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ORIGINAL ARTICLE

Large-scale spatial and temporal dynamics of the vulnerable and highly mobile superb parrot

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ABSTRACT

Aim To investigate the spatial and temporal dynamics of the vulnerable and highly mobile superb parrot (*Polytelis swainsonii*) across its range in south-eastern mainland Australia.

Location South-eastern Australia (27°–37° S latitude and 141°–151° E longitude).

Methods We used generalized additive models (GAMs) to model time-specific bird atlas occurrence data against time-specific plant productivity data, plus a range of environmental predictor variables. We then examined the effects of environmental variables on the temporal and spatial patterns of predicted abundance and distribution of the superb parrot using a correlative mapping approach.

Results Key findings from GAM analysis were: (1) there was a strong positive relationship between abundance and plant productivity in all regions, but (2) the response of abundance to other predictor variables often differed between regions. Correlative mapping predictions of the abundance and distribution of the superb parrot also indicated that: (1) predicted abundance varied through time and space, (2) predicted abundance sometimes decreased in all regions, but at other times some regions had high abundance when others had low, and (3) changes in plant productivity (and therefore climate) were associated with this variation.

Main conclusion The superb parrot favours productive landscapes that are also favoured for agriculture. Movements appear to be associated with seasonal and year to year climate variability. Thus, variation in the recorded abundance of the superb parrot may mask population trends, suggesting that existing population estimates are unreliable. Also, high abundances in some areas, and at some times, may reflect deteriorating habitat conditions elsewhere rather than species recovery. Temporal variability in the distribution of the superb parrot makes it difficult to identify specific drought refugia. Consequently, through time, as key habitat continues to deteriorate, the species will become increasingly vulnerable and threatened. Whole-landscape habitat conservation and restoration strategies are therefore needed to sustain superb parrot populations in the long-term.

Keywords

Climate, correlative mapping, fragmentation, generalized additive modelling, landscape ecology, migration, parrot conservation, plant productivity, *Polytelis swainsonii*, south-eastern Australia.

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INTRODUCTION

Statistical modelling of biological survey data in relation to remotely sensed environmental variables can be a powerful tool for filling in the gaps in knowledge about the distribution of organisms (Ferrier *et al.*, 2002). Such 'correlative mapping' combines occurrence data of a given taxon with predictor variables available for the area of interest to enable the prediction of likely occurrence across its whole distribution (Osborne *et al.*, 2001). However, the utility of correlative mapping is affected by the quality and coverage of occurrence data for the taxon of interest and the predictor variables. Prediction can be further complicated for highly mobile organisms that respond to fluctuations in climate and resources. This is because it can often be difficult to obtain coincident time-specific occurrence data and predictor variables. Furthermore, relationships between the occurrence of a species and predictor variables can be nonlinear or complicated by the effects of unmeasured variables.

In this study, we investigated factors affecting the distribution, movements and abundance of the vulnerable superb parrot (*Polytelis swainsonii*), a highly mobile, fast-flying bird from south-eastern mainland Australia (see Fig. 1; Webster, 1988; Higgins, 1999). Time-specific bird atlas occurrence data were matched and modelled with time-specific plant productivity data, plus a range other key environmental predictor variables, to examine relationships and predict temporal and spatial patterns.

The distribution and movements of the superb parrot within its range (approximately 81,000 km^2) are poorly understood at the macroscale. Regular seasonal movements are documented, but distinguishing between dispersal and migration has not been possible (Higgins, 1999; Garnett & Crowley, 2000). Hence, the superb parrot has been variously described as resident, dispersive, migratory, partly migratory, nomadic or partly nomadic (see Higgins, 1999). Movements and numbers may fluctuate in response to localized resource abundance, such as flowering intensity, and climatic fluctuations (Schrader, 1980; Higgins, 1999). These fluctuations in relation to patchy resources suggest that climate and plant productivity may influence the distribution of the species. Nix (1976) demonstrated that the breeding seasons and seasonal movements of Australian birds were closely coupled with seasonal pulses in plant growth, which in turn are driven by the physical environment in general and climate in particular.

Estimates of the population size of the superb parrot (between 5000 and 8000 individuals) are thought to be unreliable (Garnett & Crowley, 2000), due largely to the lack of understanding of distribution, movements and other factors that underpin them. General trends in the population and responses to smaller-scale habitat modification may be masked by responses to factors at broader scales. This may, in part, explain why Frith & Calaby (1953) believed the future of the superb parrot to be secure, when it now appears not to be.

Two key challenges when undertaking correlative mapping of highly mobile species such as the superb parrot are: (1) obtaining appropriate time-specific data and (2) choosing the scale appropriate to the landscape use of the organism of interest. The best sources of time-specific occurrence data for the superb parrot are the atlases of Australian birds (Blakers *et al.*, 1984; Barrett *et al.*, 2003). Bird atlases provide occurrence data in the absence of more detailed ecological studies (Osborne & Tigar, 1992; Whitehead *et al.*, 1992; Bennett & Ford, 1997), but can also suffer from sparse and patchy survey coverage. They also are often skewed towards centres of human population and contain equivocal presence-only data that may indicate either true absence or a lack of survey data (Osborne & Tigar, 1992). Reporting rates can be used to counteract this effect (Osborne & Tigar, 1992; see below). A net primary productivity index (Australian Greenhouse Office, 2002) was used for matching bird atlas data with time-specific plant productivity.

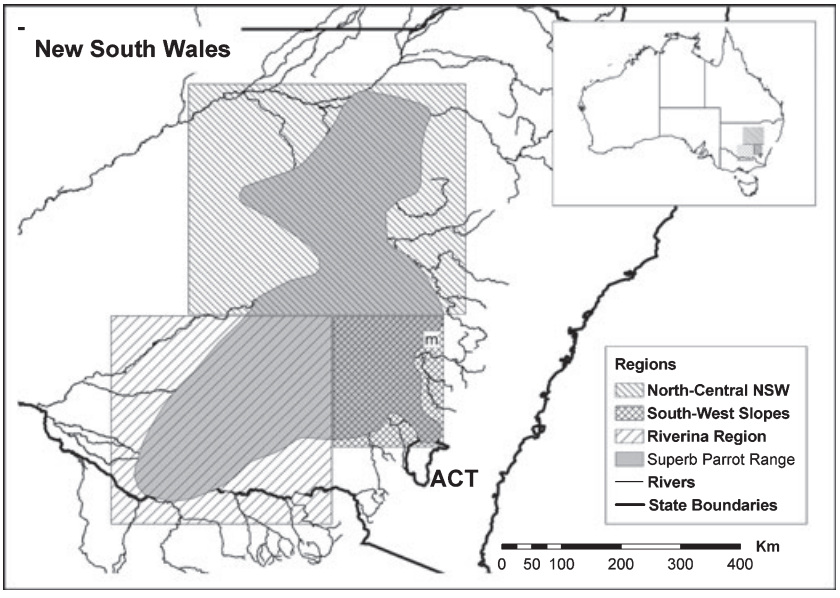


Figure 1 Approximate range of the superb parrot and the three study regions used for the analyses.

