−1.4601</td>
<td>19.35</td>
<td>3.678</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>1.0383</td>
<td>0.2736</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>NDVI</td>
<td>−8.4698</td>
<td>19.28</td>
<td>0.097</td>
</tr>
<tr>
<td></td>
<td>Road</td>
<td>0.0012</td>
<td>24.74</td>
<td>0.001</td>
</tr>
<tr>
<td>Burrow occupation</td>
<td>Intercept</td>
<td>−0.2736</td>
<td>1.02</td>
<td>14.010</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>0.8614</td>
<td>26.93</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Table 3 – Deviance explained by the final model for all three model types using the complete data set with degrees of freedom in brackets along with the area under the curve (AUC)

<table>
<thead>
<tr>
<th>Model</th>
<th>Final model</th>
<th>Null</th>
<th>Residual</th>
<th>% Deviance explained</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence-absence</td>
<td>F, 2 + B + RIV + N, 2</td>
<td>1039.7 (d.f. = 749)</td>
<td>740.9 (d.f. = 742)</td>
<td>28.7</td>
<td>754.9</td>
</tr>
<tr>
<td>Burrow clustering</td>
<td>RIV, 1 + N, 2 + B, 2 + F, 2</td>
<td>945.2 (d.f. = 754)</td>
<td>595.2 (d.f. = 746)</td>
<td>37.0</td>
<td>3719.5</td>
</tr>
<tr>
<td>Burrow occupation</td>
<td>F, 2 + N, 1 + R, 1 + B, 1</td>
<td>391.3 (d.f. = 374)</td>
<td>364.5 (d.f. = 368)</td>
<td>14.6</td>
<td>376.6</td>
</tr>
</tbody>
</table>

Symbols for predictor variables occurring in model set are distance to blackberry bush (B), percent forest cover (F), distance to river (RIV), normalised difference vegetation index (N), and distance to road (R).
The positive relationship with NDVI-SD reflects a preference for good foraging habitat near cover as wombats are typically grazers, eating almost exclusively monocot species (Evans et al., 2006). They typically refrain from burrow construction in barren or rocky areas and in areas of dense leafy vegetation, preferring instead good quality grazing land. Forests selected by wombats in this study generally had an open understorey, with a preference for 50% cover. This is supported by McIlroy (1973), and Buchan and Goldney (1998) who considered forest cover important for protection from predators and extreme weather. Similarly, Catling et al. (2000), using generalised linear models to analyse the distribution and abundance of ground-dwelling mammals, such as the common wombat, found their models reflected the species’ preference for open forests with open grassy understorey and low shrub cover. Taylor (1993) did observe a number of burrows in pasture areas; however these were all associated with Boxthorn shrubs.

The results indicate that burrow locations are clearly clumped. The $G^*_i$ model included the same predictors as the presence-absence model, although the predictive power of the model was greater than the presence-absence model. Similarly, Buchan and Goldney (1998) found the most important variable for predicting burrow usage was the presence of other active burrows. Their study found that a burrow had a greater chance of being used if it had a large number of active burrows close by.

It is almost certain that the occurrence of wombat burrows is influenced by additional habitat variables not used in our study. The inclusion of soil type and ground litter would have potentially improved the predictive capacity of all models. Buchan and Goldney (1998) observed a strong relationship between burrow location and the distribution of red earth, as opposed to yellow podsolic soil. However, as soil type is strongly correlated with vegetation and with topography, we would have partially accounted for it with these variables. It is also evident from the extent of the species range that wombats are suited to a range of soil types (McIlroy, 1973, 1976; Mallett and Cooke, 1986; Triggs, 1988).

The Blowering foreshore area has been extensively degraded since European settlement: its pastoral history, creation of an artificial lake, construction of a major highway and use as a recreational area for boating and camping. The remnant forest of the study area has been severely degraded, while blackberry bush has invaded most of the cleared land along the foreshore. Although an invasive weed, blackberry bush provides wombats with protection, enabling them to construct burrows in prime grazing areas and to move about freely. The habitat models also indicate that common wombats prefer forest edges with a mix of forest cover and grazing land for burrow placement. The use of the forest edge in this manner often places wombats in direct competition with land-holders on adjacent farms. Buchan and Goldney (1998) reported that land-holders near their study site in the Central
Tablelands believed that wombats significantly damaged their property, and there was a general perception of the need to eradicate them. Similarly the New South Wales Department of Environment and Conservation has issued several licences permitting local land-holders to exterminate wombats on their property (M. Pettit, Department of Environment and Conservation Area Manager, Personal Communication).

