Modeling Species' Distributions to Improve Conservation in Semiurban Landscapes: Koala Case Study

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Abstract: *Models of species' distributions are commonly used to inform landscape and conservation planning. In urban and semiurban landscapes, the distributions of species are determined by a combination of natural habitat and anthropogenic impacts. Understanding the spatial influence of these two processes is crucial for making spatially explicit decisions about conservation actions. We present a logistic regression model for the distribution of koalas (Phascolarctos cinereus) in a semiurban landscape in eastern Australia that explicitly separates the effect of natural habitat quality and anthropogenic impacts on koala distributions. We achieved this by comparing the predicted distributions from the model with what the predicted distributions would have been if anthropogenic variables were at their mean values. Similar approaches have relied on making predictions assuming anthropogenic variables are zero, which will be unreliable if the training data set does not include anthropogenic variables close to zero. Our approach is novel because it can be applied to landscapes where anthropogenic variables are never close to zero. Our model showed that, averaged across the study area, natural habitat was the main determinant of koala presence. At a local scale, however, anthropogenic impacts could be more important, with consequent implications for conservation planning. We demonstrated that this modeling approach, combined with the visual presentation of predictions as a map, provides important information for making decisions on how different conservation actions should be spatially allocated. This method is particularly useful for areas where wildlife and human populations exist in close proximity.*

Key Words: anthropogenic impacts, conservation planning, logistic regression, mixed effects model, natural habitat quality, spatial distribution model

Modelaje de las Distribuciones de Especies para Mejorar la Conservación en Paisaje Semiurbanos: Caso de Estudio Koala

Resumen: *Los modelos de distribución de especies son usados comúnmente para proporcionar información para la planeación paisajística y de conservación. En paisajes urbanos y suburbanos, la distribución de las especies está determinada por una combinación de hábitat natural e impactos antropogénicos. El entendimiento de la influencia espacial de estos dos procesos es crucial para la toma decisiones espacialmente explícitas en acciones de conservación. Presentamos un modelo de regresión logística para distribuciones de koalas (Phascolarctos cinereus), en un paisaje semiurbano en el este de Australia, que explícitamente separa el efecto de la calidad del hábitat natural y de los impactos antropogénicos sobre la distribución de koalas. Logramos lo anterior mediante la comparación de la distribución pronosticada por los modelos con lo que*

hubiera sido la distribución pronosticada si las variables antropogénicas estuvieran en sus valores prome-dio. Métodos similares han confiado en predicciones asumiendo que las variables antropogénicas son igual a cero, que serán no confiables si los datos no incluyen variables antropogénicas con valores cercanos a cero. Nuestro método es novedoso porque se puede aplicar a paisajes en los que las variables antropogénicas nunca están cerca de cero. Nuestro modelo mostró, promediando toda el área de estudio, que el hábitat nat-ural fue el principal determinante de la presencia de koalas. Sin embargo, en la escala local, los impactos antropogénicos podrían ser más importantes, con las consecuentes implicaciones para la planificación de conservación. Demostramos que este método, combinado con ka presentación visual de las predicciones en un mapa, proporciona información importante para la toma de decisiones sobre la asignación espacial de diferentes acciones de conservación. Este método es particularmente útil para áreas en las que la vida silvestre y las poblaciones humanas viven en cercanía.

Palabras Clave: calidad del hábitat natural, impactos antropogénicos, modelo de distribución espacial, modelo de efectos mixtos, planificación de conservación, regresión logística

Introduction

Most species of conservation concern are threatened by loss and degradation of natural habitat (Ehrlich 1988). Other anthropogenic impacts, however, such as hunting, vehicle collision mortality, pollution, and direct human-wildlife conflict also increase the extinction risk of many species (Mattson et al. 1992; Fahrig et al. 1995; Kime 1995; Woodroffe & Ginsberg 1998; Fa et al. 2002). To make spatially explicit decisions about conservation actions, we need to be able to disassociate the effect of the spatial distribution of natural habitat on population declines from the effect of the spatial distribution of anthropogenic impacts on population declines. These matters have recently become of particular interest in urban and semiurban landscapes where wildlife and human populations exist in close proximity (Miller & Hobbs 2002; Lunney & Burgin 2004).

Statistical species' distribution models such as generalized linear models are commonly used as a tool in decision making for biodiversity conservation (Watson et al. 2001; Schadt et al. 2002; Westphal & Possingham 2003). It is common to include explanatory variables representing both natural habitat and anthropogenic factors in these models, but spatial variations in the impacts of these variables on predicted distributions are rarely quantified (e.g., Mladenoff et al. 1995; Barbosa et al. 2003; Apps et al. 2004). Spatially explicit decisions about whether conservation actions should target natural habitat or anthropogenic factors, however, require an understanding of the spatial impact of each factor on populations.