Choosing the appropriate scale of analysis in correlative mapping is critical for the highly mobile superb parrot, as they may use 'whole landscapes' (i.e. numerous landscape elements, such as scattered trees and denser woodlands, over a wide spatial area). In addition, the species may perceive landscapes as a continuum, rather than discrete landscape elements, in the more 'variegated' (*sensu* McIntyre & Hobbs, 1999) parts of its range (Manning *et al.*, 2006). Many fragmentation studies have used patch-centred approaches, but have not taken into account the effect of the surrounding matrix (for discussion see McGarigal & McComb, 1995; Jokimäki & Huhta, 1996; Bennett & Ford, 1997; Saab, 1999). However, the validity of extrapolating results from patch-centred studies to landscapes has been questioned (Wiens *et al.*, 1993; McGarigal & McComb, 1995; see also Manning *et al.*, 2004a). To address these issues, bird atlas data across the distribution of the superb parrot were aggregated into 10′ grid cells, or 'landscapes' (*sensu* Bennett & Ford, 1997). This allowed analysis based on landscapes, rather than particular landscape elements, and also provided the key unit for generating reporting rates from the bird atlas data.

This study aimed to: (1) identify key factors that influence the abundance, distribution and movement of the superb parrot, (2) investigate the relationships of these factors with abundance through time and space, (3) develop parsimonious models based on these variables, (4) estimate the abundance and distribution of the superb parrot in past years and seasons, and (5) establish whether there were geographical differences in response to these variables.

METHODS

Study area

The study area encompassed the entire reported distribution of the superb parrot (27°–37° S and 141°–151° E). Due to differences in movements and distributional patterns of the superb parrot within its range (Webster, 1988; Webster & Ahern, 1992; Higgins, 1999), and concerns that the relationship between abundance and environment varies spatially, the distribution was divided into three broad areas (see Fig. 1) based on breeding and residence status: (1) the Riverina of New South Wales, constituting the Murray-Murrumbidgee Valley breeding areas and the surrounding riverine plains, where the superb parrot is generally resident throughout the year (380 landscapes, 106,952 km^2), (2) the south-west slopes of New South Wales in which birds generally only move to breed (120 landscapes, 34,015 km^2), and (3) north-central New South Wales, where many birds are thought to overwinter (525 landscapes, 153,396 km^2).

Atlas data

Observations of the superb parrot were obtained from two atlases of Australian birds (Blakers *et al.*, 1984; Barrett *et al.*, 2003). The survey data covered two 5-year periods: (1) between 1977 and 1981 (termed the 'Old Atlas') and (2) between 1998 and 2002 (termed the 'New Atlas'). In the Old Atlas, observers recorded the presence of birds within 10′ latitude by 10′ longitude grid cells, which are approximately 15 by 18.5 km, with a mean area of 292, 281 and 283 km^2 for north-central New South Wales, the Riverina and the south-west slopes, respectively. In the New Atlas, surveys were recorded at specific locations. Four survey methods were used by observers: (1) searches of two hectare areas, (2) area searches < 500 m, (3) area searches < 5 km, and (4) incidental searches. We aggregated New Atlas data into 10′ grid cells for comparability with Old Atlas data. In addition, 10′ grid cells (henceforth termed 'landscapes' *sensu* Bennett & Ford, 1997) were considered large enough to contain a reasonable number of observations in a significant number of cells, without losing local relevance. Survey coverage in the atlases was uneven, and it was necessary to control for differences in effort. Thus, reporting rates for each landscape and for each season (see below) were calculated. A reporting rate was the number of surveys with a superb parrot present, divided by the total number of surveys for that landscape (as per Osborne & Tigar, 1992).

Observations for two seasons were selected for comparison: winter (June–August) and the breeding season (September–December). Although the breeding season was longer than the winter season, differences in effort were controlled for by the calculation of reporting rates (see above). Surveys which straddled these time periods (Old Atlas only), duplicates and 'incidental' observations (considered presence-only data), were excluded.

Predictor variables

Correlative mapping operates on the assumption that predictor variables are reasonably correlated with habitat features used by the organism of interest (Osborne *et al.*, 2001). In this study, the variables were chosen based on the literature (for example, Webster, 1988; Webster & Ahern, 1992; Higgins, 1999). Variables chosen were: plant productivity, land clearing, roads, rivers/watercourses and terrain characteristics (Table 1). All data were derived using ArcGIS 8.2. 'Year' and 'season' were also included in the analysis to account for variation in abundance between years and the strong seasonal effects in some areas.

Statistical analysis

Due to the large number of variables considered and the lack of prior knowledge about the factors determining the distribution of the superb parrot, an exploratory approach was taken. Generalized additive models (GAMs) were used because with GAMs it is not necessary to define the form of the response functions (e.g. linear, cubic or exponential; Austin & Meyers, 1996), instead the GAM procedure allows the shape of the response curves to be determined by the data (Ferrier *et al.*, 2002). GAMs have a solid statistical foundation (Hastie & Tibshirani, 1987).

Table 1 Predictor variables used for analyses with descriptions, reasons for inclusion and notes on how they were derived

Variable	Description	Rationale	Notes
Land clearing	Percentage of land without woody vegetation in each landscape	The superb parrot is closely associated with trees, and it uses flowers and nectar for food and tree hollows for nesting (Webster, 1988; Webster & Ahern, 1992; Manning *et al.*, 2004b)	Two comparable vegetation data sets were used: one from 1980 and one from 2000 (to match each bird atlas period). Both were represented as percentage land clearing for each 10′ grid cell. 1980 data derived from Landsat MSS images resampled from 50 m to 25 m. 2000 data derived from Landsat ETM^+ images at 25 m (for full specifications see Australian Greenhouse Office, 2002)
Mean plant productivity index	Mean NPP index for each landscape, for each season, in each year	Spatial and temporal variations in resource availability have been associated with fluctuations in numbers and movements of the superb parrot (Schrader, 1980; Webster, 1988; Webster & Ahern, 1992; Higgins, 1999)	This data set was derived using a truncated version of the 3-PG model (for full specifications see Australian Greenhouse Office, 2002). The NPP index data for each month were derived using a combination of shortwave radiation and leaf area index (derived from the NDVI). The NPP indices for each month were summed for each winter and breeding season to produce a cumulative value for each pixel. Then, a mean for the mean NPP index was calculated
Variability in plant productivity index	Coefficient of variation of NPP index for each landscape, for each season, in each year	As above	For this index the value is given as a proportion of 1, where 0 equals no variation and 1 equals maximum variability
Roads	Kilometres of roads in each landscape	The superb parrot has been associated with vegetation along linear features such as roads (Webster, 1988). This may be a sampling artefact related to clearance history because road reserves often retain vegetation lost from the wider landscape (Bennett, 1991). Vegetation along roads is often exposed to less grazing, fertilization and weed spraying and these conditions may allow the growth of grasses and shrubs on which the superb parrot feeds (Webster, 1988)	
Watercourses/rivers	Kilometres of watercourses/rivers in each landscape	The superb parrot is thought to have an association with watercourses in the Riverina, which lessens as they move into the south-west slopes (Frith & Calaby, 1953; Webster, 1988). Watercourses in seasonally drier areas, such those occupied by the superb parrot, can extend growing seasons and associated feeding resources and can act as seasonal refuges during dry conditions (Bennett, 1999)	Drainage channels derived from a 9″ DEM using algorithms (J. Stein, personal communication)
Mean elevation	Mean elevation in each landscape	Included to investigate how distribution was affected by altitudinal gradients. Elevation is correlated with climatic variables such as temperature and rainfall	Derived from a 10″ DEM which fitted exactly within the 10′ landscapes

