Spatial models of giant burrowing frog distributions

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ABSTRACT: Spatial models of species distributions are becoming a common tool in wildlife management. Most distributional models are developed from point locality data which may limit the modelling process. Habitat variability within a species environment could be included by modelling areas of occurrence rather than point records. This may be particularly important for rare and cryptic species which often have only a small number of known localities. The giant burrowing frog *Heleioporus australiacus* is a threatened and cryptic species in south-eastern Australia. Previous attempts at modelling its distribution have been largely unsuccessful due to the extremely small number of known localities. We aimed to improve knowledge of the distribution of this species in south-eastern New South Wales (NSW) by comparing point- and area-based models. Our area-based model used watersheds as the area unit based on population data for this species. Generalized linear models were used to compare the environmental variables at 37 known localities with a set of 1000 random sites. Model performance was compared using the area under the curve from the receiver operating characteristic curve. Both modelling techniques suggest that the species may be more widely distributed than current records indicate. The species is most commonly associated with dry forest environments with high habitat complexity but avoiding large river valleys, high peaks and steep areas. These trends are consistent with an earlier BIOCLIM model for the species distribution adding support to the influence of these features as important to the species.

KEY WORDS: GIS · Generalized Linear Models · Amphibian · *Heleioporus australiacus*

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INTRODUCTION

Spatial modelling has become a commonly applied tool for wildlife/conservation managers as the technology for geographic information systems (GIS) has developed. The most common application of spatial modelling in this area is the prediction of species distributions on a landscape level. These models are used for a variety of purposes, including determining location and stratification of surveys (e.g. Claridge 2002), identifying key areas for reservation (e.g. Cantu et al. 2004), developing threat control plans (e.g. Meek & Kirwood 2003) and examining the potential impact of climate change (e.g. Meynecke 2004).

Distribution models may be most valuable for the management of rare or cryptic species. Rare and cryp-

tic species, by definition, are often difficult to detect (e.g. Hannon et al. 2004), and datasets for these species are small and mostly derived from a series of opportunistic observations rather than stratified surveys (e.g. Penman et al. 2004). Through successfully predicting sites or areas of occurrence, conservation efforts could be better directed to those habitats which are important for the species.

The giant burrowing frog *Heleioporus australiacus* is a cryptic threatened species in southeastern Australia. It is listed on threatened species legislation in New South Wales (NSW) under the Threatened Species Conservation Act 1995, in Victoria under the Flora and Fauna Guarantee Act 1988 and the Commonwealth Environmental Protection and Biodiversity Conservation Act 2000. This species spends over 97 % of its time

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in naturally vegetated areas at considerable distances from breeding sites (Lemckert & Brassil 2003, Penman 2005), where it remains burrowed below the ground during the day and is active at night when climatic conditions are favourable (Penman et al. 2006a). Areas occupied by this species include dry forest, woodlands and heath communities (Gillespie 1990, Mahony 1993, Lemckert et al. 1998, Penman et al. 2005a). Breeding occurs following heavy summer and autumn rains as the animals move into sites such as hanging swamps, pools in rocky based creeks and occasionally forest dams (Harrison 1922, Gillespie 1990, Mahony 1993, Daly 1996). This unusual behaviour means that this frog is a rarely encountered species.

The giant burrowing frog is a species that would benefit from reliable models depicting habitat requirements and distribution. However, the low number of records has greatly hindered the development of models to predict its distribution. Distribution models using Generalised Additive Models (GAM), have appeared in management documents (NSW National Parks and Wildlife Service 1998, 2000); however, the number of presence sites used by these studies was low (15 and 23, respectively). The models were considered unreliable by the authors due to the small number of sample sites relative to the number of variables used and the poor prediction of known sites. Penman et al. (2005b) subsequently conducted a bioclimatic analysis of the species distribution, which identified broad distribution trends with river valleys, high peaks and coastal lowlands providing unsuitable habitat. These models, however, did not provide detailed information of any value for managers of the species, as most of these areas have been cleared for agriculture and urbanisation or are within inaccessible areas of conservation reserves.

Our study uses 2 modelling techniques in an attempt to predict the distribution of the giant burrowing frog in southeastern NSW and employed an increased number of presence sites and a broader range of environmental variables than previous studies. The new models are compared with existing models of the species distribution to assess whether they improve our understanding of the distribution of the species.