Two exceptions are studies by Naves et al. (2003) on brown bears (*Ursus arctos*) and Mace et al. (1999) on grizzly bears (*U. arctos horribilis*). Naves et al. (2003) approached the problem by fitting two separate models to brown bear distribution data (i.e., one with only natural habitat factors as explanatory variables and one with only anthropogenic factors as explanatory variables). Habitat quality predictions are visualized as a two-dimensional phase diagram, representing a natural habitat index on one axis and a human habitat index on another. This is then translated into a spatial map of the natural habitat quality and human habitat quality predictions. An implicit assumption of modeling the two processes completely independently, however, is that there is no correlation between the natural and anthropogenic variables.

Mace et al. (1999) avoided this assumption, although high correlations can still be problematic, by modeling grizzly bear resource selection as a combined function of natural habitat and anthropogenic variables. This model is used to make spatial predictions of realized resource selection. They then set the coefficients for anthropogenic variables to zero to obtain spatial predictions of potential resource selection, in the absence of human factors. The difference between potential and realized resource selection provides a measure of the reduction in habitat potential due to anthropogenic impacts. In urban or semiurban landscapes, however, this approach may produce spurious results because human variables may actually never be close to zero. Predictions from statistical models for explanatory variable values well outside the range of the training data set are likely to be unreliable (Zar 1996).

For many koala (*Phascolarctos cinereus*) populations in eastern Australia, there is a marked conflict between human land use and koala habitat requirements (Reed et al. 1990). Human land use has resulted in extensive koala habitat loss, fragmentation, and degradation (Reed & Lunney 1990; Knott et al. 1998; Seabrook et al. 2003). Where habitat does remain, its value is often compromised by other threats such as vehicle collisions, attacks by domestic dogs, fire, and disease (Smith & Smith 1990; Phillips 2000; Dique et al. 2003*b*; Lunney et al. 2004). Therefore a combination of natural habitat and anthropogenic factors are likely to be key determinants of the distribution of koalas, yet planning for koala conservation to date has relied on models of natural koala habitat alone (e.g., Lunney et al. 1998, 2000).

We adapted the approach of Mace et al. (1999) to quantify the effect of natural habitat and anthropogenic impacts on koala distributions in a semiurban landscape in

eastern Australia. The aim was to identify the spatial contribution of these two processes to koala presence, with a view to informing conservation planning in the region. We used koala presence and absence data to model koala distributions as a function of both natural habitat and anthropogenic variables. Instead of comparing predictions from the model with predictions assuming that anthropogenic coefficients are zero (Mace et al. 1999), however, we compared predictions from the model with predictions assuming anthropogenic variables are at their mean values. With this approach we avoided having to make predictions well outside the range of the anthropogenic variables used to fit the model and having to make the strict assumption that natural and anthropogenic variables are independent. These two issues are important because, in our study area, anthropogenic variables were never close to zero and there was some correlation between the natural habitat and anthropogenic variables. We demonstrate that building the model in this way and presenting it as a map provides important information for making decisions on how different conservation actions should be spatially allocated.

Methods

Study Species and Study Area

The koala is a folivorous arboreal marsupial restricted to the eucalypt forests of eastern and southeastern Australia. Across its range koalas feed on a wide variety of tree species, predominantly from the genera *Eucalyptus* and *Corymbia*, but in any particular area show preferences for just a few species (Hindell & Lee 1987; Phillips & Callaghan 2000). Koala habitat generally consists of forests containing the preferred species of food tree, although other factors such as tree size can also contribute to habitat quality (Hindell & Lee 1987; Cork et al. 2000).