Table 1 *continued*

Variable	Description	Rationale	Notes
Terrain variability	Coefficient of variation of elevation for each landscape	Variation in aspect and terrain interacts with factors such as soil type, ground water and vegetation and affects plant growth (Nix, 1976). The superb parrot has been associated with productive agricultural landscapes (Davey, 1997) and tree species, such as yellow box and Blakely's red gum (Webster, 1988), that occur in more undulating landscapes (Banks, 1997)	Derived from a 10″ DEM which fitted exactly within the 10′ landscapes. Terrain variability is given as a proportion of 1, where 0 equals flat terrain and 1 equals complex dissected terrain

NPP, net primary productivity; NDVI, normalized difference vegetation index; DEM, digital elevation model.

Three models were produced using S-PLUS (Insightful Corporation, 2002), one for each region (i.e. the Riverina, the south-west slopes, north-central New South Wales). Nonparametric smoothing splines (four degrees of freedom) were used for continuous variables (see Austin & Meyers, 1996), and the response was modelled as a binomial distribution with logistic link and binomial variance. The models were then fitted with backwards stepwise model selection using AIC (Akaike's information criterion; Chambers & Hastie, 1992) to identify the best model. Goodness of fit was assessed using the residual deviance. It should be noted that sparseness in the data will affect the null distribution of the residual deviance and hence its utility as a goodness of fit statistic. Once a model was assessed as adequate it was then used to make predictions of parrot abundances and distributions across each region.

Because the year effect is included additively (i.e. no interaction), the environmental effects (in particular plant productivity) were averaged between years; therefore variation in the relationship between the superb parrot and environmental variables between years could not be detected. It would have been interesting to explore whether this relationship varied between years, and this could have been overcome by fitting a model for each year. Unfortunately, there were insufficient data to do this and interaction would have been rejected due to lack of power. Therefore, modelling showed general responses only. Furthermore, any correlations between productivity and abundance from year to year can be complicated by demographic effects from previous seasons. This has been observed in exploratory analysis.

The fit of the final models was examined by comparing deviance residuals to fitted values. All three models showed small amounts of lack of fit (i.e. larger than expected residuals) for small predicted values, but this appeared to be due to the sparseness of some of the binomial data. Otherwise, the plots were unremarkable. The residual deviance for all models was less than the estimated residual degrees of freedom, indicating no over-dispersion.

Reporting rates and abundance

Mac Nally *et al.* (2004) argue that reporting rates can be used as evidence of changes in abundance. Robertson *et al.* (1995) also concluded that reporting rates are reasonable estimates of abundance for some birds. We assumed that reporting rates and abundance of the superb parrot are significantly correlated (i.e. a greater abundance of superb parrots results in a higher reporting rate). A possible mitigating factor in this assumption is that variation in reporting rates could be driven largely by changes in group structure (for example, the occurrence of many small groups in one year and a few large groups in another), rather than overall abundance. However, this was considered unlikely as the superb parrot is relatively uncommon and is generally seen in small groups. Another complication is possible variation in detectability across its range.

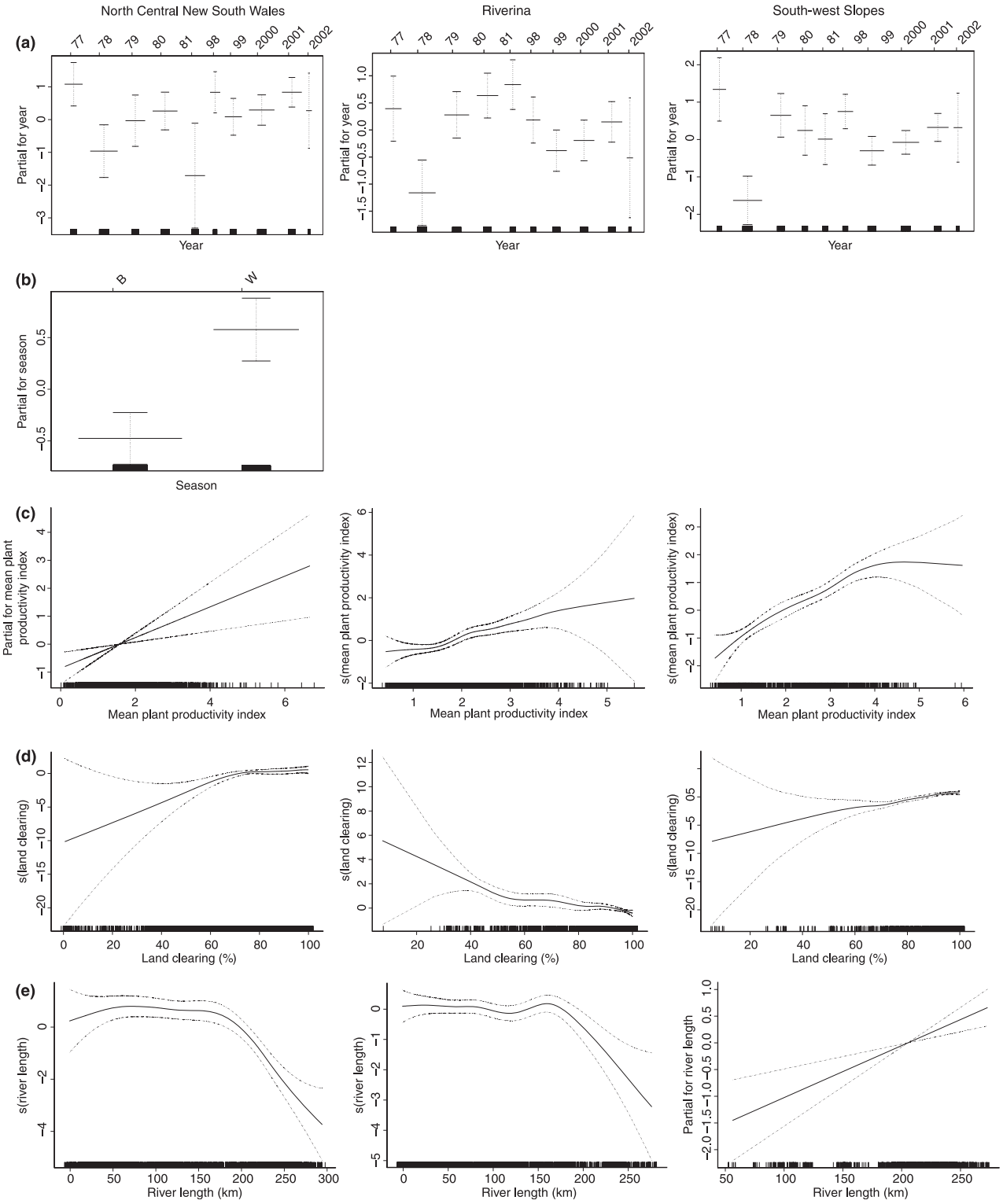


Figure 2 (a)–(i) The response of superb parrot abundance to each term. Partial effect of each term on the abundance of the superb parrot (given the effects of the other terms, s = smoothed): (a) year; (b) season; (c) mean plant productivity index; (d) land clearing; (e) river length (km); (f) road length (km); (g) mean elevation (m); (h) terrain variability. For Fig. 2(a) and (b): the central black line is the response and the perpendicular dashed lines are the point-wise 95% confidence intervals for the mean response and rug plots (short vertical lines) along the *x*-axis show the number of surveys in each year (Fig. 2a) or season (Fig. 2b). For parts (c)–(h): the central black line is the response and the dashed lines are the point-wise 95% confidence intervals for the mean response and rug plots along the *x*-axis show the number and distribution of surveys in relation to the term.

