

# A range-wide monitoring programme for a critically endangered nomadic bird

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**Abstract** Nomads challenge the prevailing approach to species conservation because their unpredictable resource-driven movements hamper data collection. We developed a monitoring approach to address the conservation needs of critically endangered, nomadic regent honeyeaters *Anthochaera phrygia*, whose unpredictable movements occur at a continental scale. We used species distribution models that incorporated lagged effects of environmental variation on habitat suitability to refine and prioritise monitoring. By incorporating lagged effects of weather on occurrence, we identified a priority area within which we selected sites to survey. We undertook 1695 surveys in 2016 at 777 priority sites, and in 2017, we conducted a further 1434 surveys at 859 sites. We discovered nesting regent honeyeaters at new locations, locating 218 regent honeyeaters over two years. We validated performance of our priority mapping with the 2016–2017 survey results and the results of Crates *et al.* (*J. Wildl. Manage.* 2017, 81, 669). Predictive performance of the priority monitoring range map was best at estimated model values of approximately 0.7 and declined at both higher and lower values. Water availability was an important predictor, but poor resolution of the underlying data used in SDMs (e.g. temporary water sources) may explain our model performance. By accounting for spatiotemporal weather variation, we show that regional habitat suitability within the range of regent honeyeaters varied dramatically among years. Incorporating dynamic weather conditions is a useful approach to designing monitoring programmes for nomads. Our approach shows how to compromise between the need to account for the dynamic environmental conditions that drive site occupancy of nomads and the practical logistic constraints of implementing monitoring with scarce resources.

**Key words:** *Anthochaera phrygia*, Australia, climate, conservation, MaxEnt, nomadism, species distribution models.

## INTRODUCTION

Ecological monitoring forms an integral part of threatened species conservation (Robinson *et al.* 2018). Effectively designed monitoring can detect population trends over time and space, empowering managers with the information necessary for recovery planning. It is comparatively simple to design monitoring schemes for sedentary and philopatric species because their site fidelity makes identifying where to monitor straightforward (Clarke *et al.* 2003). In turn, sedentary and philopatric species are often conservation success stories because monitoring captures the impact of recovery interventions measured from the individual to populations, at locations that remain stable over time (Sutherland 2002; Lavers *et al.* 2010).

Nomadic animals challenge the prevailing approach to species monitoring. Their unpredictable, resource-driven movements hamper collection of robust population data because site occupancy may vary substantially through time (Webb *et al.* 2014a). Nomads move at very large spatial scales, which limits the ability of managers to identify where in a given year they might settle. Nomads often occupy parts of the world with high resource variability and low human populations such as the Australian inland and the Arctic (Dingle 2008). High environmental variability combined with little or at best localised monitoring effort results in low detection rates in these places. This introduces high uncertainty into population size/trends of rare and nomadic species estimated using classical statistical methods from wildlife atlas or community-level monitoring data (Rayner *et al.* 2014; Runge & Tulloch 2017).

In a real-world case study, we test and evaluate a method for designing a large-scale monitoring

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scheme for a nomadic bird species. We develop an approach targeted to places and times when nomads are likely to occur (maximising detection), but with a static design (i.e. fixed sites) for straightforward implementation and management. Our focal species was the regent honeyeater (*Anthochaera phrygia*), a medium-sized (~40 g) nomadic nectarivore that follows *Eucalyptus* flowering across south-eastern Australia. Regent honeyeaters exemplify the conceptual and logistical challenges associated with the conservation of nomads. For example, the species has a population size of fewer than 400 (Kvistad *et al.* 2015), and as a result, typically <40 incidental sightings are recorded per year (BirdLife Australia, unpubl. data, 2018). The species is also mobile, with the longest confirmed individual movement being 580 km over a potential distribution of ~600 000 km<sup>2</sup> (Commonwealth of Australia 2016). Regent honeyeaters only breed where food is locally abundant, but at large scales, food availability is patchy, scattered and unpredictable. Population-wide monitoring and data collection are extremely challenging for animals such as regent honeyeaters because knowing where to search is difficult in the first place. Even if detectability is high, their rarity makes occupancy rates unavoidably low (Crates *et al.* 2017). This has important implications for conservation because quantifying the impact of threats on this species is difficult without good quality data (Crates *et al.* 2021a).