The study area consisted of the southeastern region of the Port Stephens Local Government Area, New South Wales, Australia (approximately 150 km north of Sydney, Fig. 1). Port Stephens has undergone substantial land clearing since European settlement, and most of the remaining high-quality koala habitat is now concentrated in the southeast (Knott et al. 1998; Lunney et al. 1998). The southeast is also the most urbanized part of Port Stephens and consequently contains the greatest contemporary
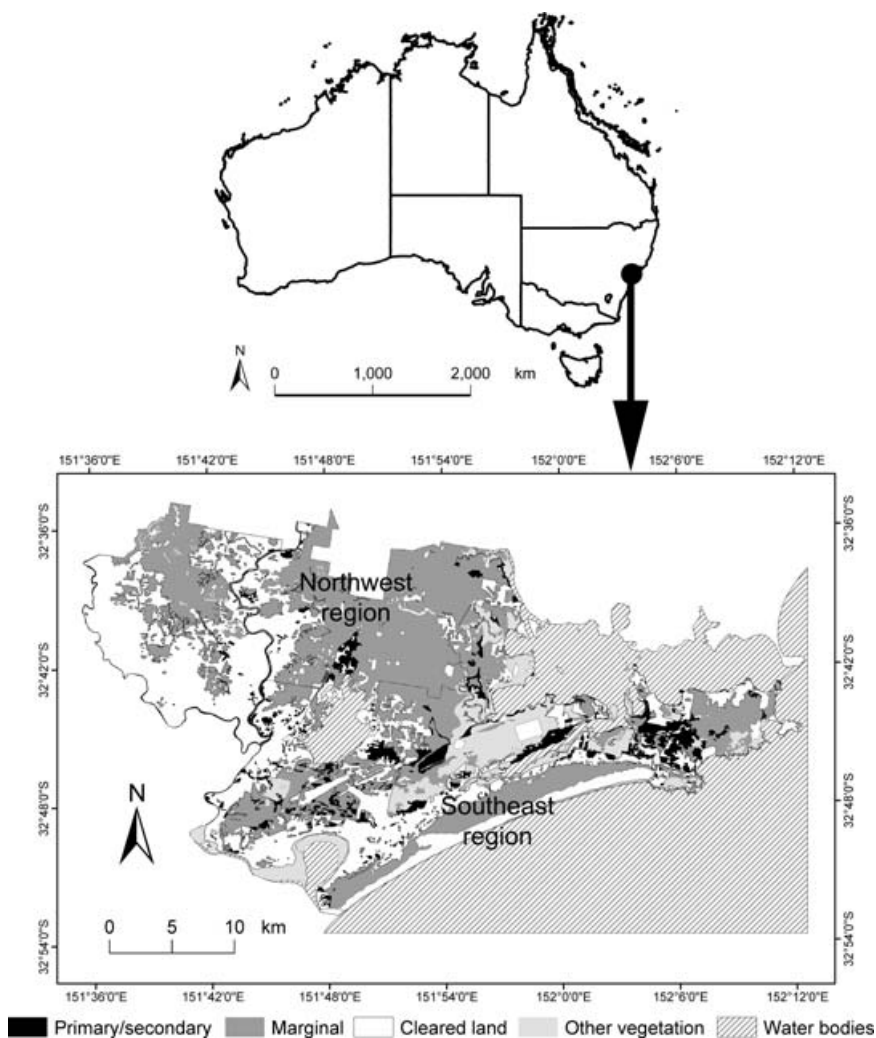

Figure 1. Port Stephens Local Government Area, with its location in Australia and the estimated distribution of natural koala habitat (based on Lunney et al. 1998). The Port Stephens map is displayed in AGD1966 zone 56 projected coordinates.

threats to koalas in the area. These threats include continued habitat loss, vehicle collisions, dog attacks, and fire (Port Stephens Council 2001).

Presence and Absence Data

Between February and April 2002 we collected koala presence and absence data across the whole of Port Stephens. We used Latin hypercube sampling (McKay et al. 1979) to select survey sites that were stratified by habitat type, patch size, proximity to other habitat patches, and proximity to roads. At each site we demarcated three subsites 100 m apart along a 200-m transect (at a few sites, logistic constraints allowed only one or two subsites to be selected). At each subsite koala presence or absence was determined using standardized searches for fecal pellets (Phillips & Callaghan 2000; Phillips et al. 2000) under the 12 trees closest to the center of the subsite. Sixty-five sites (192 subsites) were located in the southeast of Port Stephens, which is consistent with the number of sites recommended in the literature for studies of this kind (Morrison et al. 1992).

Explanatory Variables

We selected a priori several variables with which to model koala presence: habitat type, an index of fire history, road density, traffic volume, human population density, and domestic dog density (Table 1). These variables were classified as either natural or anthropogenic and mapped spatially as ESRI ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA) raster grid layers with 25×25 m cell sizes.

The distribution of habitat types was taken from habitat mapping based on an independent fecal pellet survey (Fig. 1; Lunney et al. 1998). This mapping was derived from the distribution of vegetation communities, soil types, and a model of koala preferences for tree species. We considered the distribution of two koala habitat types: (1) primary/secondary habitat and (2) marginal habitat. To construct a raster layer for each habitat type we assigned to each cell a value of 1 if it consisted of the habitat type; otherwise the value was 0.

We used data on the location of fires between January 1984 and March 2002 (New South Wales Rural Fire Service, unpublished data) to construct a raster layer for the index of fire history. This index accounted for fire frequency and time since fire. For each cell, c, with $i = 1, \ldots, n_c$ fires since January 1984, the value of the fire index, F_c, was calculated as

$$F_c = \sum_{i=1}^{n_c} \frac{1}{T_i}, \qquad (1)$$

where T_i is the time in years from the month of fire i until March 2002 (the midpoint of the fecal-pellet survey period) and the sum is over all fires in cell c. If there were no fires since January 1984, then $F_c = 0$. An assumption of this index is that the impact of each fire declines over time and that the effect of successive fires is additive.