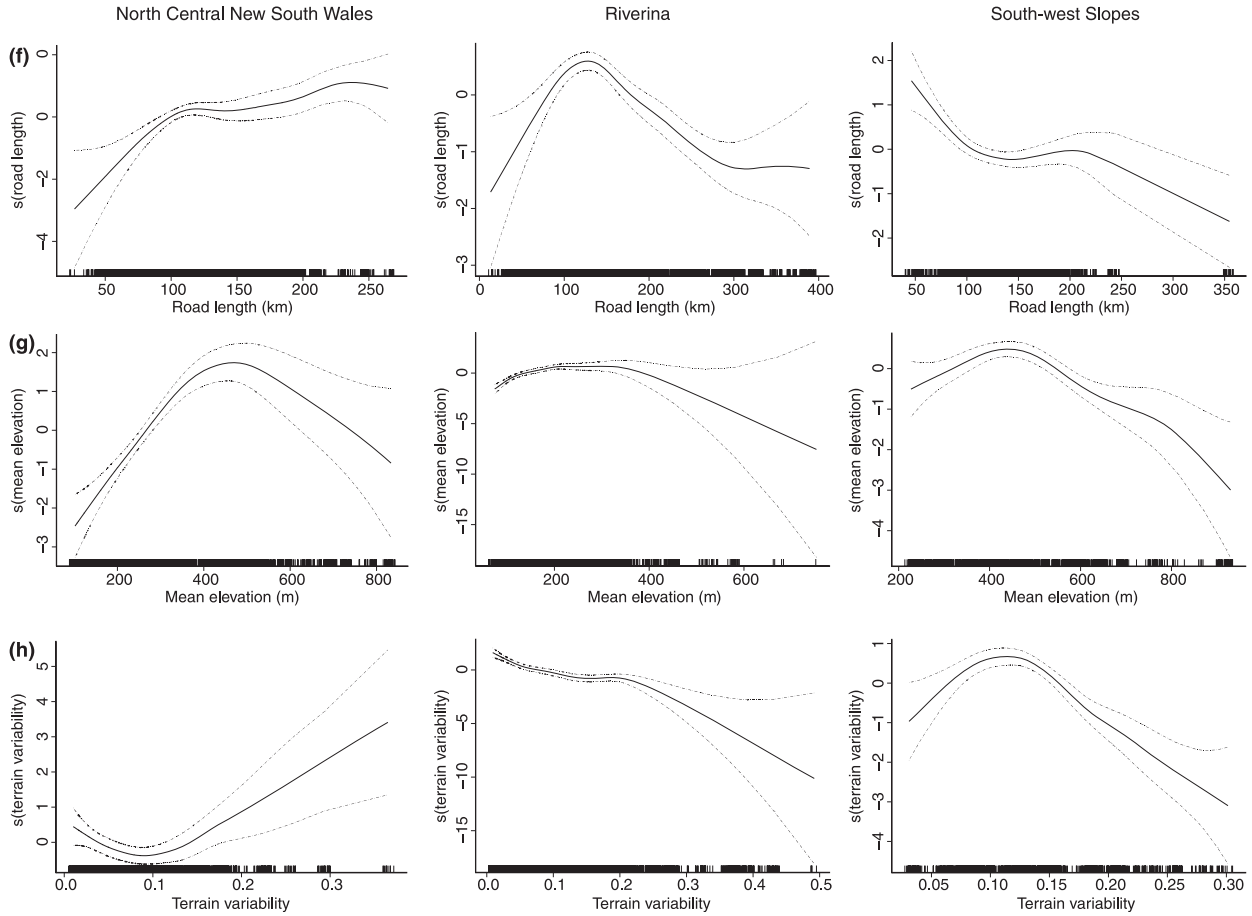


Figure 2 *continued*.

However, this was not expected to be important at the landscape scale, because the superb parrot vocalizes, is not shy of humans and is visually conspicuous. In this paper, abundances of the superb parrot used in modelling (i.e. the response on the *y*-axis) and predictions based on these models will be termed 'abundance', although predictions are essentially predicted reporting rates.

RESULTS

The results fall into two stages: (1) the modelled response of abundance of the superb parrot to the predictor variables, taking into account the other terms (see Fig. 2) and (2) correlative mapping in which predicted abundances and spatial distributions of the superb parrot are illustrated (see Fig. 3).

Stage 1: response of abundance to predictor variables

Year, mean plant productivity index, variability in plant productivity index, land clearing, rivers/watercourses, road, elevation and terrain variability were retained in the final models for each region. Season was retained in the north-central New South Wales model, but dropped from the south-west slopes and Riverina models. The three models were:

1. *South-west slopes:*
year + s(mean productivity) + s(variability in plant productivity) + s(land clearing) + river length + s(road length) + s(mean altitude) + s(terrain variability)
Degrees of freedom: 930 total; 895.16 residual.
residual deviance: 676.44;
2. *North-central New South Wales:*
year + season + mean productivity + s(variability in plant productivity) + s(land clearing) + s(river length) + s(road length) + s(mean altitude) + s(terrain variability)
Degrees of freedom: 2554 total; 2519.24 residual.
residual deviance: 558.97;
3. *Riverina:*
Year + s(mean productivity) + s(variability in plant productivity) + s(land clearing) + s(river length) + s(road length) + s(mean altitude) + terrain variability)
Degrees of freedom: 2470 total; 2432.75 residual.
residual deviance: 1331.94.

In these models 's' represents a smoothed term (see Chambers & Hastie, 1992). Note that a GAM does not provide parameters *per se*, but rather estimates of smooth functions (Fig. 2).