MATERIALS AND METHODS

Distributional models were prepared for the coastal region in the far south of New South Wales, in southeastern Australia (36°48'S, 149°36'E; Fig. 1). This region is referred to as the Eden Management Area (EMA) and was selected as it covers a large geographic area, contains a relatively large number of records of the giant burrowing frog and there are a wide variety

of data layers depicting environmental conditions within this area. Within this region a number of studies of the species have been conducted, and as a result we have a relatively good understanding of the species biology in this area (Lemckert et al. 1998, Lemckert & Brassil 2003, Penman 2005, Penman et al. 2005a,b, 2006a,b). A larger area was not used, as beyond these boundaries records of this species are extremely sparse; for example, to the north there are only approximately 5 records within an area of 500 km² (Penman et al. 2005b).

Two types of models were prepared — point-based models and area-based models. The point-based models compared the environmental conditions for point localities, i.e. those defined by a single *x* and *y* coordinate. As noted above, this type of modelling makes the assumptions that the location where the animal was found is important habitat for the species and that the data being used has been recorded to a high level of accuracy. In contrast, the area-based models calculate environmental data for an area around a species record, in this case the watershed in which the record occurs. Reviews of habitat use patterns by both Semlitsch & Bodie (2003) and Lemckert (2004) highlight the multiple habitat requirements of many anurans that are encompassed only by a broad unit of measure such as a watershed. Radio-tracking studies of this species suggest that populations occupy most areas within a watershed and rarely move outside of the watershed in which they occur (Penman 2005). For these reasons, we consider watersheds to be a biologically meaningful area unit for the giant burrowing frog and an area unit that is applicable to management of this species.

Watersheds were constructed from a 25 m digital elevation model (DEM) of the study area using inbuilt functions of the ArcInfo GIS (ESRI) software. Initially, the DEM was filled to ensure sinks (artefacts of the smoothing processes) were removed, allowing flow direction and flow accumulation to be derived. A stream network was then defined using cells with flow accumulation greater than 100 cells; subsequently, the stream order and streamline functions were applied to produce a vector stream layer. The resulting stream network was similar to existing data layers for the area; however, it was necessary to create the new layer, which was necessary for subsequent steps, as the existing layers did not match the DEM precisely. Within the network, a node formed where two stream arcs met. At each of these nodes, a calculation of the watershed area was conducted and if the area exceeded 20 ha, a watershed was formed as a polygon and the process started again. Twenty ha was chosen as a minimum size because areas smaller than this are too small to create suitable breeding habitat, too small to support a significant population of this species (Penman et al. 2006b) or

Fig. 1. Study site: Eden Management Area (EMA), southeastern New South Wales, Australia

they are of a scale that has little significance within a landscape management context (Penman 2005). This approach resulted in 14 826 watersheds being defined within the study area ranging in size from 20 ha to 173 ha, with an average area of 50 ha. The extremely large watersheds formed along long stretches of large rivers and were excluded from the analysis as this species is known not to occupy such areas (Penman et al. 2006b). Models built from the watersheds are referred to as the area-based models throughout this paper.

Presence sites for the modelling were obtained from State Forests of NSW pre-logging surveys, NSW

National Parks and Wildlife Service (NPWS) wildlife atlas and our unpublished survey records (Fig. 1). The sites in the study area all constitute non-breeding records of the species and were ground tested to ensure they were accurate to within 250 m. For the point-based model, if sites lay within 1 km of another site, the oldest site was retained and the others deleted. Removing these points meant that areas which have been extensively surveyed are not over-represented in the model. A distance of 1 km is considered sufficient to discriminate between sub-populations of this species, if not between populations

(Penman et al. 2005a). This resulted in 37 presence sites and 37 presence areas.

Random sites were created using a random point generator based on a uniform distribution (Jenness 2004) in ArcView GIS (ESRI). It was necessary to use random sites, as it is currently not possible to determine true absence sites for this species due to the low rates of detection, as discussed above. For each type of model, an independent set of 1000 random sites was chosen to create a background sample which was down-weighted in the analysis to create a balanced design (Ferrier et al. 2002, Wintle et al. 2005). A background sample provides a means of assessing the full range of habitats available in the study area and overcomes many of the problems associated with false negatives (Wintle et al. 2005). The random sites were only selected from naturally vegetated areas. By utilising only these areas for random sites, environmental variables influencing the distribution of the species within forests may become more apparent. Random sites were excluded if they were within 2 km of a known giant burrowing frog site to prevent the inclusion of known false negatives.

