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Managing the long-term persistence of a rare cockatoo under climate change

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Summary

1. Linked demographic-bioclimatic models are emerging tools for forecasting climate change impacts on well-studied species, but these methods have been used in few management applications, and species interactions have not been incorporated. We combined population and bioclimatic envelope models to estimate future risks to the viability of a cockatoo population posed by climate change, increased fire frequency, beak-and-feather disease and reduced management.

2. The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* is restricted to Kangaroo Island, Australia, where it numbers 350 birds and is managed intensively. The cockatoo may be at particular risk from climate change because of its insular geographic constraints and specialised diet on a single plant species, *Allocasuarina verticillata*. The cockatoo population model was parameterised with mark-resight-derived estimates of survival and fecundity from 13 years of demographic data. Species interactions were incorporated by using a climate-change-driven bioclimatic model of *Allocasuarina verticillata* as a dynamic driver of habitat suitability. A novel application of Latin Hypercube sampling was used to assess the model's sensitivity to input parameters.

3. Results suggest that unmitigated climate change is likely to be a substantial threat for the cockatoo: all high-CO_2-concentration scenarios had expected minimum abundances of <160 birds. Extinction was virtually certain if management of nest-predating brush-tail possums *Trichosurus vulpecula* was stopped, or adult survival reduced by as little as 5%. In contrast, the population is predicted to increase under low-emissions scenarios.

4. Disease outbreak, increased fire frequency and reductions in revegetation and management of competitive little corellas *Cacatua sanguinea*, were all predicted to exacerbate decline, but these effects were buffered by the cockatoo population's high fecundity.

5. Spatial correlates of extinction risk, such as range area and total habitat suitability, were nonlinearly related to projected population size in the high-CO_2-concentration scenario.

6. *Synthesis and applications*. Mechanistic demographic-bioclimatic simulations that incorporate species interactions can provide more detailed viability analyses than traditional bioclimatic models and be used to rank the cost-effectiveness of management interventions. Our results highlight the importance of managing possum predation and maintaining high adult cockatoo survival. In contrast, corella and revegetation management could be experimentally reduced to save resources.

Key-words: beak-and-feather disease, bioclimatic envelope, *Calyptorhynchus lathami*, climate change, glossy black-cockatoo, management, population viability analysis, revegetation, wildfire

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Introduction

Climate change may be one of the most potent extinction drivers in the future, especially because it can exacerbate existing threats, and there is an urgent need for conservation science to improve tools to predict species' vulnerability to climate change (Sekercioglu *et al*. 2008). One popular approach is the use of bioclimatic envelope models (BEMs), also known as species distribution models. These models use associations of present-day distributions with climate to forecast changes in species' bioclimatic envelopes (Pearson & Dawson 2003). BEMs have, in some cases, been used to assess extinction risk for thousands of species under climate change scenarios (e.g. Sekercioglu *et al*. 2008). However, predictions from these models are of constrained value because they (i) are correlative and yet typically require extrapolation to environmental space that is beyond the bounds of the statistical fitting (Thuiller *et al*. 2004); (ii) use range area type estimates to infer extinction risk rather than measuring threat to population persistence (Fordham *et al*. 2011); (iii) suffer from model selection uncertainty (Araújo & Rahbek 2006); and (iv) do not consider biotic interactions (e.g. Araújo & Luoto 2007).

Spatially explicit population-modelling techniques that link demographic models with BEMs are being used to add ecological realism to correlative BEM forecasts (Huntley *et al*. 2010). Combining quantitative population models and BEMs provides a more mechanistic and probabilistic approach compared to modelling distribution alone, because it links demographic parameters to climate and other explanatory variables and explores a range of uncertain outcomes using stochastic simulation (Brook *et al*. 2009). Several studies have combined habitat and population models to assess population viability (e.g. Akçakaya *et al*. 2004), but few analyses have coupled population and bioclimatic models to estimate extinction risk in the context of climate change (Keith *et al*. 2008; Anderson *et al*. 2009; Fordham *et al*. in press), and this methodology has rarely been used in birds (but see Aiello-Lammens *et al*. 2011). Ideal case-study species for this approach are those with long-term estimates of vital rates (and their variance), representative occurrence data over their geographic range and detailed knowledge of the environmental drivers influencing range and abundance.

The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* Temminck (GBC) formerly inhabited mainland South Australia, but now survives only on Kangaroo Island (located off the southern coast of central Australia) and is considered 'endangered' by the Australian government (DEH 2000; Fig. 1). When the GBC recovery program began in 1995, the cockatoo population comprised *c*. 200 individuals. From 1998 to the present, the intensively managed population has increased gradually to the current estimate of c. 350 birds (Pedler & Sobey 2008). The GBC's specialised habitat requirements and slow life history make it inherently vulnerable to decline (Cameron 2006), and its small population size and insular geographic constraints (single location) put it at high risk from population-wide catastrophes such as fire and disease (Pepper 1997). High-quality *Allocasuarina verticillata* Lam. L.A.S. Johnson, drooping