Because of differences in survey methods, comparison of abundances in the Old and New Atlas periods should be done cautiously. Irrespective of this, abundances within atlases

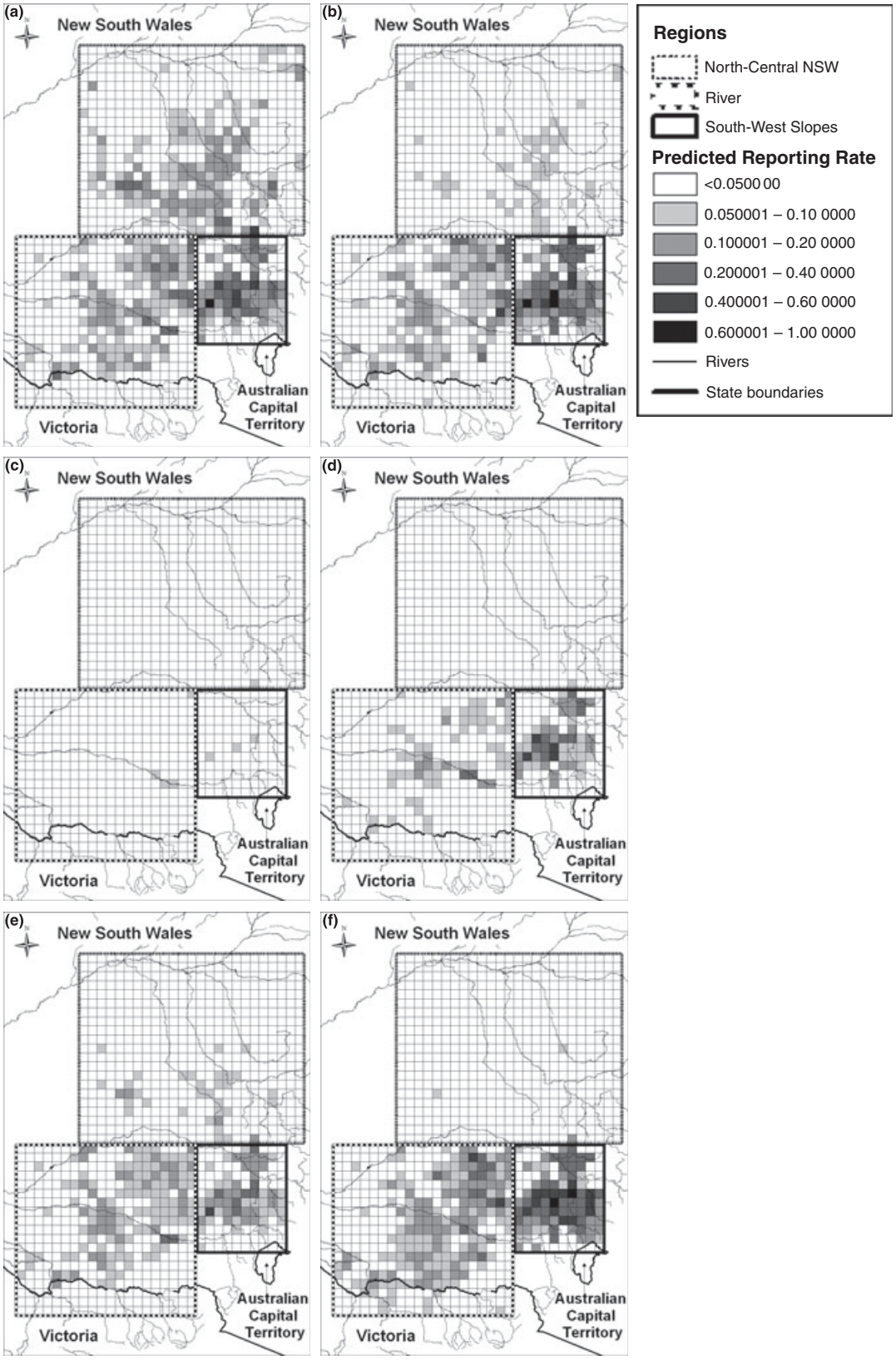
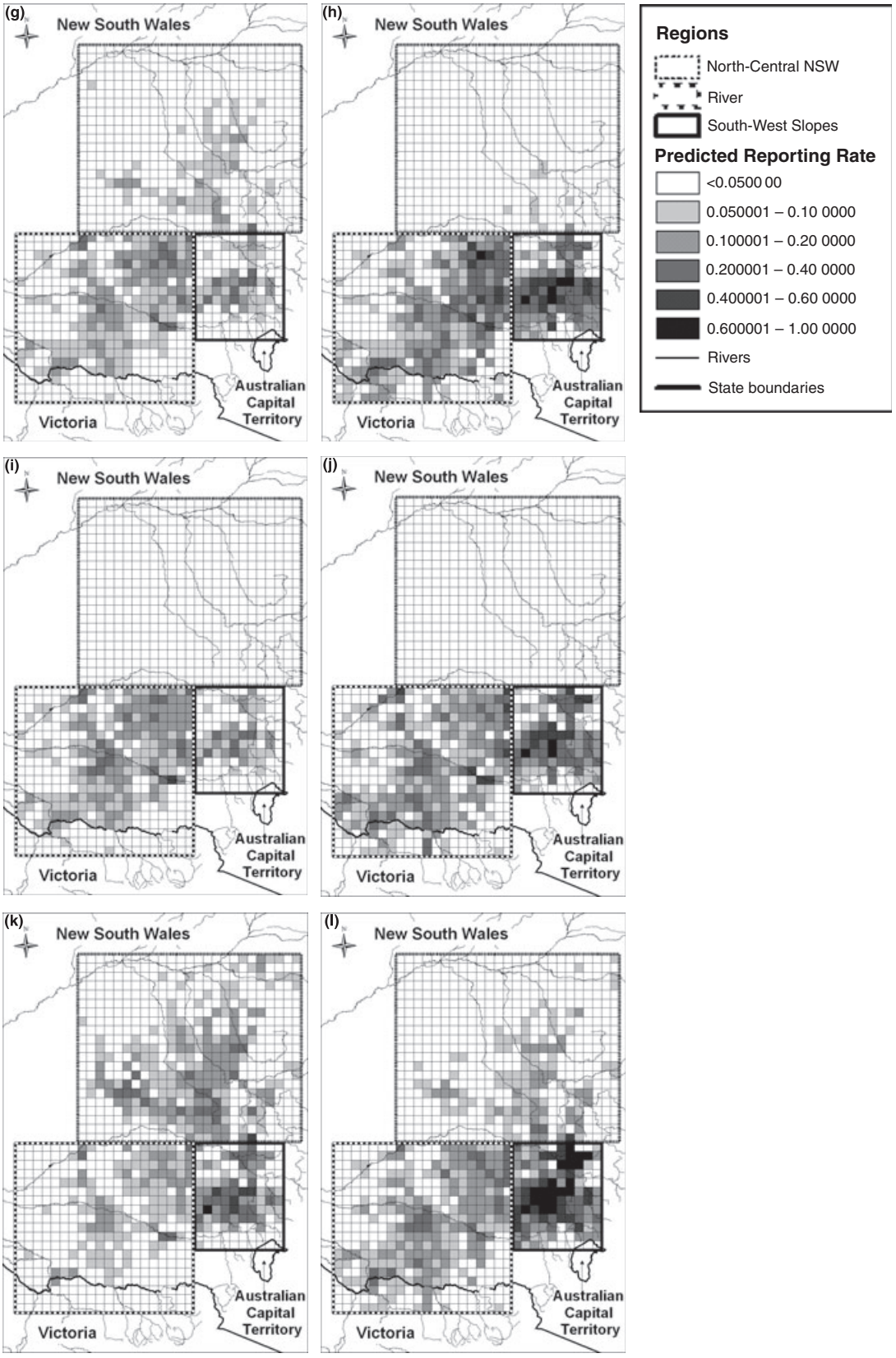


Figure 3 Predicted abundance of the superb parrot based on generalized additive modelling analyses for: (a) winter 1977, (b) 1977 breeding season, (c) winter 1978, (d) 1978 breeding season, (e) winter 1979, (f) 1979 breeding season, (g) winter 1980, (h) 1980 breeding season, (i) winter 1981, (j) 1981 breeding season, (k) winter 1998, (l) 1998 breeding season, (m) winter 1999, (n) 1999 breeding season, (o) winter 2000, (p) 2000 breeding season, (q) winter 2001, (r) 2001 breeding season, (s) winter 2002, (t) 2002 breeding season.