To construct a road-density raster layer we used data on the location of paved roads (New South Wales Department of Lands, unpublished data) to assign to each cell a value of 1 if it contained a paved road and a value of 0 if it had no roads. We used data from traffic-recording stations between 1995 and 2001 (New South Wales Roads and Traffic Authority, unpublished data; Port Stephens Council, unpublished data) to estimate traffic volumes (vehicles/day) on major roads. We then constructed a traffic-volume raster layer by assigning to each cell the estimated traffic volume if it contained a major road. If there was no major road then traffic volume was 0.

We estimated the density of humans (people/hectare) for each planning district based on records of human population sizes from 1996 (Port Stephens Council 1999). To construct a human population density raster layer we assigned to each cell the human density of the planning district in which the cell was situated. We also estimated domestic dog density (dogs/hectare) for each suburb, based on records of domestic dogs from 2003 (New South Wales Companion Animal Register, unpublished data). To construct a raster layer of domestic dog density we assigned to each cell the dog density of the suburb in which the cell was situated.

Habitat type variables were classified as natural variables, and fire index, road density, traffic volume, human

Table 1. Explanatory variables used to model the probability of koala presence.

Category	Variable	Metric description
Natural	primary/secondary habitat	negative-exponential distance-weighted density of primary/secondary habitat
	marginal habitat	negative-exponential distance-weighted density of marginal habitat
Anthropogenic	fire index	negative-exponential distance-weighted mean fire index; fire index increases with fire frequency and declines with time since fire
	road density	negative-exponential distance-weighted density of roads
	traffic volume	negative-exponential distance-weighted mean traffic volume
	human population density	human population density at the scale of the planning district
	domestic dog density	domestic dog density at the scale of the suburb

population density, and domestic dog density were classified as anthropogenic variables. Fire control measures, especially in areas close to human population centers, are key determinants of the distribution and timing of fires in Port Stephens. Therefore fire activity tends to reflect human intervention rather than an underlying natural process, so we classified fire as an anthropogenic variable.

For each variable (except human density and dog density) and for each subsite we calculated a set of distance-weighted metrics (Table 1). These metrics were weighted means of the variable values around each subsite, with an exponential decline in weighting with distance from the subsite. For subsite $j = 1, \ldots, m_i$ of site $i = 1, \ldots, M$ the metric X_{ij} was calculated as

$$X_{ij} = \frac{\sum_{c=1}^{k} V_c \exp(-\lambda d_{ijc})}{\sum_{c=1}^{k} \exp(-\lambda d_{ijc})}, \qquad (2)$$

where V_c is the value of the variable in cell c; d_{ijc} is the distance between subsite j of site i and the center of cell c; λ is the scale parameter for the negative-exponential function; and the sum is over all cells in the landscape, $c = 1, \ldots, k$. For the habitat type metrics we considered cells classified as water bodies part of the landscape, but water bodies were not considered part of the landscape for the other variables. For the human density and dog density metrics, X_{ij} was the density assigned to the raster cell in which subsite j of site i was located. All metrics were standardized to have a mean of 0 and a standard deviation of 1.

The parameter λ controls how rapidly the influence (i.e., weighting) of the variable declines with distance. If λ is small, then there is a slow decline in weighting with distance and values of the variable close to and far from each subsite determine the value of the metric. Conversely, if λ is large there is a rapid decline in weighting with distance and values of the variable close to each subsite dominate the value of the metric.

We assumed that the key determinant of the rate of decline in influence with distance was how koala movement processes connect the landscape. Therefore we considered three different values of λ, representing connectivity due to three different koala movement processes: (1) movement within the home range, (2) dispersal, and (3) long-distance dispersal. We derived the values of λ from empirical data, and they were chosen so that their corresponding negative-exponential probability distributions had: (1) a 95th percentile equal to the radius of a median 95% kernel home range (assuming it is circular) of 350 m (J.R.R., unpublished data), (2) an expected value equal to a mean dispersal distance of 3500 m (Dique et al. 2003a), and (3) an expected value equal to a 75th percentile dispersal distance of 5750 m (Dique et al. 2003a). The λ
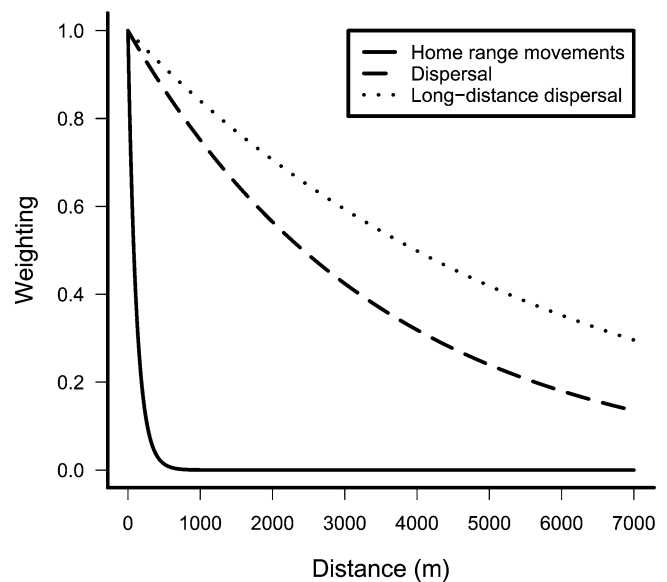

