Journal of Applied Ecology 2004
41, 213–223

Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach

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Summary

1. To develop a conservation management plan for a species, knowledge of its distribution and spatial arrangement of preferred habitat is essential. This is a difficult task, especially when the species of concern is in low abundance. In south-western Victoria, Australia, populations of the rare rufous bristlebird *Dasyornis broadbenti* are threatened by fragmentation of suitable habitat. In order to improve the conservation status of this species, critical habitat requirements must be identified and a system of corridors must be established to link known populations. A predictive spatial model of rufous bristlebird habitat was developed in order to identify critical areas requiring preservation, such as corridors for dispersal.

2. Habitat models generated using generalized linear modelling techniques can assist in delineating the specific habitat requirements of a species. Coupled with geographic information system (GIS) technology, these models can be extrapolated to produce maps displaying the spatial configuration of suitable habitat.

3. Models were generated using logistic regression, with bristlebird presence or absence as the dependent variable and landscape variables, extracted from both GIS data layers and multispectral digital imagery, as the predictors. A multimodel inference approach based on Akaike's information criterion was used and the resulting model was applied in a GIS to extrapolate predicted likelihood of occurrence across the entire area of concern. The predictive performance of the selected model was evaluated using the receiver operating characteristic (ROC) technique. A hierarchical partitioning protocol was used to identify the predictor variables most likely to influence variation in the dependent variable. Probability of species presence was used as an index of habitat suitability.

4. Negative associations between rufous bristlebird presence and increasing elevation, 'distance to creek', 'distance to coast' and sun index were evident, suggesting a preference for areas relatively low in altitude, in close proximity to the coastal fringe and drainage lines, and receiving less direct sunlight. A positive association with increasing habitat complexity also suggested that this species prefers areas containing high vertical density of vegetation.

5. The predictive performance of the selected model was shown to be high (area under the curve 0·97), indicating a good fit of the model to the data. Hierarchical partitioning analysis showed that all the variables considered had significant independent contributions towards explaining the variation in the dependent variable. The proportion of the total study area that was predicted as suitable habitat for the rufous bristlebird (using probability of occurrence at a $\geq 0{\cdot}5$ level) was 16%.

6. *Synthesis and applications.* The spatial model clearly delineated areas predicted as highly suitable rufous bristlebird habitat, with evidence of potential corridors linking coastal and inland populations via gullies. Conservation of this species will depend on management actions that protect the critical habitats identified in the model. A multi-scale approach to the modelling process is recommended whereby a spatially explicit model is first generated using landscape variables extracted from a GIS, and a second

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model at site level is developed using fine-scale habitat variables measured on the ground. Where there are constraints on the time and cost involved in measuring finer scale variables, the first step alone can be used for conservation planning.

Key-words: Akaike's information criterion, geographical information system, habitat model, hierarchical partitioning, logistic regression, information-theoretic approach

Journal of Applied Ecology (2004) **41**, 213–223

Introduction

The rufous bristlebird *Dasyornis broadbenti* (McCoy 1867) is a rare ground-dwelling passerine endemic to Australia. There are three recognized subspecies: *D. b. broadbenti* and *D. b. caryochrous*, located in south-eastern Australia, and *D. b. litoralis*, a south-western Australian species (Schodde & Mason 1999). The subspecies have suffered declines since European settlement, and the western Australian *D. b. litoralis* is now presumed extinct, while the species as a whole is listed as 'lower risk/near threatened' (IUCN 2002). Rufous bristlebirds inhabit dense, low vegetation communities ranging from coastal shrubland to wet forested gullies (Garnett & Reilly 1992; Peter 1999; Wilson *et al*. 2001).

This study concerned *D. b. caryochrous*, an endemic to south-western Victoria, Australia (Schodde & Mason 1999). This subspecies is largely restricted to a discontinuous coastal strip, although it has also been recorded in sheltered gullies extending up to 40 km inland (Emison *et al*. 1987). The rufous bristlebird is categorized as 'threatened' in Victoria under the Flora and Fauna Guarantee Act (Smith & Baker-Gabb 1993). Presumed major threats to the species include wildfire, inappropriate fire regimes and predation by cat *Felis catus* and fox *Vulpes vulpes* (Smith & Baker-Gabb 1993). Perhaps the most significant threat has been the clearing of land for agriculture and urban development, and the consequent loss and fragmentation of suitable habitat (Garnett & Reilly 1992; Smith & Baker-Gabb 1993; Peter 1999). The territorial and sedentary nature of rufous bristlebirds, combined with their apparently poor dispersal abilities and slow recolonization rates (Smith 1977; Reilly 1991; Smith & Baker-Gabb 1993; Chapman 1999), makes them particularly vulnerable to both habitat fragmentation and wildfire. As the rufous bristlebird tends to inhabit dense vegetation, management practices that involve frequent burns may be detrimental to the species because their preferred habitat may not be able to regenerate to a sufficient density (Smith 1977; Garnett & Reilly 1992; Peter 1999). It has been suggested that a high fire frequency contributed to the extinction of the western subspecies (Smith 1977).