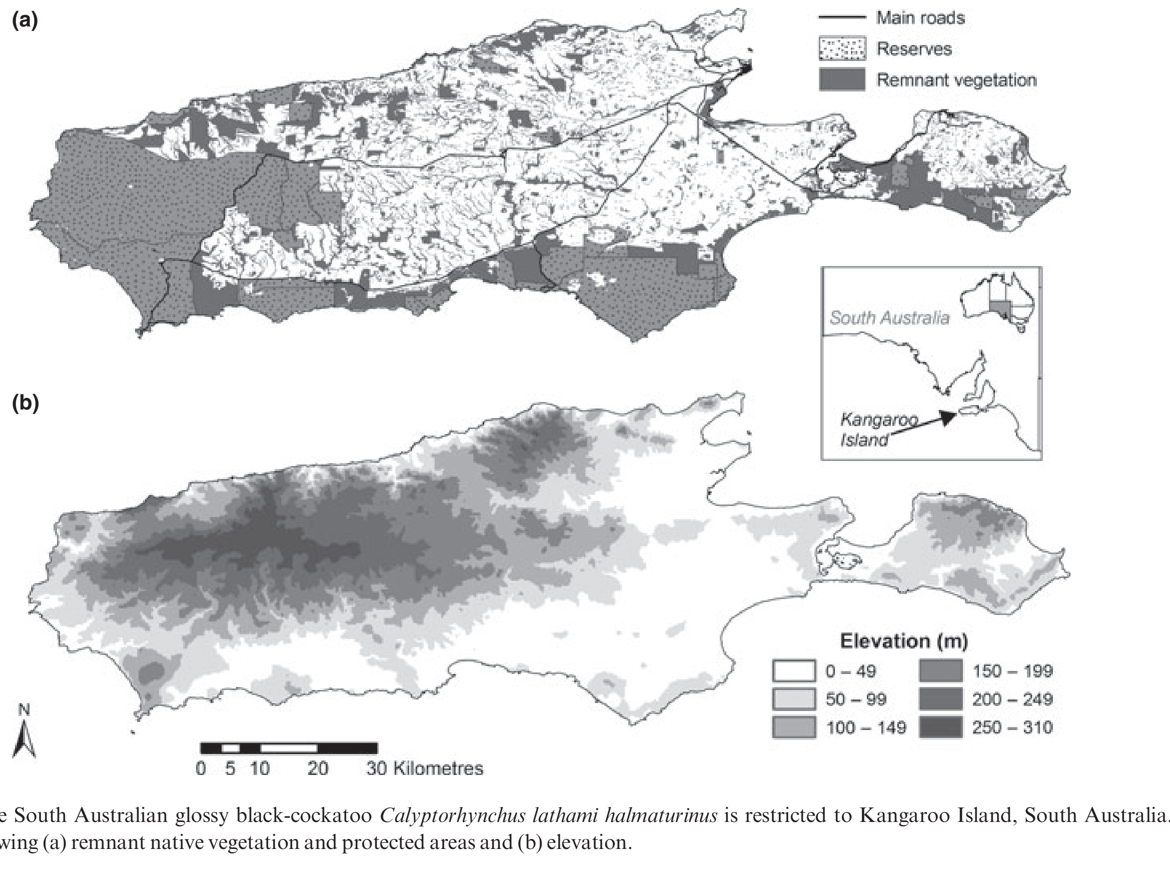

Fig. 1. The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* is restricted to Kangaroo Island, South Australia. Maps showing (a) remnant native vegetation and protected areas and (b) elevation.

she-oak, woodlands provide food and cover that are critical to the survival of the GBC; indeed, *A. verticillata* seeds make up 98% of the GBC's diet (Chapman & Paton 2006). Hollow-bearing eucalypts (primarily *Eucalyptus cladocalyx* F. Muell and *E. leucoxylon* F. Muell), which take many decades to mature and may be vulnerable to fire, are required for nesting (Crowley *et al*. 1998).

The GBC faces an interacting set of current and future threats including nest competition and predation, wildfire, climate change and disease (Mooney & Pedler 2005). GBC recruitment can be severely impaired by nest predation from arboreal brush-tail possums *Trichosurus vulpecula* Kerr. Protecting nest trees from possum predation by fitting metal collars and pruning adjacent tree crowns increased nest success from 23 to 42% (Garnett, Pedler & Crowley 1999). Approximately, 45% of nests are now placed in artificial hollows fitted by managers. Little corellas *Cacatua sanguinea* Gould and honeybees *Apis mellifera* L. are nest competitors that are also managed (Mooney & Pedler 2005). Wildfires are another threat that can kill nestlings and destroy large areas of habitat (Sobey & Pedler 2008). Kangaroo Island is expected to warm by 0·3–1·5 °C and receive 0–20% less rainfall by 2050 compared to 1990 levels, under a mid-range greenhouse-gas emissions scenario (CSIRO 2007). Climate change is likely to threaten the GBC by causing *A. verticillata*'s climatic niche to shift and compress southwards towards the southern ocean boundary (Stead 2008), causing heat- and drought-induced mortality (Cameron 2008) and an increased frequency of extreme events, such as fire and drought (Dunlop & Brown 2008). In addition, *A. verticillata* cone production may decrease as conditions become warmer and drier (D. C. Paton personal observations), limiting the GBC's food supply. Lastly, psittacine beak-and-feather disease, although not yet reported in Kangaroo Island GBCs, could potentially cause substantial declines in the population if an outbreak occurred (DEH 2005; Appendix S5).