Figure 2. Negative-exponential decay functions for the distance-weighted metrics. Lines show the weighting given to an individual raster cell as a function of distance for metrics scaled to: (1) movements within a home range, (2) dispersal, and (3) long-distance dispersal. The scale parameters, λ, for the negative-exponential distributions are (1) 8.6×10^{-3}/m for movements within a home range, (2) 0.29×10^{-3}/m for dispersal, and (3) 0.17×10^{-3}/m for long-distance dispersal.

values we used were 8.6×10^{-3}/m for movement within the home range, 0.29×10^{-3}/m for dispersal, and 0.17×10^{-3}/m for long-distance dispersal (Fig. 2).

Statistical Modeling

We modeled the probability of koala presence with mixed-effects logistic regression, with an intercept random effect between sites (Hosmer & Lemeshow 2000; Pinheiro & Bates 2000). These models had the general form

$$\ln\left(\frac{p_{ij}}{1 - p_{ij}}\right) = \beta' \mathbf{X}_{ij} + b_i, \qquad (3)$$

where p_{ij} is the probability of koala presence at subsite j of site i; β is a vector of coefficients; $\mathbf{X}_{ij}$ is a vector of explanatory variables for subsite j of site i; and $b_i \sim N(0, \sigma^2)$ is a normally distributed random effect for site i. Mixed-effects models were used to account for the hierarchical variance structure in the data (i.e., subsites nested within sites) and accounted for spatial autocorrelation within sites. We used R release 1.7.1 (package "glmmML") to fit these models to the presence and absence data by maximum likelihood (R Project for Statistical Computing, http://www.r-project.org/).

To reduce the number of possible explanatory variable combinations to a manageable level, we chose only one of the three metrics calculated for each variable. The metric chosen was the one that yielded the lowest Akaike's information criterion (AIC) from univariate models of the three metrics (Burnham & Anderson 2002). We then checked the chosen metrics for colinearity by calculating all pairwise Spearman's rank correlation coefficients. Booth et al. (1994) suggest that if a pair of variables has a correlation coefficient > 0.5, then they should be considered proxies of each other and one variable should be removed. Therefore, if a pair of metrics had a correlation coefficient > 0.5, we removed the metric that yielded the highest AIC from univariate models of the two metrics.

We constructed a set of alternative models from all linear combinations of the remaining metrics and fitted each model to the presence and absence data. We then ranked these models by their AIC values and determined the model-averaged parameter estimates (Burnham & Anderson 2002). A 95% confidence set of models was also constructed by starting with the model with the highest Akaike weight and repeatedly adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 (Burnham & Anderson 2002). The Akaike weight of a model is the relative likelihood of the model compared with all other models in the set (Burnham & Anderson 2002). Finally, for each variable, its relative importance was quantified through an index constructed by summing the Akaike weights for all models containing the variable (Burnham & Anderson 2002).

To check for spatial autocorrelation in model residuals we constructed two Moran's I correlograms (one with a lag interval of 500 m and one with a lag interval of 1000 m) from the Pearson residuals of the most parsimonious model (Cliff & Ord 1981). We then used permutation tests (with 999 permutations) and a progressive Bonferroni correction (with Type I error rate, $\alpha = 0.05$) to test for statistically significant spatial autocorrelation (Legendre & Legendre 1998; Lichstein et al. 2002). We used R release 1.7.1 (package "spdep") to conduct these tests (R Project for Statistical Computing, http://www.r-project.org/).

To assess the fit of the most parsimonious model, we used a Pearson χ^2 goodness-of-fit test, with a p value calculated from a normal approximation of the Pearson χ^2 statistic distribution (Hosmer & Lemeshow 2000). We also assessed discrimination ability by estimating the area under the receiver operating characteristic (ROC) curve for the most parsimonious model (Hanley & McNeil 1982; Pearce & Ferrier 2000). The area under the ROC curve is the probability that a randomly chosen truly occupied site is correctly ranked relative to a randomly chosen truly unoccupied site. We used cross-validation procedures (with 10 groups and 200 replicates) to estimate the area under the ROC curve (Fielding & Bell 1997; Pearce & Ferrier 2000). The ROC curves were constructed with R release 1.7.1 (package "ROC") (BioConductor Project, release 1.3, http://www.bioconductor.org/).

Relative Spatial Impact of Natural and Anthropogenic Factors

We evaluated the relative spatial impact of natural and anthropogenic factors based on model-averaged predictions. First we made model-averaged predictions of the spatial distribution of koalas, with a probability cut-off that equalized specificity (proportion of unoccupied sites correctly predicted) and sensitivity (proportion of occupied sites correctly predicted). Then we made model-averaged predictions with the same probability cutoff but with anthropogenic variables fixed at their mean values. Finally, we used the difference between these two sets of predictions to create a map showing the change in predicted occupancy patterns due to variation in anthropogenic variables from their means.