Smith & Baker-Gabb (1993) assessed the conservation status of the rufous bristlebird in Victoria and identified key management actions. Priority was given to ascertaining the critical habitat requirements common to both the inland and coastal populations, as well as enhancing a system of corridors to link known populations, and assessing the sustainability of current populations. Habitat models generated using generalized linear modelling techniques can assist in delineating specific habitat requirements of a species and, coupled with geographic information system (GIS) technology, these models can be extrapolated to produce maps displaying the spatial configuration of suitable habitat (Guisan & Zimmermann 2000). By providing baseline information about the spatial arrangement of potentially suitable habitat for a species, habitat suitability maps can be used to facilitate protection and restoration of critical habitat, and hence they have broad applicability in conservation biology and wildlife management (Manel *et al*. 1999; Jaberg & Guisan 2001; Elith & Burgman, in press). The aim of the current study was to develop a predictive habitat suitability model for the rufous bristlebird, and thereby address the priorities identified by Smith & Baker-Gabb (1993) above. In particular, we aimed to identify critical areas that require preservation, such as corridors for dispersal.

Applying a predictive distribution model within a spatial context relies on the existence of landscape-scale variables that define suitable habitat for a species (Osborne, Alonso & Bryant 2001; Austin 2002a,b) and for those variables to be biologically important to that species. Landscape variables are likely to have no direct physiological relevance for a species' performance but can act indirectly on causal variables, such as temperature, that have direct influence on a species' distribution (Guisan & Zimmermann 2000; Austin 2002a,b). Because GIS coverage of causal variables is difficult to obtain, the use of direct variables for predictive distribution mapping is likely to be impractical (Austin 2002b). In this study, various terrain (indirect) variables, derived from a digital elevation model (DEM), and hydrology information were selected as potential predictors. In addition, the availability of a spatial layer of vegetation structure for the study area permitted the inclusion of vertical vegetation density as a potential predictor variable.

The study region experienced a wildfire in 1983 that burned large areas (40 000 ha) and left few refuges (Reilly 1991). The recovery of the rufous bristlebird in coastal sections of this region post-fire has been assessed (Reilly 1991; Wilson *et al*. 2001); however, the population status of an adjacent inland area is unclear. A further objective of the current study was to determine the distribution of the species inland from the coast and to identify possible corridors linking the coastal and inland populations.

Methods

STUDY AREA

The study was centred on the Anglesea Heath and adjacent coastline (9706 ha) in south-west Victoria, Australia (38°23′S, 144°08′E; Fig. 1). The Anglesea Heath is leased to Alcoa of Australia Ltd for the purpose of brown coal extraction. The area surrounding the mine and associated power station is recognized for its significant flora and fauna communities, and a Land Management Co-operative Agreement was established in 2002 to protect its biodiversity values (McMahon & Brighton 2002).

The area experiences a temperate climate, with cool wet winters and warm dry summers, and an average yearly rainfall of between 600 and 800 mm (Laidlaw 1997). The vegetation consists of a diverse mosaic of predominantly sclerophyllous forests, woodlands and heathlands, interspersed with dense shrublands in the wetter and coastal areas (Land Conservation Council 1985; Meredith 1986). The species composition of the vegetation communities has been determined in detail (Land Conservation Council 1985, 1987). The undulating landscape is traversed by the main drainage systems of Salt and Marshy Creeks, and the Anglesea River. Minor drainage systems forming deep gullies extend from the Heath to the coastline.

Fig. 1. Location of study site in southern Victoria, Australia.

BIRD SURVEYS

Surveys were conducted from October to December 2002. Tracks selected at random were traversed slowly on foot (Fig. 2) in the early morning (07:00–11:00) and the location of bristlebirds either heard and/or observed was recorded using a global positioning system (GPS), with an accuracy of ±10 m. While bristlebirds are often described as shy and cryptic, they can be located reliably by their loud and distinctive call (Parker & Reid 1978;

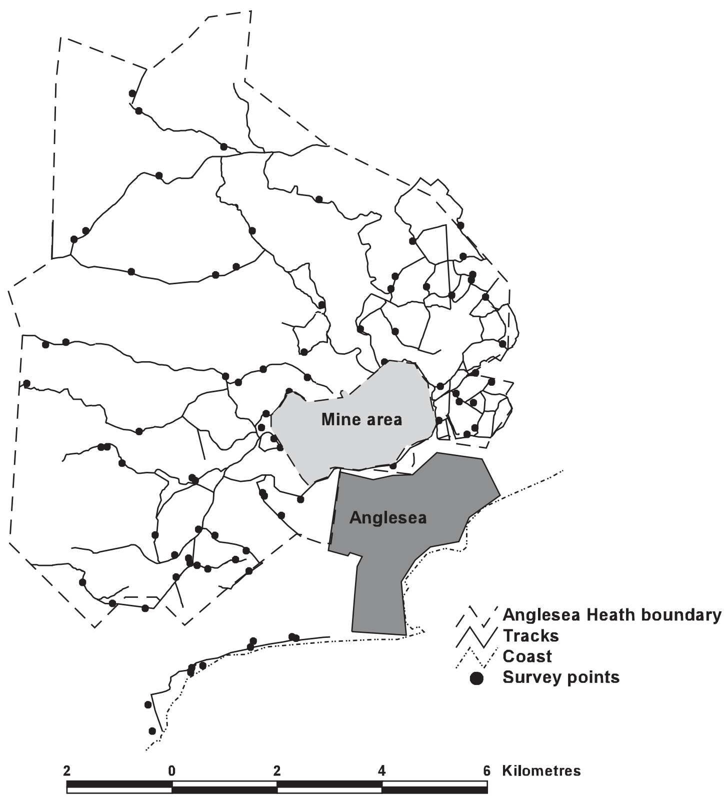

Fig. 2. Study area showing locations of surveyed tracks and survey points.