A variety of biological and physical variables were used in the analyses (Table 1). Due to the different data required for point and area models, some variables were included in only 1 type of model. Variables used in both models were represented as a single value for the point-based models and as mean values for the area-based models. All data layers had a 25 m grid cell resolution and aligned to the DEM.

The list of potential variables is relatively large and it is possible that one of these variables may be significant by chance alone. In selecting factors, preference was given to 'proximal' rather than 'distal' variables (following Austin 2002). Harrell et al. (1996) recommend as a rule of thumb $n/10$ predictor degrees of freedom (PDF), where n is the number of observations in the least prevalent class (in this case, the presence sites). For our data set, this represents approximately 4 PDF. In the process of model building (see 'Statistical analysis'), models were built on sets of 4 or less variables.

We used logistic regression within a generalized linear model (GLM) framework as the primary statistical analysis (Guisan & Zimmerman 2000). GLM

Table 1. Data layers used in the 2 modeling techniques, point and area

Factor	Model type	Description
Solar radiation	Both	Measure of the total solar radiation received in a 12 mo period (NSW National Parks and Wildlife Service 1998)
Wetness index	Both	Estimate of the quantity of water draining to a point in the landscape and the landscape's ability to retain water due to slope (NSW National Parks and Wildlife Service 1998)
Stream order	Both	Defined by Strahler (1952), a rough measure of stream size
Habitat complexity	Both	Following Catling & Burt (1995), provides a measure of structural complexity of the vegetation
Temperature	Both	Average annual temperature, layer derived from the BIOCLIM program
Annual rainfall	Both	Annual rainfall, layer derived from the BIOCLIM program
Elevation	Both	Either a point-based elevation or average for the area
Slope	Both	Measure of either slope at the point or mean slope for the area
Aspect relative to north	Both	Measure of aspect relative to north: either a point measure or the median for the area
Roughness within 1km	Point	Standard deviation of the elevations within a radius of 1 km
Area roughness	Area	Standard deviation of the elevations within the area
Dry forest	Point	Dummy variable derived from habitat type indicating either the presence (1) or absence (0) of dry forest habitat
Proportion of area that is dry forest	Area	Proportion of the area that comprised dry forest communities: values 0–1
Flow accumulation	Area	Measures the number of grid cells flowing to a point. Values taken at the end of the area to provide a quantitative measure of stream size
Topographic position landscape	Point	Measure of where the point lies within the landscape. Numerical measure of gully through to the ridgeline

extends regression modelling to encompass response variables which belong to the exponential family of distributions (McCullagh & Nelder 1989). All analyses were conducted in SAS version 8.2 (SAS).

We utilised binary presence/absence data with 37 presence sites and 1000 absence sites in each model. It is not possible to create abundance scores for the giant burrowing frog at any of these sites, as reliable and comparable survey techniques are not available for this species (Penman et al. 2004). Of the sites used in the analysis, 31 are from observations of 1 frog at each site and the remaining 6 are from observations of 2 (2 sites), 4 (2 sites), 6 (1 site) or 10 frogs (1 site). This variation is a function of survey effort and does not necessarily reflect the abundance of the species at each site (T. D. Penman, F. L. Lemckert unpubl. data).

Each factor was tested using linear and quadratic relationships. Higher order relationships were not examined, due to the relatively low number of presence sites (after Wintle et al. 2005). The models were then built incorporating factors significant at the $p = 0.05$ level. Individual factors and sets of factors were tested with only significant variables included in the final model.

Model fit was then compared using the Receiver Operating Characteristic curve (ROC curve). The ROC curve represents the relationship between the true positive (sensitivity) and the false positive fraction (1-specificity) over a range of threshold values. A good model maximises the sensitivity for low values of the false positive fraction (Woodward 1999). The fit of a model is measured by the area under the curve (AUC) with 0.5 representing an entirely random model. Thuiller et al. (2003) use the traditional academic point system (Swets 1988) as a rough guide for classifying the fit of the model with AUC values. Models with AUC values under 0.70 are considered poor, values of 0.70 to 0.80 are rated as fair, 0.80 to 0.90 as good and those over 0.90 as excellent.