Here, we develop a detailed spatial population viability model for the GBC by building a demographic model, linking the demographic model to landscape and climate variables and testing scenarios in a population viability analysis. The analysis is based on a comprehensive location-specific data set and incorporates climate change and its interaction with fire, disease and management. Two earlier attempts at modelling the GBC used non-spatial simulations to investigate extinction risk (Pepper 1996; Southgate 2002), but both were limited in scope and made simplifying assumptions. For instance, in contrast to known population increases, Pepper (1996) predicted a rapid decline to extinction, and Southgate (2002) suggested the population would decline by 10% annually (Appendix S1). These studies were hampered by the limited data available when the analyses were performed and did not consider fire, disease, climate change or the positive influence of management. By contrast, we use a detailed data set collected by the GBC recovery program since 1995, consisting of 13 years of mark-resight and reproductive data and extensive documentation of catastrophes and management intervention, to parameterise our models. Few parrots have such complete demographic data available (Snyder *et al*. 2004).

Our approach incorporates a critical biotic interaction between the GBC and its primary food source, *A. verticillata*, by incorporating projected changes in the plant's range in the spatially explicit cockatoo model to provide direct measures of extinction threat (e.g. expected minimum abundance) as well as implied measures calculated from changes in habitat suitability and range size (Fordham *et al*. 2011). Similar approximations of species interactions have been used with BEMs (e.g. Araújo & Luoto 2007; Barbet-Massin & Jiguet 2011), but never in combination with a demographic model. Specifically, we sought to (i) model the population trajectory and extinction risk of the GBC up to the year 2100; (ii) determine the possible future effects of current and emerging threats to the subspecies; (iii) assess the impact of choosing different management strategies on GBC population trends; and (iv) evaluate the relative importance of demography and anthropogenic extinction drivers on the GBC's population viability.

Materials and methods

POPULATION MODEL

For the demographic component of the model, we used 13 years of mark-resight surveys to estimate survival rates using program MARK v.5.1 (Cooch & White 2008). Birds are marked with numbered bands as nestlings at several sites across the island (some areas are better sampled than others), and telescopes are used to resight marked birds during the annual post-breeding census. The mark-resight analysis was used to test the importance of management and environmental variables on survival rates of juvenile (<1 year old) and sub-adult/adult GBCs (Table S1). Fecundity was calculated as the number of fledglings of each sex produced per female of breeding age from 1996 to 2008 (see Appendix S2 for details on the mark-resight analysis, fecundity calculations and standard deviations used in the population model). Survival and fecundity estimates were combined with other life-history information, such as age of first breeding, to build a stage- and sex-structured, stochastic population model of the GBC (Table 1). We used RAMAS GIS (Akçakaya & Root 2005) to create a spatially explicit metapopulation model that links the subspecies' demography to landscape data, comprising dynamic bioclimatic maps for *Allocasuarina verticillata* (the GBC's primary food source), and raster layers of native vegetation, substrate and slope (see below).

BIOCLIMATIC SUITABILITY MAPS FOR *ALLOCASUARINA VERTICILLATA*

Climate change was incorporated by modelling the potential distribution of *Allocasuarina verticillata*, as a function of three key climate variables that influence the species' distribution (annual rainfall, January temperature and July temperature; Stead 2008). We used meteorological data to estimate long-term average annual rainfall and mean monthly January and July temperature (1980–1999) for Australia (Fordham, Wigley & Brook 2012). We used thin-plate splines and a digital elevation model to interpolate between weather stations (Hutchinson 1995; Appendix S3). An annual time series of climate change layers was generated for each climate variable based

Table 1. Stage matrices used in the model with stable age distribution (SAD) of each age class

	Age 0	Age 1	Age 2+	SAD(%)
Female				
Age 0	0	0	0·2324 (0·0951)	7·3
Age 1	0·612 (0·0951)	0	0	4·3
Age 2+	0	0·913 (0·0951)	0·913 (0·7148)	32·4

	Age 0	Age 1	Age 2	Age 3	Age 4+	SAD(%)
Male						
Age 0	0	0	0	0	0*	9·3
Age 1	0·612	0	0	0	0	5·5
Age 2	0	0·913	0	0	0	4·9
Age 3	0	0	0·913	0	0	4·3
Age 4+	0	0	0	0·913	0·913	32·0

The top row in each matrix represents fecundities, and the subdiagonal and diagonal in the bottom right elements represent survival rates. The first stage (age 0) for both sexes is the sub-adult stage. The final stages (female, age 2+; male, age 4+) are the adult stages. The intermediate stages are pre-breeding sub-adult stages. The proportional sensitivities of the finite rate of increase to small changes in each of the non-zero elements of the female matrix (elasticities) are in parentheses.
*In RAMAS, we specified fecundity values of 0·2324 and 0·296 for females and males, respectively (Appendix S2).

on two emission scenarios: a high-CO_2-concentration stabilisation reference scenario, WRE750, and a strong greenhouse gas mitigation policy scenario, LEV1 (Wigley *et al.* 2009). WRE750 assumes that atmospheric CO_2 will stabilize at about 750 parts per million (ppm), whilst under the LEV1 intervention scenario CO_2 concentration stabilizes at about 450 ppm. Future climate layers were created by first generating climate anomalies from an ensemble of nine general circulation models and then downscaling the anomalies to an ecologically relevant scale (*c.* 1 km^2 grid cells) (Fordham, Wigley & Brook 2012; Fordham *et al.* 2012; Appendix S3). Averages from multiple climate models tend to agree better with observed climate compared to single climate models, at least at global scales (Fordham, Wigley & Brook 2012).