Chapman 1999; Peter 1999). In order to maximize probability of detection, surveys were timed to coincide with the breeding season from July to December, and during the early morning (Wilson *et al.* 2001). This census technique has been used routinely for bristlebirds (Bramwell *et al.* 1992; Baker 1997; Wilson *et al.* 2001). Sites where bristlebirds were located were visited at least twice on separate occasions, and presence of the bird was confirmed. Care was taken to avoid double-detections of the same bird by ensuring that there was sufficient distance between successive calls and the direction from which successive calls come was different.

Random points (53) were generated along the surveyed tracks where the birds were not detected (during the census), and these were used as 'absent' sites (Osborne, Alonso & Bryant 2001). Random points were offset from the tracks by 20 m.

GIS COVERAGE

As the essential components of suitable habitat of the rufous bristlebird are unclear (Smith & Baker-Gabb 1993), an exploratory approach was taken in the initial selection of potential predictor variables. However, selection of variables did depend on their availability in digital format for the study area, and the small number of survey sites precluded the use of a large number of variables (Harrell 2001). Raster (grid) layers of slope, aspect and elevation were derived from a 20-m resolution DEM provided by the Victorian Department of Sustainability and Environment (DSE), using spatial analysis tools in ArcView (ESR1). Layers of slope and aspect were further combined to generate a sun index grid according to the equation:

$$SI = \cos(aspect) \times \tan(slope) \times 100 \qquad \text{eqn 1}$$

(Wilson, Aberton & Reichl 2001; Wilson, Lewis & Aberton 2003). Sun index was used on the premise that the amount of solar radiation received at a site will be influenced by the steepness and orientation of the landscape at that site. Aspect and slope alone were not used in the modelling process. Grid layers of 'distance to coast' and 'distance to creek' were also generated in the GIS from digitized hydrology information (supplied by DSE). Ideally, the resolution, or pixel size, of the raster data should relate to the home range of the species under investigation (Austin 2002b). Although the home range of the rufous bristlebird has not been accurately measured, their territory size has been estimated to be between 1 and 3 ha (Chapman 1999; Wilson *et al.* 2001). In this case, to avoid losing resolution a neighbourhood function in ArcView Spatial Analyst software was used to calculate the mean value of a 100 × 100-m moving window for each 20-m pixel in each layer.

A multispectral digital image (mosaic of video-graphic imagery) at 2-m resolution was purchased for the study area (Specterra, Leederville, Australia). The image was further processed (CSIRO Division of Forestry and Forest Products, Victoria, Australia) to produce a digital data layer that represented the complexity of the vegetation structure. This technique is based on the relationship between local variance of the near infrared spectral band and habitat complexity. Habitat complexity was used here as an index of vegetation structure that was independent of individual plant species but incorporated habitat components and vegetation strata such as tree canopy, shrub canopy and ground herbage coverage, the cover of rocks, logs and litter and general soil moisture condition (Newsome & Catling 1979). Full specifications of the methodology used to derive this layer are given in Coops & Catling (1997a,b).

The GPS locations of the survey points were input into the GIS and checked for accuracy against aerial orthophotography. Landscape values for each survey point were then extracted using ArcView.

STATISTICAL ANALYSIS

The information-theoretic approach described by Burnham & Anderson (2002) was used to model the data, based on the second-order Akaike's information criterion corrected for small sample size (AIC_c). Burnham & Anderson (2002) recommend the use of AIC_c when the sample size divided by the number of variables is less than 40, which applied in this case. All possible subsets of the five predictor variables were modelled using logistic regression, with presence or absence of the rufous bristlebird as the dependent variable. In addition, 5000 bootstrapped samples were generated from the data set (i.e. resampling the data with replacement) and the AIC_c was computed for each model, refitted to the bootstrap sample. The proportion of times each candidate model returned the lowest AIC_c when fitted to each bootstrap sample was recorded. Calculation of this proportion determines the relative frequency (or π_i) that any candidate model is found to be the best, and provides a measure of relative support for alternative statistical models, which due to the use of bootstrap resampling is robust to the effects of sampling error in the original data. A given Akaike weight (ω_i) is considered as the weight of evidence in favour of a candidate model being the best model out of the set of models considered. In other words, the weights are relative model likelihoods normalized to sum to 1. If no single model is clearly superior compared with the others in a set (i.e. ω_{max} = 0·9), as was the case here, a (weighted) model-averaging approach should be used where inference is based on the entire set of models. Model coefficients are weighted either using Akaike weights or bootstrap selection probabilities; the former were used here.

The predictive performance of the model-averaged model was evaluated using the receiver operating characteristic (ROC) technique. The use of this threshold-independent method has increased in ecological applications in recent years (Manel *et al.* 1999; Marsden & Fielding 1999; Pearce & Ferrier 2000; Osborne, Alonso & Bryant 2001; Luck 2002b; Scott *et al.* 2002).