Habitat suitability maps were prepared for the best model for each approach. These are simplistic maps which predict either presence or absence. The classification values or cut-off points were calculated from a plot of the sum of sensitivity and specificity over a range of threshold values. Where this plot reaches its maximum, the model is considered to have the highest discriminatory power (Woodward 1999). If 2 peaks were present, the peak with the higher sensitivity value was used; this minimises the occurrence of false negatives. Using the equations described above and the classification values, spatial models were then prepared with the model builder function within the spatial analyst extension of ArcView GIS.

RESULTS

The final models for the point and the area datasets are presented in Table 2. In the point-based model, the probability of occurrence for *Heleioporus australiacus* was increased in the more complex dry forests and lowered as roughness values increased. A quadratic relationship was seen, with elevation suggesting that the species is more likely to be encountered in the intermediate elevation areas within the study area. AUC for the point model was 0.829, suggesting a good fit. We do acknowledge that this model has 5 variables which exceeded the PDF recommended by Harrell et al. (1996), therefore caution has been taken in interpreting this model. Testing against the global null hypothesis, the model was significant ($\chi^2 = 29.66$, $p < 0.001$). The model based on the area data suggested that the species is most commonly encountered in dry forest areas. This model included a quadratic relationship, with the wetness index suggesting the species is more common in the intermediate wetness values for the study area. Model fit for the area-based model was 0.722, indicating an average to poor fit. Testing against

Table 2. Final models in the GLM analysis for point- and area-based data

Parameter	Estimate	Standard error of the estimate	Wald Chi-squared	p-value
Point model				
Intercept	-6.3074	1.9274	10.7089	0.0011
Roughness	-0.0558	0.0197	8.0332	0.0046
Dry forest	2.1008	0.7639	7.563	0.006
Complexity	0.7003	0.2129	10.8226	0.001
Elevation	0.0141	0.00487	8.348	0.0039
Elevation ²	-0.00001	4.70×10^{-6}	6.8199	0.009
Area-based model				
Intercept	-211.1	100.5	4.4145	0.0356
Proportion of dry forest	1.4854	0.7724	3.6982	0.0545
Wetness	2.8617	1.4024	4.1637	0.0413
Wetness ²	-0.00971	0.00489	3.938	0.0472

the global null hypothesis, the model was significant, ($\chi^2 = 12.04$, $p < 0.001$).

Classification values for these models were different. For the point dataset, the sum plot of sensitivity and specificity peaked at $p = 0.30$ (Fig. 2), at which point sensitivity was 97% and specificity was 57%. Two peaks exist in the area dataset with the first peak at $p = 0.48$ and the second at $p = 0.68$ (Fig. 2). At these points, the sensitivity values were 76 and 42%, respectively, and the specificity values were 59 and 90%. The first point ($p = 0.48$) was chosen as, at this point, the sensitivity values were closest in the 2 modelling approaches, thus allowing for better comparisons of the distributional predictions.

The predicted distributions from the point- (Fig. 3) and area-models (Fig. 4) were broadly similar, although some notable differences were observed. Distributions were only predicted for the forest areas within the region for the reasons outlined above. Within the forested area of the EMA, a much larger area was predicted as suitable by the point model (377 475 ha) than the area-based model (153 686 ha). Many of the forest areas were predicted as suitable in both models; however, the Wadbilligia wilderness area in the north-west of the region and many of the high peaks and several pine plantation areas in the south-west were predicted as unsuitable for the species. Forests immediately to the west and to the south of Eden were predicted as unsuitable to varying degrees in the 2 models. The main differences between the 2 models were the prediction of the Tantawangelo section of the South East Forest National Park, the Dangelong Nature Reserve and the western slopes as suitable in the point model but not in the area-based model.