Occurrence records for *A. verticillata* (n = 572) came from cleaned records from the South Australian biological survey. An equal number of pseudoabsences were generated randomly within the study region (Appendix S3). Although our focus was on Kangaroo Island, we modelled the distribution of the species across South Australia (325,608 grid cells) to better capture its regional niche (see Barbet-Massin, Thuiller & Jiguet 2010). We modelled the potential current and future climatic suitability of the landscape for *A. verticillata* with an ensemble of seven bioclimatic modelling techniques, including simple surface-range envelope models and more complex machine learning approaches, in BIOENSEMBLES software (Diniz-Filho *et al.* 2009; Appendix S3). Ensemble modelling generates consensus projections that circumvent some of the problems of relying on single-model projections of climate change impacts on species' potential distributions (Araújo & New 2007). We used BIOENSEMBLES models to forecast annually for 90 years (i.e. climate suitability maps for each year were created from 2010 to 2100). Nonetheless, our model assumed that the *A. verticillata*–GBC relationship would remain strong and we were unable to consider other species interactions.

INTEGRATING THE POPULATION MODEL AND SPATIAL INFORMATION

Binomial generalised linear models (GLMs) were used to relate GBC occurrence records to *A. verticillata* present-day climate suitability (above) and three landscape variables that are known to influence the distributions of the GBC and *A. verticillata*: substrate (Raymond & Retter 2010), native vegetation cover (http://www.environment.gov.au/erin/nvis/index.html), and slope (http://www.ga.gov.au/meta/ANZCW0703011541.html; Appendix S4). Verified GBC occurrence records (n = 349) consist of presences only. Pseudoabsences were generated by down-weighting cells close to a known sighting (Appendix S4). The analysis was performed with package MuMIn (Bartoń 2012) in R (v. 2.12.1; R Development Core Team, http://www.R-project.org). The best model (determined by AIC_c) from this analysis was used to parameterise the habitat-suitability function in RAMAS (Appendix S4).

RAMAS uses the habitat-suitability function to assign a habitat-suitability value to each grid cell of the study area based on values of the input rasters (in this case *A. verticillata* climatic suitability, substrate, native vegetation and slope). Every grid cell above the habitat-suitability threshold is considered suitable, and suitable cells are aggregated based on neighbourhood distance (the spatial distance at which the species can be assumed to be panmictic; Akçakaya & Root 2005). The habitat-suitability threshold (0·83) and neighbourhood distance (four cells) values were derived iteratively to match the well-known current extent of suitable habitat for the GBC on the island (Mooney & Pedler 2005).

The initial population size in all scenarios was 350 birds, in accordance with recent estimates (Pedler & Sobey 2008). The island's current carrying capacity was estimated at 653 birds by combining feeding habitat requirements (Chapman & Paton 2002) with data on *A. verticillata* area (Appendix S4). Dispersal estimates came from data on movements of marked individuals (Fig. S1). A ceiling model of density dependence was used to approximate the GBC's intraspecific competition for nest hollows and feeding habitat (Mooney & Pedler 2005). Population dynamics were linked to habitat via the density dependence function: habitat determines carrying capacity that conditions demographic rates (survival and fecundity) in each year, as a function of population size and carrying capacity in that year (Akçakaya & Root 2005). Each simulation incorporated environmental and demographic stochasticity and was run 10 000 times (Akçakaya *et al.* 2004).

Our main measures of population viability were expected minimum abundance (EMA) and mean final population size of persisting runs. EMA, which is equivalent to the area under the quasi-extinction risk curve (McCarthy 1996), provides a better (continuous, unbounded) representation of extinction risk than probability of extinction or quasi-extinction (McCarthy & Thompson 2001). We calculated EMA by taking the smallest population size observed in each iteration and averaging these minima.

We also calculated three spatial measures that are commonly used to infer extinction likelihood: change in total habitat suitability (from RAMAS), occupied range area (area of cells greater than habitat-suitability threshold) and average cockatoo density (see Fordham *et al.* 2011 for details). Density was calculated by relating the population size at each time step to habitat-suitability values per grid cell in suitable patches.

MODEL SCENARIOS

We generated RAMAS models for three climate scenarios: WRE750, LEV1 and a control scenario with no climate change. For each climate scenario, we assessed GBC population viability given changes in fire frequency, disease outbreak and changes in management from funding constraints. We modelled severe fires as reducing GBC fecundity by 10% and adult and sub-adult survival by 3%, based on responses measured in 2007 (Sobey & Pedler 2008; P.A. Mooney personal communication). Wildfire frequency was modelled as increasing with building fuel loads. Baseline scenarios include an annual probability of severe fire of 6·8% (Appendix S5). We modelled 5%, 25% and 220% (i.e. 2·2-fold) increases in fire frequency under climate change (Lucas *et al.* 2007). It was not realistic to model any fire increases for the no climate change scenario or the 25% or 220% increase for the mitigation LEV1 scenario (Appendix S5). Psittacine beak-and-feather-disease outbreaks were modelled as reducing sub-adult survival by 50%, with an annual probability of an outbreak of 5% (DEH 2005; Appendix S5). We modelled ending brush-tail possum, little corella and revegetation management as causing 44%, 7% and 3% reductions in fecundity, respectively (Mooney & Pedler 2005).