A ROC curve is a plot of true positive cases (or sensitivity) against corresponding false positive cases (or 1 – specificity) across a range of threshold values (Fielding & Bell 1997). The area under the curve (AUC) provides a measure of discrimination ability, and varies from 0·5 for a model with discrimination ability no better than random, to 1·0 for a model with perfect discriminatory ability (Pearce & Ferrier 2000). ROC analyses were performed using SPSS Version 11·5 (SPSS 1998). The calculation of the AUC and standard error was based on a non-parametric assumption.

A hierarchical partitioning (HP) protocol (MacNally 2000, 2002) was used to identify the predictor variables most likely to influence variation in the dependent variable. Due to the difficulty of dealing with multicolinearity in generalized linear modelling approaches, MacNally (2000, 2002) uses HP to examine the independent, as opposed to joint, contribution of each predictor variable. MacNally (2002) goes further to describe a technique for deciding which predictor variables to retain in the analysis based on a randomization procedure. The final sets of predictor variables selected in each approach (AIC_c and HP) were compared.

Data analyses were run in the R statistical package (Ihaka & Gentleman 1996) using algorithms to calculate the AIC_c, bootstrap frequencies, model-averaged estimates and unconditional standard errors, and to run the HP analysis (Walsh & MacNally 2003).

Results

MODEL SELECTION

Bristlebirds were detected at 30 locations within the study area and the following were calculated: the maximized log-likelihood values [$\log(\mathscr{L})$], number of predictor variables (K), AIC_c values, differences between the model with the lowest AIC_c value and each candidate model (Δ_i), relative Akaike weights (ω_i) and bootstrap selection frequencies (π_i) (Table 1). Note that it is not the absolute size of the AIC_c value but the relative values that are important (Burnham & Anderson 2002). In Table 1, the models are ranked according to their AIC_c differences (Δ_i), from best to worst. Model 1 was indicated to be the best approximating model; however, an Akaike weight of 0·33 suggested substantial model selection uncertainty. The difference in Akaike weights between the first and second ranked models was only 0·09, also indicating strong support for the latter model. According to Burnham & Anderson (2002), models with AIC_c differences between 0 and 2 have substantial support, values of 4–7 have considerably less support, while values greater than 10 have

Table 1. Results of AIC_c-based model selection for the rufous bristlebird; the table also shows maximized log-likelihood function ($\log(\mathscr{L})$), number of predictor variables (K), AIC_c differences (Δ_i), Akaike weights (ω_i) and bootstrap selection frequencies (π_i)

Number	Model*	$\log(\mathscr{L})$	K	AIC_c	Δ_i	ω_i	π_i
1	H + E + Co + Cr	−17·938	5	46·66	0·00	0·333	0·296
2	E + Cr + Co	−19·115	4	46·74	0·09	0·319	0·310
3	H + S + E + Co + Cr	−17·489	6	48·08	1·43	0·163	0·142
4	S + E + Co + Cr	−18·992	5	48·76	2·11	0·116	0·063
5	H + E + Co	−21·393	4	51·30	4·64	0·033	0·038
6	H + S + E + Co	−21·075	5	52·93	6·27	0·014	0·029
7	E + Co	−23·489	3	53·28	6·63	0·012	0·023
8	S + E + Co	−23·486	4	55·49	8·83	0·004	0·002
9	H + S + E + Cr	−23·018	5	56·82	10·16	0·002	0·025
10	H + E + Cr	−24·274	4	57·06	10·41	0·002	0·004
11	H + S + Co + Cr	−24·225	5	59·23	12·57	0·001	0·043
12	H + E	−26·505	3	59·31	12·66	0·001	0·001
13	H + S + E	−25·970	4	60·45	13·80	< 0·001	0·002
14	S + Cr + Co	−26·601	4	61·71	15·06	< 0·001	0·015
15	H + Cr + Co	−26·918	4	62·35	15·69	< 0·001	0·002
16	E + Cr	−28·038	3	62·38	15·72	< 0·001	0·000
17	Cr + Co	−28·559	3	63·42	16·77	< 0·001	0·002
18	S + E + Cr	−27·520	4	63·55	16·90	< 0·001	0·001
19	E	−30·376	2	64·90	18·25	< 0·001	0·000
20	S + E	−30·282	3	66·87	20·21	< 0·001	0·000
21	H + S + Co	−32·150	4	72·81	26·16	< 0·001	0·000
22	H + S + Cr	−33·232	4	74·98	28·32	< 0·001	0·001
23	H + Co	−34·559	3	75·42	28·77	< 0·001	0·000
24	S + Co	−35·748	3	77·80	31·14	< 0·001	0·000
25	Co	−37·157	2	78·46	31·81	< 0·001	0·000
26	H + Cr	−38·954	3	84·21	37·56	< 0·001	0·000
27	H + S	−40·288	3	86·88	40·22	< 0·001	0·000
28	S + Cr	−41·042	3	88·39	41·73	< 0·001	0·000
29	H	−45·153	2	94·46	47·80	< 0·001	0·000
30	Cr	−46·136	2	96·42	49·77	< 0·001	0·000
31	S	−49·575	2	103·30	56·64	< 0·001	0·000

*Model includes variables: H, habitat complexity; S, sun index; E, elevation; Cr, creek; Co, coast.