Fig. 2. Sum of the specificity and sensitivity for the point and area models used to derive classification values for each model

DISCUSSION

Statistical models of amphibian distributions have rarely been presented in the literature (but see Wardell-Johnson & Roberts 1993, Parris & Norton 1997), and where such models have been derived they are usually over smaller geographic areas (e.g. 56.3 km² in Joly et al. 2003). The main difficulty in modelling amphibian distributions has been that most amphibian surveys, hence records, are derived from breeding sites (e.g. Hamer et al. 2002, Parris 2002) which are difficult to model at the landscape scale. Despite their importance there is a limited understanding of the non-breeding habitat requirements for most amphibian species (Lemckert 2004), and spatial models provide a means of assessing habitat requirements of amphibian species on a landscape scale as they are able to incorporate both breeding and non-breeding environments in a single analysis.

The predicted distributions for the giant burrowing frog in this study support the notion that the species occurs more widely than current records indicate. The models suggest that the species occurs in dry forests under 900 m in elevation, but usually above 150 m. The species does not appear to occur in areas that are steep, possibly because such environments are rocky and unlikely to support a suitable soil for the species to burrow into. Alternatively, these areas may not be able to create suitable breeding streams for the species. The models also reflect the unwillingness of the giant burrowing frog to use large streams as breeding sites. Large streams are often associated with river flats and hence low area roughness values. This species is thought to breed only in slow-flowing, small streams (e.g. Harrison 1922, Gillespie 1990, Daly 1996, Penman 2005, Penman et al. 2006b), as the species does not possess the morphological characteristics for swimming, (i.e. long legs and webbed feet Cogger 2000); which would be necessary within larger streams. The association of the species with dry forest habitats predicted in these models is consistent with reports from other studies (e.g. Webb 1987, Lemckert et al. 1998, Penman et al. 2005b).

The trends in the predicted distributions are similar to the BIOCLIM model of Penman et al. (2005a) despite the absence of climatic factors in the point or area final models. Large river valleys (e.g. Bega valley), high peaks (e.g. Mumbulla mountain) and coastal lowlands (e.g. the southeast corner) were generally considered unsuitable in the BIOCLIM, point and area models. The consistency across the modelling techniques suggests that these areas are unsuitable for the species or that sampling to date has been inadequate in these areas. More detailed comparisons are not possible as BIOCLIM models show broad trends in distributions

Fig. 3. *Heleioporus australiacus*. Predicted distribution in the EMA, based on point data. For geographical locations see Fig. 1

and do not account for non-climatic biophysical variables.

Future survey effort for this species should be directed into 2 main areas: those that are consistently predicted as suitable and those that are consistently predicted as unsuitable. Areas that are consistently predicted as suitable include the Nadgee Nature Reserve, Nadgee State Forest, Yambulla State Forest and the majority of the coastal forests. With the exception of the Nadgee Nature Reserve, most of these areas have been subject to relatively high survey effort. As access to the Nadgee Nature Reserve is restricted, particularly during wet periods, surveys for *Heleioporus australiacus* have not

yet been conducted there. Thus, it would be valuable if future surveys for this species were conducted in this reserve. Wadbilliga Wilderness area is predicted as unsuitable by both modelling approaches. There has been little or no survey effort in this area which supports vegetation communities and geologies that are not represented elsewhere within the region (Keith & Bedward 1999). The predicted absences may indeed be true absences or may simply be an artefact of the surveys conducted to date. We recommend that this area be considered a survey priority for the Eden Management Area.

Verification of these models is required to assess their accuracy but this has not yet been possible. Tech-

Fig. 4. *Heleioporus australiacus*. Predicted distribution in the EMA, based on area data

niques such as cross-validation (Agresti 2002) could not be conducted on such a small dataset. Cross-validation builds a model on a subset of the data and then tests the predictive ability of the model on the remaining data. Our sample size was small (37 presence sites) and therefore we could not justify building a model on a reduced number of presence sites. Conducting field surveys to determine the accuracy of the model is difficult. The behaviour of this species is influenced strongly by climatic conditions, and it is difficult to detect even in areas where it is known to occur (Penman et al. 2006a). For example, in 3 yr of intensive surveys, only 4 independent locations were identified

(Penman 2005). Even if this effort could be repeated, such a small number of sites would be insufficient to verify the quality of a statistical model. Only significantly more effort resulting in a greatly expanded number of records would allow for verification of these models. It is recommended therefore that the models be refined when at least 10 new independent records for this species exist within the EMA.

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