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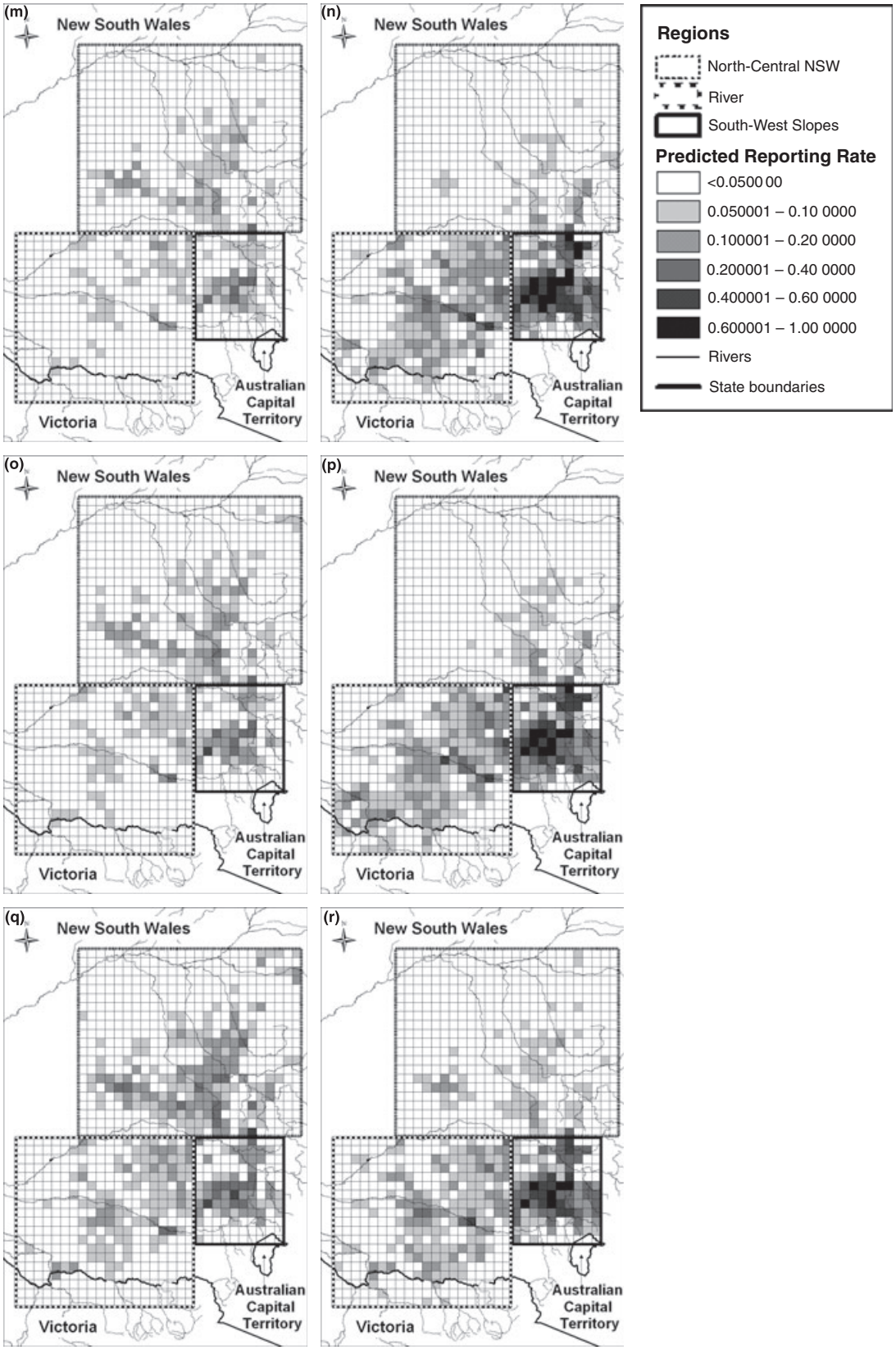

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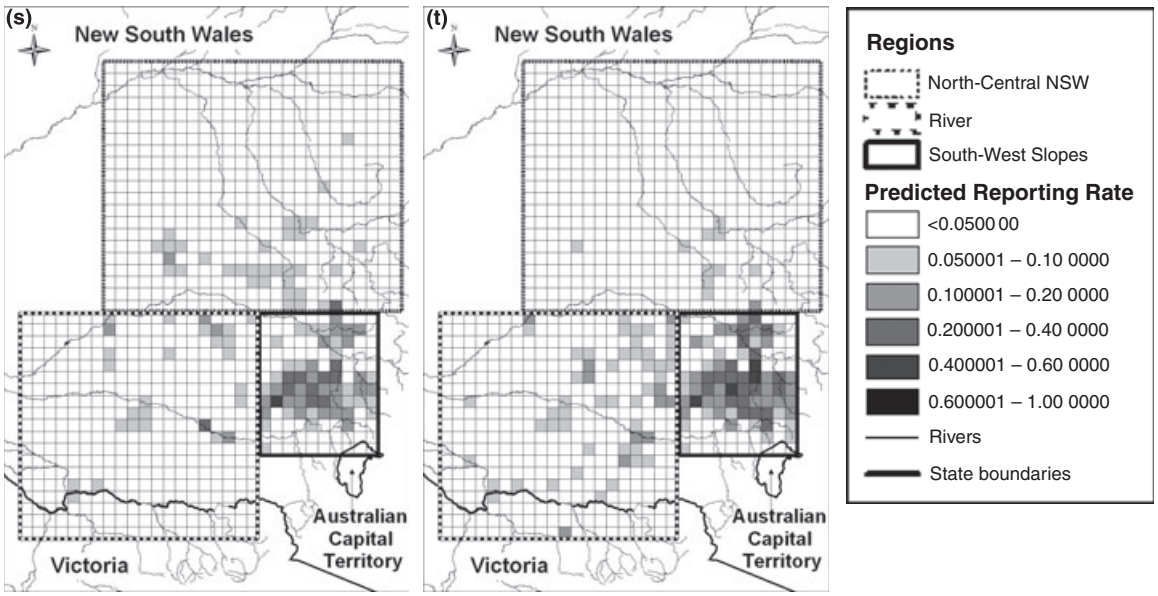

Figure 3 *continued*.

varied greatly between years and seasons for all three regions (Fig. 2a). For example, in the Old Atlas period, parrot abundances were highest in north-central New South Wales and the south-west slopes in 1977 and in 1981 in the Riverina. Abundances were lowest in the Riverina and the south-west slopes in 1978, and 1981 in north-central New South Wales. In the New Atlas period, abundances were highest in 1998 in all regions and lowest in north-central New South Wales and the south-west slopes in 1999 and in 2002 in the Riverina. Season was only retained in the north-central New South Wales model.