4.2. Burrow occupation

The probability of the presence of an occupied burrow increased with increasing distance from road, presumably because wombats living in close proximity to the highway would be struck by vehicles more often. Burrows further from the highway may be preferred as they would incur fewer disturbances from people and traffic using the foreshore area for recreation. Burrow occupation was also positively associated with percent forest cover. This finding supports our burrow location model and can be interpreted as a reflection of the importance of proximal forest for weather and predator protection. Similarly, Buchan and Goldney (1998) found that burrows were more frequently used when they were situated within a 2 m radius of an overstorey tree; this variable was also significant in their study as a predictor of the frequency of burrow use. The probability of an occupied burrow was also correlated with NDVI-SD. This supports the findings that wombats seek out high quality forage, but actively select areas away from dense foliage. Given the lack of performance of the occupancy model, our results suggest that other factors, such as density dependence, may play more important roles in determining burrow occupation.

4.3. Limitations of burrows as presence data

Although we can be confident that all burrow locations were true presences, we cannot demonstrate undoubtedly that the randomly generated absence points were in fact true absences. However, by choosing to model a fixed location, we were not relying on locations of calls, or species sightings, which can be problematic in their failure to distinguish between where animals forage and the territory they pass through (Burgman et al., 2001; Wintle et al., 2005a; Ray and Burgman, 2006). In addition, species sightings and call loca-
tions are more subject to false absences that occur when an observer fails to record a resident species (Wintle et al., 2005b). False absences often occur via misidentification of species, adverse weather, and random chance (including temporary absence of wide-ranging species) (Wintle et al., 2005b); use of burrows greatly reduces the risk of these occurring. Burrows are important in driving wombat ecology (Taylor, 1993; Walker et al., 2007), such that burrow presence can be thought to not only reflect suitable burrowing conditions but also proximity to optimal foraging habitat. A caveat associated with using burrow locations is that they may not incorporate the true structure of randomness present in the data, as distinct areas of burrow clumping were observed. However, the Getis-Ord spatial clustering model accounts for incidence of spatial autocorrelation. As this and the presence-absence model exhibited similar results, pseudo-replication is not a major concern in this dataset.

4.4. Population sustainability

Extrapolation of the habitat models across the study region identified an abundance of habitat suitable for burrows but the number of occupied relative to abandoned burrows was low. Buchan and Goldney (1998) observed 80% occupancy rates, compared to the 27% observed in this study. Given the availability of suitable habitat the common wombat populations in the region should be thriving. McIlroy (1973) noted that very high densities of wombats (0.5 wombats ha$^{-1}$) could be found in forest that was very close to high quality grazing areas, like the Blowering foreshore. However, given that common wombats are thought to use as many as four burrows on a regular basis, the 81 occupied burrows likely reflected a total population size in the area ranging from 20 to 40 individuals (McIlroy, 1973; Rishworth et al., 1995; Skerratt et al., 2004). This population size was

Fig. 5 – Partial plots of the relationship between the Getis-Ord statistic of positive and negative burrow clusters and the predictor variables included in the final model. The X-axis represents the range of values for each environmental variable [(riv) distance to river, (n) normalised difference vegetation index, (b) distance to blackberry, and (f) percent forest cover]. Dashed lines represent 95% confidence intervals around the fitted response shape.

Table 4 – Model results for burrow occupation model

<table>
<thead>
<tr>
<th>Model</th>
<th>Loss function</th>
<th>Total #models</th>
<th>B</th>
<th>F</th>
<th>S</th>
<th>RIV</th>
<th>H</th>
<th>N</th>
<th>R</th>
<th>Median # variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability occupation</td>
<td>Misclassification error rate</td>
<td>51</td>
<td>0.61</td>
<td>0.78</td>
<td>0.55</td>
<td>0.51</td>
<td>0.66</td>
<td>0.61</td>
<td>0.76</td>
<td>4</td>
</tr>
<tr>
<td>Deviance</td>
<td>Deviance</td>
<td>128</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>4</td>
</tr>
</tbody>
</table>

Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion.