Table 2. Model-averaged coefficients, unconditional standard errors and standard errors conditional on the best model (model 1) for each variable

		SE	
Variable	Coefficient	Unconditional	Conditional
Constant	4·934	4·908	4·400
Elevation	−0·077	0·026	0·026
Coast	−0·001	0·000	0·000
Creek	−0·018	0·009	0·009
Habitat complexity	0·472	0·511	0·556
Sun index	−0·015	0·042	N/A

essentially no support in terms of explaining variation in the data. That the AIC_c differences of the first four models were within approximately 2 units suggested that all these models were plausible candidates as the best model. Moreover, of the 5000 bootstrap samples generated, model 1 was selected as the best 29·6% of the time ($\pi_i = 0{\cdot}296$), while model 2 was actually higher at 31·0% ($\pi_i = 0{\cdot}310$), further indicating considerable uncertainty in the selection of model 1 as the best model. Summing the Akaike weights for the first four models showed that they represented an approximate 93% confidence set. Clearly, these results indicated that a model-averaging approach was appropriate.

The model-averaged logistic regression coefficients were calculated together with unconditional standard errors and standard errors conditional on the best model (model 1; Table 2). The term 'unconditional' used here means not conditional on any particular model. Unconditional standard errors were calculated using the conditional sampling variances from each model and their Akaike weights. Usually, conditional standard errors are underestimates as a measure of precision because the variance component due to model selection uncertainty has not been included, while unconditional standard errors better reflect the precision of a given model coefficient (Burnham & Anderson 2002). The small differences in unconditional and conditional standard errors observed in Table 2 were likely to be a reflection of the relatively strong support for the best model out of all the candidate models. The high unconditional standard errors of both habitat complexity and sun index suggested that considerable uncertainty existed as to the true effects of these variables on the pattern of rufous bristlebird presence/absence.

Negative associations between bristlebird presence and elevation, distance to coast, distance to creek and sun index, and a positive association with habitat complexity, were observed. The AUC of the ROC plot was 0·969 ± 0·018, indicating that the model could correctly discriminate between rufous bristlebird presence and absence 97% of the time.

HP analysis showed that all the variables considered had significant independent contributions towards explaining the variation in the dependent variable (Table 3). Therefore, all the variables should be retained. The percentage contributions of each variable in Table 3 are shown in decreasing order, with elevation making the highest contribution, followed by distance to coast, distance to creek, habitat complexity and then sun index. The relative importance of variables can also be examined using the information-theoretic approach by summing the Akaike weights for each variable across all models that contain that variable (Burnham & Anderson 2002). In this case, the values were as follows: elevation 0·999, coast 0·995, creek 0·936, habitat complexity 0·549 and sun index 0·301; the same trend was apparent in the HP analysis.

Table 3. Results of HP analyses showing independent percentage contributions for each variable. *Z*-scores calculated as [observed-mean (1000 randomizations)]/SD (1000 randomizations) and statistical significance (*) based on the upper 0·95 confidence limit (Z = 1·65) are also shown

Variable	Contribution	*Z*-score	Significance
Elevation	22·33	18·74	*
Coast	16·27	13·80	*
Creek	9·00	7·13	*
Habitat complexity	7·25	5·15	*
Sun index	3·48	2·08	*

MODEL IMPLEMENTATION IN THE GIS

The logistic regression equation of the final (model-averaged) model:

$$Y = 4{\cdot}934 - 0{\cdot}077(\textit{elevation}) - 0{\cdot}018(\textit{distance to creek}) - 0{\cdot}001(\textit{distance to coast}) - 0{\cdot}015(\textit{sun index}) + 0{\cdot}472(\textit{habitat complexity}) \quad \text{eqn 2}$$

was implemented in the GIS by combining the grid layers of elevation, distance to creek, distance to coast, sun index and habitat complexity as defined by equation 2, using the map calculator function in ArcView Spatial Analyst. The inverse logistic transformation:

$$\text{Probability of occurrence} = \exp(Y)/(1 + \exp(Y)) \quad \text{eqn 3}$$

was then applied to the linear predictor (Y) of equation 2 to transform the predictors from the logit scale to the