Plant productivity had a strong effect on the abundance of the superb parrot in the models in all regions (Fig. 2c). However, variability in plant productivity had little overall effect, and is not shown. The abundances of the superb parrot increased with land clearing in the south-west slopes and north-central New South Wales, but decreased with clearing in the Riverina (Fig. 2d). The response to the other variables (rivers, roads, elevation and terrain variability) was more complex and varied between the regions. River length had little effect on superb parrot abundance in the Riverina and north-central New South Wales until approximately 175 km of rivers per landscape, after which there was a rapid drop off (Fig. 2e). In the south-west slopes abundance increased with river length.

The superb parrot also exhibited different responses to roads in each region (Fig. 2f). In the south-west slopes, abundance decreased as the length of roads increased. In north-central New South Wales, the abundance of the superb parrot increased with roads. In the Riverina, numbers initially increased, then decreased with road length. Elevation had a similar effect in both north-central New South Wales and the south-west slopes (Fig. 2g). Both show an optimum elevation for the superb parrot between *c.* 350 and 550 m. Below 350 m abundance increased with elevation and above 550 m there is a reduction in abundance as elevation increases. In north-central New South Wales the superb parrot also seems particularly averse to low elevation environments. In the Riverina, lower elevations seem to have no effect until approximately 350 m, after which there is a steady reduction in abundance. In addition, the Riverina and the south-west slopes show a general reduction in abundance of the superb parrot as the terrain variability increases (Fig. 2h). In north-central New South Wales, the response is the opposite with increased numbers with terrain variability.

Stage 2: predicted abundance and distribution

There was great variability in predicted abundance and distribution between seasons, years and regions (Fig. 3). Receiver operating characteristic (ROC) curves for the proportions of correctly and incorrectly classified predictions were used to assess the levels of discrimination of the predictions based on the three regional models (Ferrier *et al.*, 2002). All levels of discrimination were high, with 90%, 85% and 85.9% for the predictions for the south-west slopes, Riverina and north-central New South Wales, respectively.

Winter 1977 had high predicted abundance, particularly in north-central New South Wales and the south-west slopes (Fig. 3a). Winter 1978 had low predicted abundance for the superb parrot in all regions, with very low predictions in almost all landscapes (Fig. 3c). Winter 1981 was a poor season in north-central New South Wales (Fig. 3i).

The 1977 breeding season was a good season in north-central New South Wales (Fig. 3b), suggesting that some birds may have remained in the region. The 1978 breeding season was poor in all regions (Fig. 3d). The 1979 breeding

season was reasonably good in the Riverina and the south-west slopes but predicted abundance was limited in north-central New South Wales (Fig. 3f). In the 1980 breeding season, predicted abundance was low in north-central New South Wales but high in the other regions (Fig. 3h). The 1981 breeding season was good in the Riverina and the south-west slopes (Fig. 3j). At the same time, this was the worst season in the Old Atlas period for north-central New South Wales, with 100% of landscapes predicted to have no more that 5% abundance.

Winter 1998 was a good season in all regions (Fig. 3k). Winter 1999 had low predicted abundances in all regions (Fig. 3m). Winter 2002 was poor in both north-central New South Wales and the Riverina (Fig. 3s). In contrast, the situation in the south-west slopes was relatively good (Fig. 3s), suggesting that while fewer birds are predicted to have wintered in north-central New South Wales, some probably stayed in the south-west slopes.

The 1998 breeding season was the best season in all regions for this period (Fig. 3l). Predictions indicate that some birds remained in north-central New South Wales throughout the season. In contrast, the 2002 breeding season was poor in all regions, particularly the Riverina.

DISCUSSION

The GAMs indicate that: (1) there was a strong positive relationship between abundance and plant productivity in all regions but (2) the response of abundance to other predictor variables often differed between regions. The correlative mapping predictions of parrot abundance and distribution also indicate that: (1) the predicted abundance of the superb parrot varied in time and space, (2) the predicted abundance sometimes fell in all regions, but at other times some regions had high abundance when others had low, and (3) changes in plant productivity (and therefore climate) were associated with this variation.

Response of abundance to predictor variables

The superb parrot was associated with more productive landscapes in all regions, and these landscapes are also highly valued for agriculture. Remnant vegetation in these areas is poorly protected. For example, the south-western slopes and Riverina bioregions are the areas with the fewest reserves in New South Wales and much of the area which is reserved is on low-productivity, upland areas (Benson, 1999). These latter areas are least-favoured by the superb parrot. Habitat loss as a result of agricultural intensification is thought to have contributed to a decline in the abundance of the superb parrot (Higgins, 1999).

In the Riverina, the abundance of the superb parrot decreased with increased land clearing, as might be expected This region had the most clearing (92.3%) of the three, and the landscapes are much more open and treeless, in part due to natural conditions (grassland) and also because large paddocks have been cleared, and often the only remaining large eucalypts are along watercourses. Given this, the increase in the abundance of the superb parrot in the south-west slopes and north-central New South Wales with increased land clearing may seem counterintuitive, considering the strong association of this species with woodlands (see Webster, 1988; Webster & Ahern, 1992; Higgins, 1999). However, this may be explained by patterns of vegetation clearance and the resolution of land clearing data. In the south-west slopes and north-central New South Wales, scattered and isolated trees left after thinning and grazing, but not total clearing, of woodlands, are a common feature of the landscape (Ozolins *et al.*, 2001; Gibbons & Boak, 2002). The characteristics of favoured landscapes in the south-west slopes (those supporting lower tree cover and higher plant productivity) are consistent with studies that show that the superb parrot uses modified scattered box-gum woodlands, containing species such as yellow box (*Eucalyptus melliodora*), Blakely's red gum (*Eucalyptus blakelyi*) and white box (*Eucalyptus alba*) (Manning *et al.*, 2004b, 2006). In the past, it has sometimes been assumed that remnant trees and small patches in the agricultural 'matrix' (i.e. where agriculture is the dominant land use) had little conservation value (for discussion see Guevara *et al.*, 1998; Reid & Landsberg, 1999; Ozolins *et al.*, 2001). However, scattered paddock trees not only have high ecological value for the superb parrot (see Manning *et al.*, 2004b, 2006) but also many other species (e.g. Fischer & Lindenmayer, 2002). Land clearing data used in this analysis provide a reliable index of gross vegetation cover/clearing; however, these data appeared to miss many scattered trees. Therefore, less tree cover may mean more scattered trees for the superb parrot. This sort of habitat is threatened by lack of tree regeneration, rural tree dieback, removal of trees and collection of firewood (see Manning *et al.*, 2004b; Manning, unpublished thesis and references within). These issues pose a serious threat to the long-term sustainability of superb parrot populations.

The response to rivers, roads, elevation and terrain variability was complex and varied between regions. This was not unexpected, as organisms can respond differently in different parts of their range. For example, two species of Australian arboreal marsupial, the yellow-bellied glider (*Petaurus australis*) and the greater glider (*Petauroides volans*) respond quite differently to landscape conditions and other factors in southern Victoria than in southern New South Wales (Lindenmayer, 2002). Similarly, Lindenmayer *et al.* (2001) found that population and distributional responses of the common ringtail possum (*Pseudocheirus peregrinus*) and the sacred kingfisher (*Todirampus sanctus*) varied markedly between native forest/plantation and woodland landscapes located just 15–30 km apart.