Symbols for predictor variables occurring in model set are distance to blackberry (B), percent forest cover (F), slope (S), distance to river (RIV), hillshade (H), distance to road (R), and normalised difference vegetation index (N).
extremely low, as estimates of mortality from threats would appear to match this population estimate on an annual basis. At least 4–22% of the population was infected with the fatal disease sarcoptic mange (based on averages of prevalence reported in Skerratt et al., 2004), while an average of 28 were killed on the highway each year (Ramp et al., 2005). As common wombats are slow breeders, there is little chance that this mortality was being replenished solely by local reproduction. It is more likely that the habitat of the study region was a sink for populations within the interior of the national park. Given that the majority of the study area has historically supported a large wombat population by providing an abundance of food and shelter, the apparent influx of wombats from surrounding areas (or source populations) suggests that the region is now acting as an ecological trap (Battin, 2004). Ecological traps occur when species are unable to identify the suitability of a habitat accurately, perceiving it as good when in fact it is bad (Kokko and Sutherland, 2001; Kristan, 2003). One would predict that an ecological trap would be associated with changes in the fine-scale distribution of subpopulations, such as increases in the number of isolated or semi-isolated subpopulations. We are currently gathering data to test this hypothesis. Certainly, the identification of source and sink populations becomes crucial for resource managers, who may wish to conserve source but not sink habitats (Runge et al., 2006).

4.5. Conservation implications

Common wombats play an important role in preserving ecosystem health, as native grazers and as ecosystem engineers (sensu Jones et al., 1997), increasing rates of soil turnover, and impacting soil nutrition (Kinlaw, 1999). The loss of such a species would have serious environmental implications, and their status as a common, wide ranging species cannot simply be assumed. Lunney and O’Connell (1988) found that, due to the excessive logging and burning of large forest areas, near Bega, New South Wales, that the common status of large forest herbivores, such as the common wombat and swamp wallaby, could not be guaranteed. Similarly, Buchan and Goldney (1998) noted that common wombats in the Central Tablelands were patchily distributed and appeared to be declining in the region. Little else has been reported on the status of the species, but what is recognised is that there is increasing isolation of populations of common wombats in remnant forest patches scattered over much of the species’ former range (Lunney and O’Connell, 1988; Triggs, 1988). This isolation, in conjunction with other drivers of change, like road-kill, is a major threat to the conservation of local populations (McIroy, 1995; Buchan and Goldney, 1998). Our findings suggest that although areas may have an abundance of suitable habitat for wombats, suitable habitat does not necessarily equate with high densities of animals. We suggest that wombats are drawn to cleared areas, and this movement is often to their detri-
ment. Management needs to evaluate common wombat populations in this context, and strive to preserve habitat linked to optimal suitability, while mitigating limiting factors.

Constructing habitat models is an important step in highlighting species relationships with environmental variables to assist in the development of conservation strategies. Localised habitat models are limited to quantifying suitability within the study area, and are often criticised for their limited ability to be extrapolated to larger scales and other populations. Our final models demonstrated how wombat occurrence is influenced by both local and landscape spatial scales, and it is likely that habitat selection processes inherent to the common wombat operate on both spatial scales. Therefore, mechanisms of burrow selection may be similar between locations, despite the broad-scale heterogeneity of wombat habitat, and may enable the application of predictive models throughout their range. Comparison of historic and current records of common wombat distribution challenges the opinion that common wombats are currently common and that perceptions of abundance are often clouded by socio-political factors rather than informed by biological and ecological factors. Given the risks facing wombat populations, we recommend the expansion of biomonitoring of wombat habitat, and may enable the application of predictive models throughout their range. Comparison of historic and current records of common wombat distribution challenges the opinion that common wombats are currently common and suggest that perceptions of abundance are often clouded by socio-political factors rather than informed by biological and ecological factors. Given the risks facing wombat populations, we recommend the expansion of biomonitoring of common wombats along a gradient of human disturbance and land-use areas to determine metapopulation function and localised population decline.

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