Impact of Map Boundaries

A number of sites were situated close to the boundary of the mapped area, which could affect model inferences and predictions. We assessed this effect by excluding subsites within 5750 m of a map boundary and repeating the modeling procedures on the reduced data set. The expected value of the negative-exponential function that we used for calculating the metrics scaled to long-distance dispersal was 5750 m. Therefore, for metrics scaled to long-distance dispersal, landscape characteristics within 5750 m of a subsite had a greater influence on metric values than landscape characteristics farther than 5750 m away. Further, metrics scaled to within home range movements and dispersal were even less influenced by landscape characteristics farther than 5750 m from a subsite. Hence we investigated the influence of map boundaries on model inferences by excluding sites within 5750 m of a boundary.

Results

Metrics scaled to long-distance dispersal produced the most parsimonious univariate models for all explanatory variables, except traffic volume. The most parsimonious metric for traffic volume was scaled to home range movements. Therefore we chose the home range scaled metric for traffic volume and long-distance dispersal scaled metrics for the other variables. We found high correlations between fire and road density (Spearman's rank correlation $= -0.74$) and human density and dog density ($+0.87$). Therefore, to reduce the effect of multicolinearity, we removed (based on AIC comparisons of the univariate models) the fire and human density metrics from further analysis. Consequently we considered only the chosen metrics for primary/secondary habitat, marginal habitat,

road density, traffic volume, and dog density in the model selection procedures.

The most parsimonious model (AIC = 198.9) contained the metrics, scaled to long-distance dispersal, for primary/secondary habitat, marginal habitat, road density, and dog density (Table 2). Based on the correlogram analyses, we did not find any significant spatial autocorrelation in the Pearson residuals ($p > 0.05$). Also, the Pearson χ^2 goodness-of-fit test revealed no evidence of a significant lack of fit ($Z = -0.055$, $n = 192$, $p = 0.96$). Finally, the cross-validation area under the ROC curve was 0.79, indicating reasonable discrimination ability (Pearce & Ferrier 2000). Therefore we concluded that the structure of the most parsimonious model was appropriate.

The 95% confidence set of models contained four models, revealing some model uncertainty (Table 2). A common feature of these models, however, was that they all contained primary/secondary habitat, marginal habitat, and road density. The mean relative importance of the natural variables was 0.98, and for the anthropogenic variables it was 0.71. For individual variables the order of importance was: (1) primary/secondary habitat (relative importance index = 1.00), (2) road density (1.00), (3) marginal habitat (0.95), (4) dog density (0.85), and (5) traffic volume (0.28). Model-averaged coefficients for primary/secondary habitat, traffic volume, and dog density were positive, whereas model-averaged coefficients for marginal habitat and road density were negative (Table 2). The model-averaged coefficients for traffic volume ($t = 0.07$, df = 184, $p = 0.95$) and dog density ($t = 1.51$, df = 184, $p = 0.09$) were not significantly different from 0.

Model-averaged predictions revealed three broad areas of koala presence: (1) south and east of Grahamstown Lake, (2) on the Tilligerry Peninsula, and (3) on the Tomaree Peninsula (Fig. 3). With anthropogenic variables fixed at their mean values, however, predictions differed, such that koala absence was predicted east of Grahamstown Lake, presence was predicted farther to the east on the Tilligerry and Tomaree peninsulas, and presence was predicted south of Raymond Terrace (Fig. 3). To the east of the Tilligerry and Tomaree peninsulas, koala presence was predicted at mean anthropogenic variable values because of a high proportion of primary/secondary habitat. The above-average road density, however, resulted in predictions of absence from the full model. To the south of Raymond Terrace the presence of some primary/secondary habitat meant that koala presence was predicted at mean anthropogenic variable values. Once again, however, above-average road densities in the area meant that absence was predicted from the full model. The area east of Grahamstown Lake is dominated by marginal habitat. Therefore, at mean anthropogenic variable values, koala absence was predicted, but because the density of roads is well below average in this area, the full model predicted presence.

The effect of map boundaries on model inferences and predictions was minor; therefore we did not consider this further. For the reduced data set compared with the full data set, the most parsimonious model was the same, model ranking was almost identical, and the ranking of variables by relative importance was the same. The model-averaged predictions obtained from the reduced data set were also very similar to predictions obtained from the full data set. The key differences were that the full model predicted koala presence slightly farther to the west near Raymond Terrace and, with anthropogenic variables at their mean values, koala presence was predicted slightly farther to the east, south of Grahamstown Lake. However, the same broad conclusions were obtained from both data sets.