Given their vast extent of occurrence, it is logistically unfeasible to monitor the entire regent honeyeater range with uniform sampling intensity. Accordingly, we aimed to refine the search area to an achievable but ecologically relevant spatial scale by identifying potential monitoring sites where the species is most likely to be present for feeding or breeding. To do this, we used species distribution models (SDM) including bioclimatic data. Static species distribution models (SDMs) that predict over large scales (Gormley *et al.* 2011) can excessively overestimate the extent of habitat and species occurrence (Reside *et al.* 2010). This over-prediction limits their applicability to nomadic species (Webb *et al.* 2017). We overcome this limitation for regent honeyeaters using SDMs that incorporate time-lagged effects of environmental variation. Time-lagged environmental conditions can explain why animals in variable environments occur where and when they do (Greenville *et al.* 2016; Runge *et al.* 2016). Time lags account for delayed animal responses to, for example, periods of rainfall and subsequent flowering of food plants (Greenville *et al.* 2016). This approach explicitly accounts for the temporal variation in environmental conditions that underpin the ecology of nomads, with the aim of focusing survey effort on places and times when there is most consistently a higher than average chance of detection. Similar approaches have

predicted impacts of changing climate and human land use on the locations of important habitat of nomads (Stojanovic *et al.* 2019). Further, temporal trends in the number of occupied sites and the relationship between occupancy and abundance counts at those sites may be a reliable surrogate for population trends, which may be too impractical to monitor directly in nomads (Webb *et al.* 2019).

We aimed to develop a monitoring programme that increased the quality and quantity of data available to help address the most pressing conservation needs of regent honeyeaters. To achieve this aim, we:

1. Identified priority objectives for monitoring, supported by research questions linked to critical conservation knowledge gaps for our target species;
2. Used SDMs to design and implement range-wide monitoring of 'priority breeding habitat' to collect population data on our target species; and
3. Evaluated performance of our monitoring design, including SDM validation, using two years of monitoring survey data.

## MATERIALS AND METHODS

### Study area and species

Sighting data used to build the SDMs came from the entire extent of occurrence of the regent honeyeater between 2000 and 2010 (BirdLife Australia, unpubl. data; Appendix S7). Our study was conducted across >26 000 km<sup>2</sup> of the contemporary breeding range of the regent honeyeater in the temperate woodlands of south-eastern Australia (−28.17° north, 151.49° east, −36.62 south and 145.91° west). Regent honeyeaters occupy a wide range of wooded habitats (Australian Department of the Environment & Energy 2016; Commonwealth of Australia 2016). All monitoring sites had one or more plants preferred by regent honeyeaters for food or nests. These plants included the following: river she-oak (*Casuarina cunninghamiana*) with needle-leaf mistletoe (*Amyema cumbagei*), yellow box (*Eucalyptus melliodora*), red ironbark (*E. sideroxylon*), white box (*E. albens*), grey box (*E. molluccana*), spotted gum (*Corymbia maculata*) and broad-leaved ironbark (*E. fibrosa*) with long-flowered mistletoe (*Dendrothoe vitellina*, Commonwealth of Australia 2016).

### Identifying monitoring objectives

Addressing key knowledge gaps about the regent honeyeater was the objective of the monitoring programme. Based on expert advice and the current National Regent Honeyeater Recovery Plan (Commonwealth of Australia 2016), we targeted the following questions:

- Q1. Where does important contemporary breeding habitat occur?

- Q2. What factors drive breeding habitat occupancy?  
 Q3. Do population parameters vary over the breeding range?  
 Q4. What are the contemporary threats to nest success?  
 Q5. Do current conservation actions enhance reproductive output?

The purpose of the present study is to explain the rationale and methods applied to design a cohesive monitoring programme to answer these questions. As a result, we do not explicitly answer the above questions in this study, but further information is available elsewhere (Crates *et al.* 2017, 2019; Crates *et al.* 2021b) and is subject to ongoing research.