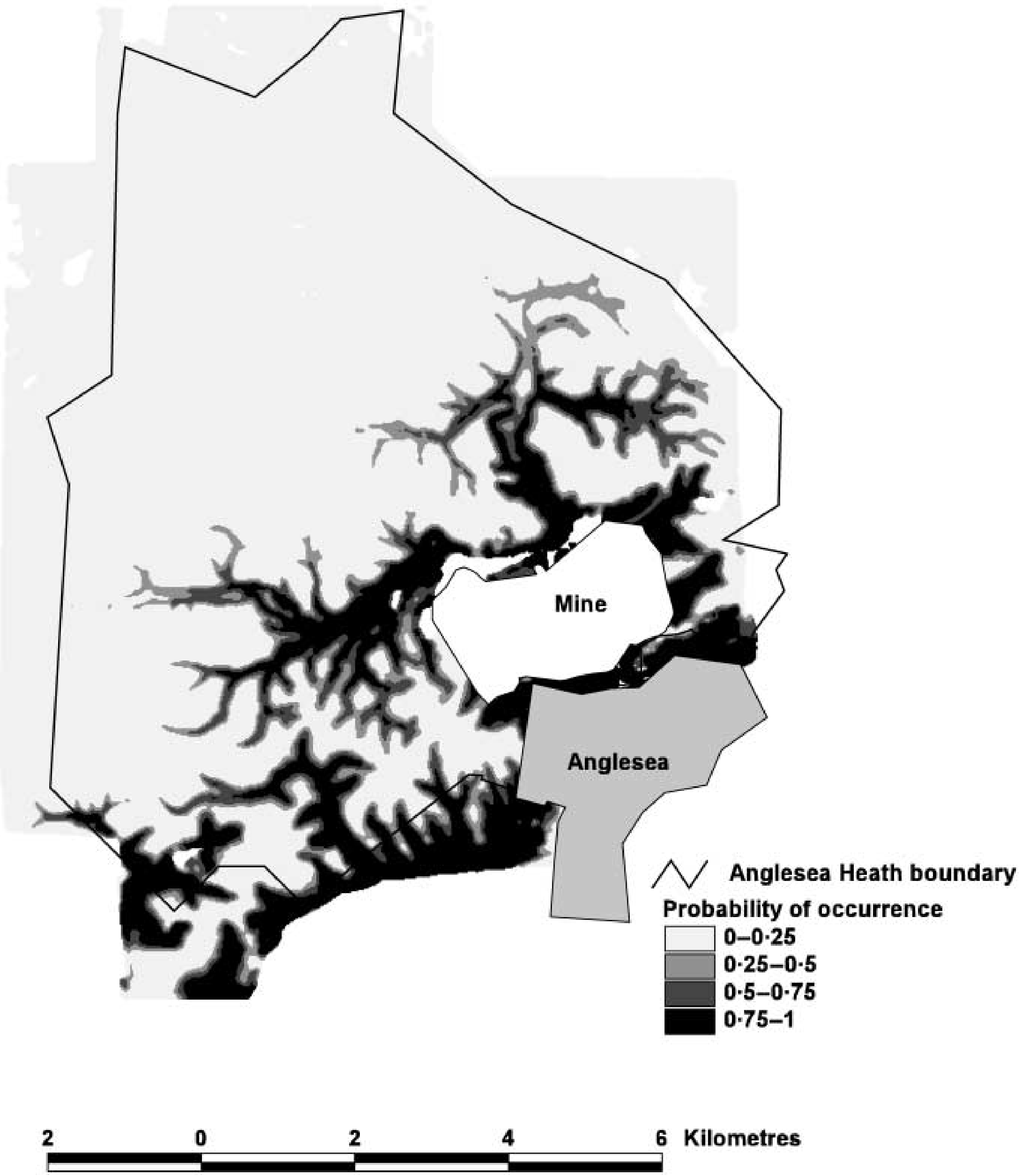

Fig. 3. Habitat suitability model representing an index of the probability of occurrence of the rufous bristlebird.

probability scale. The resulting habitat-suitability model depicted the modelled/fitted probability of rufous bristlebird presence within any given pixel (Fig. 3). The proportion of the study area predicted as suitable habitat for the bristlebird (i.e. probability of occurrence ≥ 0·5) was 16% (Table 4). The majority of the study area (excluding the town and mine) was predicted as low suitability (77·3%), and only a small proportion of the area was predicted as highly suitable (10·1%) (Table 4).

Table 4. Proportion of the total study area predicted as suitable habitat for the rufous bristlebird, as guided by probability of species occurrence. Figures in parentheses represent areas within the Anglesea Heath (excluding the mine area)

Probability of occurrence	Percentage of total area	Area (ha)
0–0·25	77·3 (79·7)	7504 (5420)
0·25–0·5	6·7 (7·4)	647 (501)
0·5–0·75	5·9 (6·1)	573 (412)
0·75–1	10·1 (6·9)	982 (469)

Discussion

HABITAT ASSOCIATIONS

Previous studies have concentrated on identifying habitat requirements of the rufous bristlebird in terms of vegetation composition and structure (Belcher 1992; Peter 1999; Wilson *et al.* 2001). These studies concur that vegetation structure, rather than floristic composition *per se*, is a major determinant of habitat suitability for this species, with areas containing low, dense vegetation preferred. The current study sought to explore both topographic and vegetation attributes that may define habitat suitability for the rufous bristlebird that can be applied at a broader spatial scale. The negative associations between rufous bristlebird presence and increasing elevation, distance to creek, distance to coast and sun index identified in this study suggest that this species prefers areas at relatively low altitude, in close proximity to the coastal fringe and drainage systems, and receiving lower solar radiation. The observed positive association between increasing habitat complexity and rufous bristlebird presence indicates that it also prefers a dense vertical vegetation structure. Although previous studies have identified an association between vegetation density and rufous bristlebird habitat, a preference for lower altitudes had not previously been identified. Rufous bristlebirds have been reported to occur on coastal cliff-tops (Garnett & Reilly 1992; Peter 1999) but these areas are generally lower in altitude than the adjacent inland region. In the Otway Ranges of south-western Victoria, the species has been recorded in the low-lying forested valleys of the region (Emison *et al*. 1987). Also in this region, rufous bristlebirds occur in the heavily vegetated gullies of both coastal and inland habitats (Emison *et al*. 1987; Garnett & Reilly 1992; Smith & Baker-Gabb 1993). In the current study, rufous bristlebirds were similarly located in gullies adjacent to the coast and in close proximity to drainage systems further inland, with 70% of detections within 100 m of a drainage line. Presumably these wetter areas provide denser vegetation preferred by the species. The negative association with sun index indicates a preference for areas that have a gentle slope and southerly aspect. As these areas are exposed to less direct sunlight (in the southern hemisphere), this response is probably related to the moister soil conditions and hence denser vegetation at these sites. Likewise, Wilson, Aberton & Reichl (2001) observed a negative association between the sun index and the presence of swamp antechinus *Antechinus minimus*, a small mammal also preferring dense vegetation.