SENSITIVITY ANALYSIS

We used a Latin Hypercube sensitivity analysis to assess the impact of varying the values of six key input parameters (adult survival, varied by $\pm 5\%$; sub-adult survival, $\pm 10\%$; fecundity, $\pm 10\%$; carrying capacity, $\pm 20\%$; and proportion of population dispersing annually, $\pm 20\%$) on GBC mean final population size (Iman, Helson & Campbell 1981). Latin Hypercube sampling, which simultaneously varies the values of the input parameters and then estimates sensitivity by fitting a spline regression model, is arguably preferable to other Monte Carlo techniques because it requires many fewer iterations to sample the parameter space whilst allowing for co-variation in parameter choices (McKay, Beckman & Conover 1979). We fit a Poisson GLM with all six predictors (a segmented linear model was used for adult survival; segmented package in R; Appendix S5) and calculated standardised regression coefficients (fitted slopes divided by their standard errors) to rank the importance of the input parameters (Conroy & Brook 2003). We also tested the model's sensitivity to parameterisation of disease outbreaks by doubling the frequency of simulated outbreaks, increasing the impact to a 75% reduction in survival and combining these parameterisations.

Results

DEMOGRAPHY

The best-supported mark-resight survival model was stage-structured and time invariant (Table S2). There was also statistical support for the next eight models (Δ AIC$_c$ < 2), yet the majority of model structural deviance was explained by the most parsimonious model (88% compared to 99%). The annual survival estimates so derived were 0·612 ± 0·0388 SE for juveniles and 0·913 ± 0·0123 SE for adults. All of the top-ranked 10 survival models incorporated stage structure with two age classes. There was little evidence for differences in survival between the sexes over the study period from the mark-resight data. Models including environmental covariates were suboptimal regardless of stage structure. All covariate models with no stage structure had wAIC$_c$ < 0·01.

We used a mean annual fecundity estimate of 0·232 ± 0·0053 SE female nestlings produced per female of breeding age, and 0·296 ± 0·0068 SE male nestlings produced per female of breeding age, from 1996 to 2008, such that the finite rate of increase in the resultant matrix model was 1·0345, indicating a population increasing deterministically by 3·5% per year (Table 1; Appendix S2). The elasticities suggest that the rate of increase is most sensitive to adult survival.

SPATIAL RESULTS

There was considerable overlap between *Allocasuarina verticillata* patches and GBC presences. Approximately, 32% of GBC presences (feeding, nesting and band observations) were inside an *A. verticillata* patch, and 79% of presences were within 1 km of an *A. verticillata* patch (only 19% of the island is within 1 km of a patch).

The bioclimatic envelope modelling predicts that most of *A. verticillata*'s range (and consequently the GBC's habitat) will remain intact under the reduced emissions (LEV1) scenario, whilst the range is likely to contract substantially under the high-CO_2-concentration scenario (WRE750) (Fig. 2). The majority of suitable habitat that is predicted to remain at the end of the century under the WRE750 emissions scenario is on the island's higher-elevation western plateau (Figs 1, 2). By 2100, total habitat suitability declined substantially (decreasing by 12%) in the WRE750 scenario, whereas suitability decreased by just 1% under LEV1 (Fig. 3). Range area was inversely related to average cockatoo density per cell (Fig. 3). This was especially evident for WRE750, where range area contracted by 77% and predicted density increased by 57% by 2100. Range area declined by only 6% in the LEV1 scenario (Fig. 3).

POPULATION VIABILITY

Habitat changes caused by unmitigated climate change had a strong effect on population viability, with simulated final population size and expected minimum abundance always <160 birds, which is roughly equivalent to a return to the population