Table 2. Distribution model ranking, Akaike's information criteria (AIC), coefficient estimates (± 1 SE) for the 95% confidence set of models and the model average, and the relative importance indices.

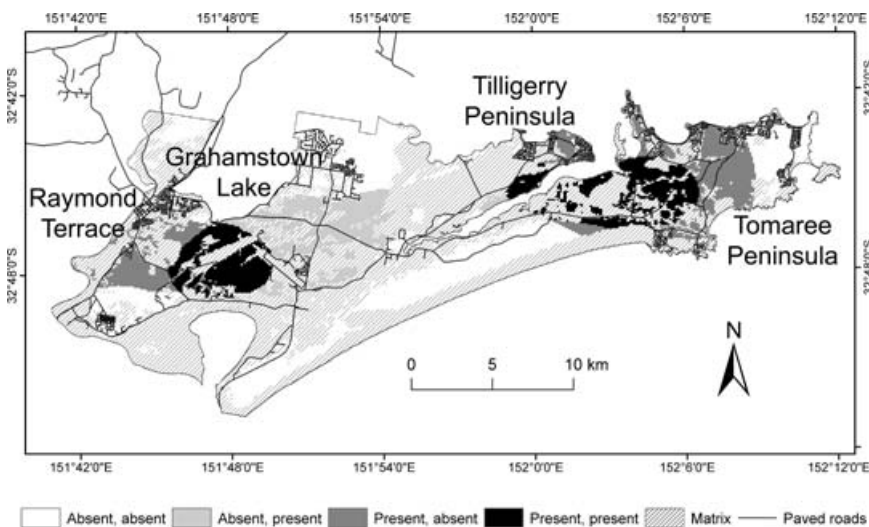|				Natural explanatory variables		Anthropogenic explanatory variables			
Model ranking	AIC	w^a	Intercept	Primsec-ldd[b]	Marg-ldd[b]	Road-ldd[b]	Tvol-hr[b,c]	Dogs[b,c]	σ^d
1	198.9	0.61	0.02 ± 0.35	2.90 ± 0.72	-2.40 ± 0.91	-3.88 ± 1.21		1.08 ± 0.51	1.90 ± 0.52
2	200.9	0.23	0.02 ± 0.35	2.91 ± 0.73	-2.39 ± 0.91	-3.88 ± 1.21	0.06 ± 0.27	1.08 ± 0.51	1.91 ± 0.52
3	203.0	0.08	0.14 ± 0.35	2.38 ± 0.59	-1.34 ± 0.67	-2.40 ± 0.82			1.92 ± 0.52
4	204.9	0.03	0.13 ± 0.35	2.39 ± 0.60	-1.34 ± 0.67	-2.40 ± 0.82	0.10 ± 0.27		1.93 ± 0.52
Model average			0.04 ± 0.36	2.79 ± 0.75	-2.16 ± 0.96	-3.58 ± 1.32	0.02 ± 0.28	0.91 ± 0.54	1.91 ± 0.52
Relative importance[e]				1.00	0.95	1.00	0.28	0.85	

[a]*Akaike weight.*

[b]*Primsec-ldd, primary/secondary habitat metric scaled to long-distance dispersal; Marg-ldd, marginal habitat metric scaled to long-distance dispersal; Roads-ldd, road density metric scaled to long-distance dispersal; Tvol-hr, traffic volume metric scaled to within home range movements; and Dogs, domestic dog density at the scale of the suburb.*

[c]*Blank space signifies variable not in the model.*

[d]*Standard deviation of the random effect.*

[e]*Mean relative importance index for the natural and anthropogenic variables was 0.98 and 0.71, respectively.*

Figure 3. Model-averaged predictions of the distribution of koalas in the southeastern region of Port Stephens with anthropogenic variables fixed at their mean values and for the full model, both with probability thresholds of 0.55. Each grouping in the legend shows the predicted occupancy state (presence or absence) first for anthropogenic variables at their mean values and second for the full model (e.g., unshaded areas are where koalas are predicted to be absent with anthropogenic variables fixed at their mean values as well as for the full model). Matrix consists of cleared land and other vegetation not classified as koala habitat. Predictions are shown at a resolution of 100 × 100 m, and the map is displayed in AGD1966 zone 56 projected coordinates.

Discussion

We have presented a statistical model of koala distributions in which the probability of koala presence was conceptualized as a function of natural and anthropogenic variables. Our approach demonstrated that both natural and anthropogenic variables were important for determining the distribution of koalas in the Port Stephens study area but that their effects varied spatially (Fig. 3).