The rufous bristlebird has previously been associated with coastal habitats, with some records of the species a short distance inland (Emison *et al*. 1987; Smith & Baker-Gabb 1993). In this study, rufous bristlebirds were located up to 5 km inland, with the majority of detections (60%) less than 2 km from the coast. Again, the high density of shrub cover relatively close to the coast (Peter 1999) probably explains the preference for coastal regions. Historical records of the species regularly place it just north-east of the Anglesea Heath (*c.* 9 km inland) from 1979 to 1981 (Atlas of Victorian Wildlife 2001). The first records of the species within the Heath were in 1985 and then 1987 (Atlas of Victorian Wildlife 2001), just 2 and 4 years following the 'Ash Wednesday' wildfires of 1983 that swept through this region. However, these two records came from Salt Creek, an area that was only lightly and patchily burnt and may have provided a refuge for the bristlebird. As the rufous bristlebird has a slow recolonization rate (Smith 1977; Reilly 1991), the population may still be recovering in this area, and this is reflected in the negative association with the variable 'distance from coast'. The most recent record of the species occurring within the Heath prior to this study was in 1999 (Atlas of Victorian Wildlife 2001). In the current study the rufous bristlebird was detected at 20 locations within the Anglesea Heath. However, this survey was not exhaustive, as birds calling from distances larger than 100 m from the surveyed tracks were less likely to be heard, although this did depend on the prevailing weather conditions and the density of the vegetation. Chapman (1999) reports that the call of the eastern bristlebird can carry for about 400 m in still conditions. In situations where an exhaustive search is beyond the resources available, the utility of a predictive distribution model becomes apparent.

MODEL PERFORMANCE

It has been suggested that abiotic environmental variables, in addition to vegetation structure and composition, may improve the accuracy of wildlife habitat descriptions (Dettmers & Bart 1999). In the current study, both abiotic variables describing the topography and a measure of vertical vegetation structure provided the basis for modelling the distribution of rufous bristlebird habitat. The limited number of sites where the species was located (i.e. 30) restricts the number of variables that can be used in the modelling process. While it is certain that additional variables influencing the occurrence of the rufous bristlebird exist, a larger number of 'present' sites are required to explore this possibility. This problem is inherent when modelling rare species using logistic regression, as the ratio of absent to present sites is most likely to be large, with only a relatively small number of present sites ever likely to be discovered. As such, a priori decisions on which variables to include in the analysis based on expert scientific knowledge are crucial.

A small data set also means that the power to detect or distinguish deviations from linearity is small. Moreover, the inclusion of, for example, quadratic terms in the model set, means that when using a model-comparison approach the number of candidate models greatly increases, which is likely to be unproductive with only 30 positive cases. Burnham & Anderson (2002) emphasize the importance of defining a small set of candidate models and state 'Researchers routinely err by building models that are far too complex for the data at hand'. For these reasons, only linear response functions were examined in this study.

Information criteria such as the AIC_c are useful for selecting the best model out of a set of candidate models. However, if the best model is not strongly supported, rather than basing inferences on a single model inferences can be based on the entire set by using model averaging. This concept of 'multimodel' inference reduces model selection bias effects on regression coefficient estimates in all subset selection (Burnham & Anderson 2002). As the essential components of suitable habitat of the rufous bristlebird were unclear, an exploratory approach was taken and all possible subsets of predictor variables were modelled and considered in the analysis. The use of model averaging for the entire set of models meant that all the variables considered were included in the final model. However, the high unconditional errors observed for habitat complexity and sun index suggests that their influence on the dependent variable is relatively weak. The ranked second-best model (model 2), based on Akaike weights, did not include these two variables. Furthermore, model 2 was selected most frequently as the best model in the bootstrapped data set, indicating strong support for this model. However, as the HP analysis recommended that all the predictor variables be retained, this suggests that all the variables were meaningful in terms of their independent contributions (MacNally 2000, 2002).

Post-hoc evaluation of the predictive performance of the selected model is also crucial (Fielding & Bell 1997; Guisan & Zimmermann 2000; Pearce & Ferrier 2000). The majority of ecological modelling studies agree that model evaluation should involve a comparison with independent data (Fielding & Bell 1997; Manel *et al.* 1999; Pearce & Ferrier 2000; Scott *et al.* 2002). In studies involving rare species, such an independent data set is not always readily available, as was the case here. The predictive success of the model-averaged model, as evaluated by ROC analysis, was shown to be high (AUC 0·97), indicating a good fit of the model to the original data. However, habitat modelling is an iterative process whereby the development, evaluation and refinement of models should be ongoing until consistent trends are observed (Luck 2002a). The collection of an independent data set in future studies will allow a full assessment of the adequacy of the model to predict rufous bristlebird presence.