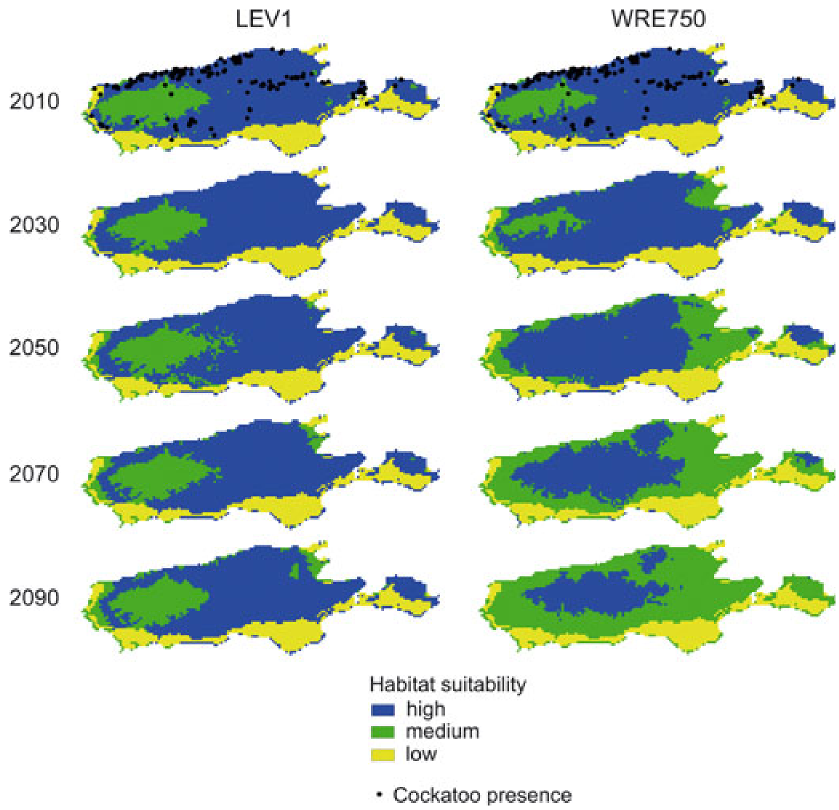

Fig. 2. Climate-change-driven maps of habitat suitability for *Calyptorhynchus lathami halmaturinus* according to a greenhouse gas mitigation policy scenario (LEV1) and a high-CO_2-concentration stabilisation reference scenario (WRE 750). Recent cockatoo presences are shown on the 2010 maps. Habitat suitability is classified from a continuous variable into three categories to aid visual interpretation: high (above the habitat-suitability threshold), medium (below threshold) and low (unsuitable substrate for *A. verticillata*) suitability.

bottleneck of the 1980s (Fig. 4, Fig. S2). In contrast, all simulations in the no climate change (control) case had final population sizes >635, and EMA >350, unless brush-tail possum management ceased. The strong mitigation (LEV1) simulations had slightly lower final population sizes than the no climate change case, but still had all final population sizes >595 unless there was no possum management. The simulations predicted that stopping possum management would have a serious effect on the population with all EMAs below 90 birds. Scenarios that ceased possum management were the only cases when the population did not stay close to carrying capacity. Unlike all other scenarios, possum scenarios had considerable probabilities of quasi-extinction (falling below 50 individuals): 10% for no climate change, 11% for LEV1 and 36% for WRE750. Stopping all management actions caused severe declines, with EMAs <26 birds for each scenario. The other catastrophes and changes in management had much more minor effects compared to possum management, although they did impact the population in the hypothesised directions (e.g. increased fire management caused slightly higher population sizes in LEV1 and no climate change). In this group of scenarios, beak-and-feather-disease outbreak had the strongest effects, but still only resulted in final population size reductions of 13, 12 and 1, compared to the baseline for no climate change, LEV1 and WRE750, respectively.

SENSITIVITY ANALYSIS

The Latin Hypercube sensitivity analysis indicated that model results were most heavily influenced by parameterisation of adult survival (top-ranked in each climate scenario) and carrying capacity (ranked second in each scenario; Fig. 5; Table S4). The standardised regression coefficients show that adult survival (low + high values from the segmented model) accounted for 35% (WRE750) to 52% (no climate change) of total sensitivity, whilst carrying capacity accounted for 21–32% of total sensitivity, respectively (Table S4). Decreased adult survival resulted in severe declines in GBC final population size, whilst increased adult survival had only slight or moderate effects because the modelled population, with the current survival estimate of 0·913, tracks carrying capacity with a positive population growth rate. Accordingly, varying carrying capacity also had substantial effects on final population size, especially for the WRE750 scenario where range area declines sharply. The other input parameters had small effects with sub-adult survival, fecundity and dispersal listed in order of decreasing importance. The additional disease outbreak sensitivity analysis indicated that increasing disease frequency or impact did not have substantially different effects on the population unless they were combined in the same scenario (Table S5).

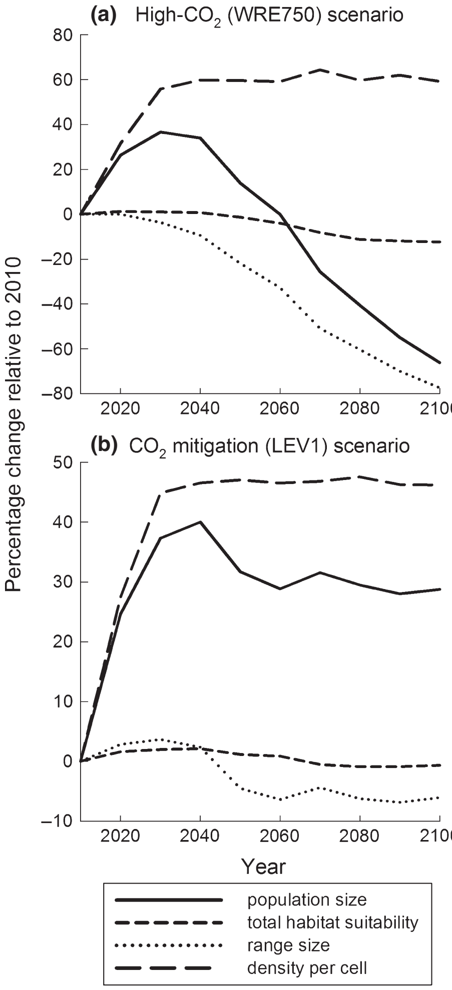

Fig. 3. Percentage changes in total habitat suitability (output from RAMAS GIS), range size (area of suitable habitat), cockatoo density per cell and population size according to two climate change scenarios: (a) high-CO_2-concentration stabilisation reference scenario (WRE750), (b) greenhouse gas mitigation policy scenario (LEV1).