Model Interpretation

The most important determinant of the probability of koala presence, averaged across the landscape, was the distribution of natural habitat, with anthropogenic factors of secondary importance. As the amount of primary/secondary habitat increased so did the predicted probability of koala presence. Conversely, the predicted probability of koala presence decreased as road density increased. These were the two most important variables and they had the largest effect sizes. Therefore we concluded that natural habitat quality was correlated with the amount of primary/secondary habitat and anthropogenic impacts were correlated with road density. The negative model-averaged coefficient for marginal habitat indicated that areas with high proportions of marginal habitat were of low natural habitat quality. The positive model-averaged coefficients for traffic volume and dog density were somewhat counterintuitive, but these coefficients were not significantly different from zero and were of low relative importance.

For brown bears, Naves et al. (2003) explicitly linked natural variables to reproductive output and anthropogenic variables to mortality. This enhanced the biological interpretation of their model. Anthropogenic impacts mainly increase mortality risk for koalas, but the effect of natural habitat on demographic rates is less clear. Koala reproduction and mortality rates, however, do not seem to vary substantially with natural habitat quality in Port Stephens (J.R.R., unpublished data). It may be that distributions are largely determined by strong habitat selection preferences (Rhodes et al. 2005) that have evolved in response to difficult-to-detect differences in the fitness rewards between habitats. These uncertainties prevent a more in-depth biological interpretation of the effect of natural habitat on population dynamics, and they form an important area for future research.

A further consideration is how habitat selection processes interact with spatial variation in natural and anthropogenic factors because this can have important implications for population viability. Areas of high natural habitat quality can have negative population growth rates if these areas are subject to high anthropogenic impacts (Gaona et al. 1998). Over evolutionary time scales, habitat selection strategies have evolved to use cues from the natural environment. Anthropogenic influences have appeared only recently, and habitat selection responses to them may not have evolved yet. Therefore, individuals may falsely perceive areas as being good-quality habitat where, in fact, population growth rates are negative because of high anthropogenic impacts. This can result in maladaptive habitat selection and the formation of "attractive sinks," with an associated reduction in population

viability (Remes 2000; Delibes et al. 2001). In Port Stephens, areas that have high natural habitat quality but adverse anthropogenic impacts, such as on the Tomaree Peninsula (Fig. 3), could be attractive sinks. Therefore, understanding the link between habitat selection processes and the spatial locations of natural and anthropogenic effects is an important area of research.

The distance-weighted metrics we used produced much better models than simple buffer measures (J.R.R., unpublished data). Moilanen and Nieminen (2002) also show that these types of metrics are more likely to detect significant connectivity effects than nearest-neighbor or buffer measures. These metrics tend to be more biologically meaningful than simple buffer measures of landscape composition because they encapsulate connectivity between different locations. The fact that metrics, scaled to long-distance dispersal, produced the most parsimonious models suggests that the spatial extent of the influence of natural and anthropogenic factors were determined mainly through natal dispersal processes. However, we did not consider other spatial processes, such as the movement of domestic dogs, that may also be important.

Model Limitations

The capacity to transfer the model to other areas appeared to be low. The model did not predict koala distributions well in the northwestern region of Port Stephens (Fig. 1), which has a more agricultural landscape and where the threatening processes are different (J.R.R., unpublished data). However, the aim of the model was to predict the distribution of koalas in a particular area of Port Stephens in order to inform conservation planning, rather than as a general model for koalas.

Implications for Conservation

In semiurban landscapes, conservation planning requires the spatial locations of natural habitat and anthropogenic impacts be considered. In Port Stephens, there are two broad categories of possible management actions: (1) protect and reconstruct natural habitat and (2) reduce anthropogenic influences, such as mortality from dog attack and vehicle collisions (Port Stephens Council 2001). The model of koala distributions we developed supported both these strategies as being important but indicated that priorities vary spatially. For example, the high natural habitat quality and above-average anthropogenic influences on the Tomaree Peninsula (Fig. 3) indicate that a reduction in anthropogenic influence is a priority in this area. This especially will be the case if this area is acting as an attractive sink. On the other hand, to the east of Grahamstown Lake (Fig. 3), natural habitat improvement may be a priority because anthropogenic influence is low and natural habitat quality is not particularly high. In such a

way, our modeling approach can assist in identifying conservation priorities in a spatial context.

Ideally these types of models should be integrated into a decision-theory framework (Possingham et al. 2001). This involves the specification of clear objectives, such as maximizing the probability of koala presence. Model predictions can then be used to find good landscape planning strategies to meet these objectives within economic and social constraints (e.g., Westphal & Possingham 2003). This then allows decision-making processes to link explicitly with the underlying ecological models, and moves from qualitative to quantitative advice. This will be a key area of research for the effective application of our approach to conservation planning.

Conservation planning requires the identification of conservation priorities and invariably involves compromises with other socioeconomic objectives. The ultimate benefits of conservation planning depend largely on the effectiveness of decision making and priority setting in this context. Successfully communicating our understanding of ecological impacts to policy and decision makers is crucial in this process (Dovers et al. 1996). We believe that explicitly separating the effect of natural and anthropogenic factors, in the way we have done, will improve communication with planners and policy makers on how the two different processes affect species' distributions.

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