CONSERVATION APPLICATIONS

A predictive distribution model, or habitat suitability model, usually consists of a probability map depicting the likelihood of occurrence of a species (Pereira & Itami 1991; Store & Kangas 2001). The categorization of habitat quality displayed in the spatial model can be used to prioritize areas requiring protection based on their value. This statement is made on the premise that the probability of species presence is positively correlated with the quality of the habitat. Elith & Burgman (in press) discuss the plausibility of making such an assumption and, despite the recognition that some population processes can create considerable noise in the relationship between occupancy and habitat quality, they agree that distribution models are usually the best available representation of habitat.

One disadvantage of using indirect variables, such as those used here, is that a model can only be applied within a limited geographical extent (Guisan & Zimmermann 2000; Austin 2002a,b). This is because the same topographic position in a different region may experience a different environmental gradient (Austin 2002a,b). For example, average temperature and rainfall at a given altitude is likely to vary between regions (Austin 2002b). Similarly, the same species may respond to a combination of a different set of variables in different parts of its distributional range. Within this context, the habitat suitability map provides baseline information about the spatial arrangement of potentially suitable habitat for the rufous bristlebird in the area of concern. In the spatial model, areas predicted as highly suitable (i.e. probability of occurrence $\geq 0{\cdot}75$) are clearly delineated, surrounded by areas of lower quality (Fig. 4).

Drainage systems are likely to be important corridors for rufous bristlebird dispersal, lending significance to 'creeks' as landscape correlates. Gullies extending inland from the coast are likely to be particularly important in linking coastal and inland populations of the bristlebird. Evidence was provided in the current study by the presence of bristlebirds at either end of Hut Gully, a drainage system extending from the southern section of the Anglesea Heath to the coastal fringe. This same area was predicted as highly suitable habitat for the bristlebird. The protection of these potential corridors should be a high priority for management, so that further fragmentation of suitable habitat of the species is prevented.

The inclusion of habitat complexity in the analytical model meant that the spatial model was restricted to the area contained within the available multispectral image. As the importance of this variable in the model was questionable in this study (see above), and given that the acquisition of the imagery for large areas is costly, this variable could be removed to allow for the future application and assessment of the model at a larger spatial scale. The calculation of the AUC of the ROC plot for the best available model excluding habitat complexity (i.e. model 2) showed that it performed equally as well as the model-averaged model (0·967 compared with 0·969).

The effective conservation of the rufous bristlebird in the Anglesea Heath is one of many priorities for its managers (McMahon & Brighton 2002). Given that the proportion of the Heath that was predicted as suitable habitat for the rufous bristlebird (i.e. probability of occurrence $\geq 0{\cdot}5$) was only 13% (881 ha), protection of this area is likely to be crucial to ensure the long-term persistence of this species within the Heath. An important consideration in the development of management guidelines for rufous bristlebird habitat is the inclusion of an appropriate fire regime. Rufous bristlebirds are known to be fire sensitive (Smith 1977; Reilly 1991; Peter 1999) and burning of suitable habitat, particularly the interconnecting gullies, should be avoided where possible. Further work is needed to establish the size and spatial continuity of areas of suitable habitat required by the rufous bristlebird.

In common with all models using predictor variables derived from GIS layers, the selection of variables in the formulation of these models is constrained by the availability of digital data layers that approximate the ecological requirements of the species under investigation (Osborne, Alonso & Bryant 2001; Austin 2002a). While models developed from coarse-grained landscape variables can predict species distribution effectively (Jaberg & Guisan 2001; Osborne, Alonso & Bryant 2001), some studies suggest that predictive success can be improved by the inclusion of more detailed habitat data (Lindenmayer, Cunningham & McCarthy 1999; Manel *et al*. 1999; Osborne, Alonso & Bryant 2001). Unfortunately, finer scaled habitat variables, such as food availability, are unlikely to be captured at a landscape level (Austin 2002a). However, the modelling process could involve two steps whereby a spatially explicit model is first generated using landscape variables extracted from a GIS, and a second model at site level is developed using fine-scale habitat variables measured on the ground. Such multiscale approaches to modelling habitat are not new (Hall & Mannan 1999; Luck 2002a) but studies involving analyses combining both GIS and on-ground variables are rare (Loyn *et al*. 2001). This approach is likely to advance the understanding of the habitat requirements of a species but, due to the time and cost involved in measuring finer scale variables, the first step alone is most likely to be used for conservation planning. Additionally, as a trade-off exists between improving the predictive power of a model by incorporating more detailed data, and the wider application of the model by using more general predictor variables (Luck 2002a), the objectives of the modelling process must be clear. Future research will involve the measurement of finer scale habitat variables in areas occupied by rufous bristle-birds, both in coastal and inland localities, and this information will be incorporated into multiscale models using the above approach.

Acknowledgements

A special thanks to John Aberton, Ros Gibson, Tim Gibson, Gwen Hall, John Hall, Evelyn Jones, Margaret MacDonald, Mike Traynor and Kay Traynor for assistance in the field. The statistical advice of John Aberton, Jane Elith and Michael Scroggie was much appreciated. John Aberton, Janet Gwyther, Graeme Newell and Michael Scroggie provided valuable comments on the manuscript. The research was funded by an ARC/SPIRT grant to B. A. Wilson, D. M. Cahill and J. Hill. The research was conducted under a Department of Natural Resources and Environment Scientific Permit and with ethics approval from Deakin University Animal Ethics Committee.

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Received 20 June 2003; final copy received 5 January 2004