Discussion

The population viability analysis for the South Australian glossy black-cockatoo illustrates the type of applied management questions that can be addressed using coupled demographic-bioclimatic approaches, as well as a method for incorporating dynamic vegetation-driven habitat change into animal population forecasts. The modelling indicates that the outlook for this small population depends strongly on continuous funding for management and global efforts to mitigate CO_2 emissions. The simulations suggest that GBC population size will increase under a low emissions future even if disease outbreaks were to occur, most management actions were reduced, and fire frequency was to increase. The gradual increase in the population over the last 15 years, combined with the large stands of underused *Allocasuarina verticillata* on the island, shows the potential for continued population growth. In contrast, a failure to mitigate CO_2 emissions could severely reduce GBC range area, critically threatening long-term population viability. Regardless of emissions scenario, our predictions indicate that the GBC's insular geographic constraints and low population size, which is well-below estimates of minimum viable estimates for most species (Traill *et al.* 2010), may leave the species vulnerable to decline.

Climate change under high CO_2 emissions (WRE750) caused a large reduction in range area, and contraction to the cooler and wetter western plateau, whilst habitat changes under low emissions (LEV1) were minimal, with range area decreasing modestly and habitat suitability remaining almost constant. Under high emissions, population size did not decrease as rapidly as range area because habitat suitability and cockatoo density initially increased in the remaining habitat (Fig. 3). These results indicate that range area is unlikely to be linearly related to GBC abundance. Habitat differences translated into much lower EMA for all high emissions scenarios compared to low emissions and no climate change. A population of 150 animals is inherently at risk of extinction from stochastic small-population processes (Traill *et al.* 2010). We did not run simulations beyond 2100 because of uncertainty in climate projections, but such small population sizes at the end of the century do not bode well for the GBC's persistence under a high-CO_2-concentration scenario.

Simulating reduced brush-tail possum management had a profound impact on GBC EMA, whilst reduction in little corella management was almost negligible because of the resilient GBC population. The absence of a strong response to corella management indicates that culling could be experimentally stopped in some areas in an adaptive management framework to save resources. Simulated psittacine beak-and-feather-disease outbreaks also had only slight effects on the GBC population. If mortality rates become higher and outbreak frequency is increased, disease could become a potent threat (Table S5). We suggest that continued vigilance and communication with organisations involved with disease management in other threatened parrots (e.g. orange-bellied parrot *Neophema chrysogaster* Latham) is needed.

Our results indicate that revegetation is only having small effects on the population at present, but altered spatial patterns of *A. verticillata* abundance from climate change and the carrying capacity of 653 individuals will probably necessitate revegetation in the future. Our model assumed full dispersal and establishment of habitat trees (with implicit instantaneous seed production), which may overestimate *A. verticillata*'s ability to colonise new areas. Given the strong likelihood that emissions will exceed LEV1 levels (IPCC 2007) and that *A. verticillata* recruitment is limited by herbivores such as tammar wallaby *Macropus eugenii* Desmarest, managers will probably need to revegetate to maintain *A. verticillata* and GBC populations. Although revegation effort could be reduced over the short term, key model assumptions (full dispersal and unlimited recruitment of *A. verticillata*) and model sensitivity to variation in carrying capacity (driven by climate related changes in *A. verticillata*) mean that managers should be ready for intensive revegetation in the future.

Management and monitoring should focus on maintaining adult survival and fecundity at their current levels. The acute

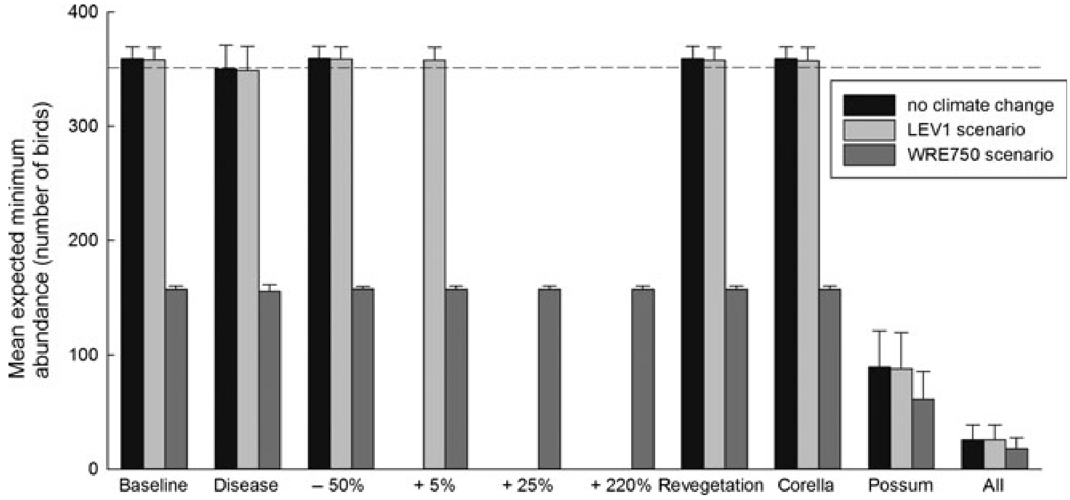

Fig. 4. Mean expected minimum abundance (±SD) of *Calyptorhynchus lathami halmaturinus* under no climate change, a greenhouse gas mitigation policy scenario (LEV1) and a high-CO_2-concentration stabilisation reference scenario (WRE750). The initial population size was 350 individuals (dashed line). Baseline = baseline scenario that includes observed fire frequency and ongoing use of current population management methods; disease = beak-and-feather-disease outbreak; -50% indicates 50% reduction in fire frequency from increased management; +5%, +25% and +220% (i.e. 2·2-fold increase) indicate increasing fire frequency from climate change. It was not realistic to model some fire increases for the no climate change or LEV1 scenarios. The last four groups of bars show the effects of ceasing management. 'Revegetation', 'corella' and 'possum' indicate stopping revegetation, little corella *Cacatua sanguinea* and brush-tail possum *Trichosurus vulpecula* management, respectively. 'All' indicates stopping all management actions.