Road reserves are less intensively managed than surrounding private agricultural land. This allows grasses and shrubs to grow and set seeds that the superb parrot feeds on (Webster, 1988; A.D. Manning, personal observation). In the south-west slopes, the abundance of the superb parrot decreased with road length. This implies that the superb parrot depends on

elements in the wider landscape, such as scattered trees (see above), rather than roadside vegetation alone. In north-central New South Wales, there was a positive relationship between the abundance of the superb parrot and road length. This could be because the roads were providing better habitat than the surrounding agricultural landscape. It also could be partially explained by: (1) the low number of bird observers in this region (particularly in winter), (2) many surveys are along roads, and (3) road density is the lowest of the three regions. The response to roads in the Riverina was complex and difficult to interpret.

The responses to terrain variables indicate that the superb parrot was found in low to moderate elevations and in landscapes of limited relief. This negative response in relation to increased elevation towards the east and south of these regions probably reflects a combination of poorer soils with lower temperatures at higher elevations – all of which affect plant productivity and types of vegetation.

Interannual variation

Fluctuations in plant productivity were associated with spatial and temporal variation in abundance, distribution and, by implication, movements of the superb parrot. Schrader (1980) argued that migration routes and abundances of the superb parrot were influenced by the availability of blossom. It has been shown that *Eucalyptus* flowering varies spatially (Wilson & Bennett, 1999) and is influenced by variation in climate in preceding years (Porter, 1975,1978). The results of this study support suggestions by Schrader (1980) and Webster & Ahern (1992) that the superb parrot may be influenced by variation in the favourability of different seasons.

Climatic variability (and its effect on plant productivity) is the most likely explanation for interannual variation in abundance and distribution. The Southern Oscillation index (SOI) is a key driver of climate variability in Australia and is linked to rural productivity, particularly in Queensland and New South Wales (Commonwealth Bureau of Meteorology, 2003a). When the SOI is strongly negative it indicates an El Niño episode where the climate is much drier (Commonwealth Bureau of Meteorology, 2003a,b). Nix (1976) argued that bird breeding seasons and migratory movements were closely coupled to seasonal pulses in plant productivity. Porter (1975, 1978) demonstrated that climatic conditions in preceding years affected the growth and flowering of red ironbark (*Eucalyptus sideroxylon*) and associated honey production. Porter (1978) argued that this could affect the movements, feeding and breeding of birds. Hence, there can be a lag in the time it takes for climate to affect birds. Thus the changes in the abundance and distribution of the superb parrot shown in this study may be influenced by the climate in preceding years.

In 1981, the abundance of the superb parrot was the lowest in north-central New South Wales of all years, yet abundance in the Riverina was at its highest (see Fig. 2a). Predictions for the Riverina in particular show little change between both winter and breeding season. These patterns may reflect a response to the onset of drought conditions, and predicted abundances indicate that the superb parrot remained in, or retreated to, the Riverina – possibly to the riparian areas. In 1982 there was a severe drought (Smith *et al.*, 1992). However, this was probably the culmination of poor rainfall conditions in the preceding years (Smith *et al.*, 1992). The SOI in 1982 was severely negative, but not for a sustained period in 1981 (see Commonwealth Bureau of Meteorology, 2003c). The effect of drought may also be seen in 2002 (where the SOI was negative for a sustained period; see Commonwealth Bureau of Meteorology, 2003c) and all areas appear affected with low predicted abundances. While results in 2002 may have been influenced by fewer surveys (because it was the end of the New Atlas project), overall results suggest that the superb parrot was affected by drought, but the nature of the response varied with the year or sequence of successive years.

Interseasonal variation and predicted abundance

Generally, the predicted abundance and spatial distribution of the superb parrot in the south-west slopes and the Riverina was reduced in winter while at the same time there was an increase in north-central New South Wales. In the breeding season, the opposite occurred and predicted abundance and spatial extent increased in the south-west slopes and the Riverina and reduced in north-central New South Wales. However, in some years the superb parrot was predicted to occur in north-central New South Wales during the breeding season. This indicates that, contrary to current understanding, the superb parrot may breed in this area in favourable years. Predictions support the belief that the superb parrot occurred in low numbers in the centre and west of the south-west slopes in winter and bird atlas data support this conclusion.

Geographical differences and conservation approaches

The modelling and predictions of abundance and distribution revealed geographical differences in responses to landscapes between the regions. This highlights the need for consideration of different conservation measures appropriate to particular regions and areas. For example, the superb parrot in the Riverina uses flight paths connecting breeding areas and feeding areas (see above and Webster, 1988; Webster & Ahern, 1992), whilst this study (and others; Manning *et al.*, 2006) suggests that the superb parrot in the south-west slopes (and probably north-central New South Wales) has a broader use of the whole landscape.

Population estimates and conservation status

The abundance of the superb parrot in the south-west slopes was consistently predicted to be high. This indicates that the

south-west slopes area is of higher conservation value for this species than has been previously realized. This is strongly supported by systematic field surveys in the region, which showed that the superb parrot is found throughout the agricultural matrix (Manning *et al.*, 2006). While the importance of this region to the superb parrot may not have been fully realized, this may be a result of other parts of its range becoming less favourable. Furthermore, variation in abundance in response to climatic variation may mask long-term population and distributional trends in relation to threats such as habitat loss. Understanding the effects of habitat changes on the superb parrot is made more complex by responses to intra- and interannual fluctuation in plant productivity. For example, irruptive population aggregations and fluctuation in response to localized food abundance cannot necessarily be interpreted as 'species recovery', and may simply reflect: (1) short term abundance of localized resources in relation to macroscale variation in climate/plant productivity and/or (2) relatively poor climatic conditions elsewhere (e.g. drought) and/or degradation of habitats elsewhere causing relocation to other areas.

CONCLUSIONS

Climate change and its interaction with habitat loss could threaten the persistence of the superb parrot. Webster & Ahern (1992) argued that if the population fluctuated in response to the favourability of different seasons, the species could be vulnerable if numbers were reduced after drought. The combination of a restricted range (Forshaw & Cooper, 1981), ongoing habitat loss and response to climatic fluctuations suggest that the superb parrot is at risk. Widespread and continuing habitat loss as a result of tree senescence, dieback, clearing (particularly for firewood) and lack of regeneration are clearly threats to the long-term survival of the superb parrot (see Webster, 1988; Webster & Ahern, 1992; Higgins, 1999; Manning *et al.*, 2004b).

The variability of climatic conditions means that the spatial location of 'refugia' could be different at different times. Therefore, conservation of remaining habitat, including scattered trees, as well as restoration must be implemented throughout the range of the superb parrot. In addition, increases in the frequency and severity of droughts associated with climate change (Australian State of the Environment Committee, 2001), might be expected to exacerbate the risk to the superb parrot. Therefore, targeted preservation of specific refugia is not possible and landscape-scale conservation and restoration measures are essential.

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