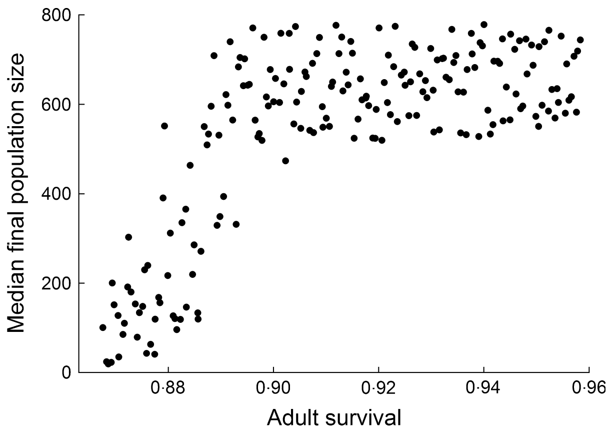

Fig. 5. Relationship between uncertainty in adult survival and median final population size in a Latin Hypercube sensitivity analysis for the no climate change scenario. The breakpoint for the segmented generalised linear model was 0·89, and the slopes were 78·9 and 0·76 for the low and high parameters, respectively. The mean estimate for adult survival from the mark-resight analysis is 0·913 (95% confidence interval from 0·88 to 0·93).

sensitivity of the model to lower (but still plausible) values of adult survival in the range of 85–90% emphasises the importance of monitoring adult survival over time. Predation from raptors such as wedge-tailed eagles *Aquila audax* Latham, climate variation, fire frequency and food availability may be important drivers of adult survival (Mooney & Pedler 2005), but there was no evidence of changing survival during the study period, and these relationships are incompletely known. Threats to the GBC may change over time, and the effects of climate variation on survival can be difficult to detect without monitoring data sets that span decades (Grosbois *et al.* 2008). Therefore, we suggest that mark-resight and reproductive data should continue to be collected to build this unique data set and allow ongoing analysis of the drivers of adult survival.

In addition to collecting data on the GBC, studies of *A. verticillata* are needed to improve forecasts of the GBC's extinction risk. In particular, studies on the effects of drought, warmer temperatures and fire on *A. verticillata* survival, recruitment and seed production are needed, especially given that climate change is likely to cause more extreme environmental events that would affect the life cycle of this food plant. New data could then be integrated with analyses that combine demographic models of both *A. verticillata* and the GBC.

Our approach minimised uncertainty by combining a comprehensive demographic data set with rigorous methods, including mark-resight estimation of survival and ensemble bioclimatic and global climate modelling, yet the model's assumptions should be considered when interpreting our results. The projected range contraction of *Allocasuarina verticillata* under the high emissions scenario assumes that the species' distribution–climate relationship remains the same as today and that climate is the main driver of range changes (species interactions are not considered for this plant). In addition, our model assumes that the relationship between *A. verticillata* and the GBC will remain strong in the future.

In conclusion, the results of our coupled demographic-BEM simulations suggest that the GBC is likely to continue its population increase over time until carrying capacity is reached, provided the climate remains similar to today and intensive possum control continues. However, should unmitigated climate change or reduced adult survival occur, severe declines are probable. We recommend continued intensive life-history monitoring on the GBC, possum management and research on *A. verticillata*, to promote the persistence of the GBC. The methods illustrated here demonstrate how species interactions can be included in coupled demographic-bioclimatic modelling approaches to add realism to forecasts of population viability under climate change for well-studied species of conservation concern. Furthermore, our analysis shows how coupled models can provide practical management advice in the face of broader issues and uncertainties such as global emissions mitigation.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. Annual dispersal-distance curve for the *Calyptorhynchus lathami halmaturinus* population on Kangaroo Island.

Fig. S2. Mean final population size of persisting runs ($\pm$SD) of *Calyptorhynchus lathami halmaturinus* under no climate change, a greenhouse gas mitigation policy scenario (LEV1) and a high-CO_2-concentration stabilisation reference scenario (WRE750).

Table S1. Covariates and their data sources for the mark-recapture survival analysis of *Calyptorhynchus lathami halmaturinus* on Kangaroo Island.

Table S2. Comparison of survival model results from Cormack-Jolly-Seber models in program MARK.

Table S3. Results of binomial GLMs relating spatial variables to *Calyptorhynchus lathami halmaturinus* presences on Kangaroo Island.

Table S4. Latin Hypercube sensitivity analysis results.

Table S5. Sensitivity of results to parameterisation of disease outbreaks.

Appendix S1. Previous modelling studies on the Kangaroo Island GBC.

Appendix S2. Detailed population-modelling methods.

Appendix S3. Climate change forecasts and bioclimatic envelope modelling methods.

Appendix S4. Integrating population and distribution models (methods).

Appendix S5. RAMAS scenarios and sensitivity analysis methods.

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