Based on these questions, our monitoring design needed to maximise spatial coverage while maintaining collection of fine-scale data. To achieve this, we (Crates *et al.* 2021b) designed the monitoring programme to include complementary surveys at two spatial scales. First, rapid range-wide surveys across the entire potential distribution of the species would locate regent honeyeaters and track variation in food availability (addressing questions 1 and 2). Second, landscape-scale intensive nesting surveys where regent honeyeaters were detected in range-wide surveys would improve finer scale resolution (questions 3–5). This approach was a compromise on resourcing and feasibility. For example, a fully dynamic approach – where a new search area might be defined annually (Greenville *et al.* 2016; Runge *et al.* 2016) – is unfeasible because the specialist analytical skills and intensive ground-truthing required are unlikely to be adequately resourced in the long term. Instead, we preferred a static search area (logistically feasible for long-term planning and implementation) that represented the area where the odds of detecting the target species were optimised based on the results of multiple, discrete, time-lagged component models (i.e. refugia, Reside *et al.* 2014).

## Species distribution model construction

### *Modelling data*

We first generated presence-background SDMs in MaxEnt (Phillips *et al.* 2006) to refine the area where monitoring would occur within the very large potential distribution of the species. Due to decades of severe deforestation across the range of the regent honeyeater, we only used occurrence records between 2000 and 2010 to target more recent habitat use since historical deforestation. We therefore excluded historically important sites where the species is now locally extinct (due to deforestation or range contraction) from analysis. The study area (i.e. the total range of the regent honeyeater) has an average annual rainfall of 58–239 mm per year (Atlas of Living Australia [www.ala.org.au](http://www.ala.org.au)), but the 10-year period of monitoring used for this analysis included the millennium drought as well as years of high rainfall (in 2001 and 2010). This range in rainfall is representative of the fluctuations in rainfall experienced by the regent honeyeater over the past 50 years and is therefore a useful sample from which to generalise habitat use. A shorter period of time (e.g. 2003–2007) would not have sufficed due to the chance of missing the wet years.

We sourced data from the BirdLife Australia Bird Atlas and the Regent Honeyeater Recovery Team sightings database. Data could include records collected using any type of survey design or sampling protocol, but we excluded records without GPS coordinates. We removed duplicates and errors, leaving 1328 unique observations (presences) from 995 unique locations for analysis (Appendix S7). Regent honeyeater observations extended from Victoria, through New South Wales and into Queensland, with many points occurring near urban areas and known regent honeyeater hot spots (these hot spots are shown in Appendix S7). SDMs based on opportunistic sighting data have similar accuracy to those based on systematic monitoring surveys for uncommon species (Sardà-Palomera *et al.* 2012), and in the context of our study aims, we considered this a reasonable starting point.

### *Time-sliced modelling*

We accounted for time lags between environmental conditions and species occurrence (Runge *et al.* 2016) using ‘time-sliced models,’ representing time lags of different lengths. We related species occurrence data to 10 environmental variables (Appendix S2). Six environmental variables reflected weather (Xu & Hutchinson 2011) and varied temporally over the study period. These were daily precipitation (mean and total), daily maximum temperature (mean and maxima) and daily minimum temperature (mean and minima). We matched weather data to the latitude, longitude, year and month of each regent honeyeater sighting. We identified the most appropriate time slice to apply to weather data by comparing the area under the curve (AUC) scores among global models incorporating 3-, 6-, 9- and 12-month time lags (Appendix S3). Using this procedure, we identified rolling 12-monthly averages and totals as the most appropriate lag to predict regent honeyeater distribution over time (Appendix S4).

The remaining four environmental variables were habitat derived and held constant over the study period. These variables and their respective sources were as follows: extent of suitable vegetation, where ‘suitable’ included known feed trees and commensurate vegetation associations (Australian Department of the Environment & Energy 2016), extent of historically cleared land (Australian Department of the Environment & Energy 2016), distance to major streamline (Bureau of Meteorology 2014) and landscape position. We matched habitat data to the latitude and longitude of each regent honeyeater sighting. Detailed data on habitat characteristics at the locations where regent honeyeaters were observed in the source data were unavailable, but we consider that the above approach provided a reasonable approach for refining the monitoring area given the large spatial scale of our study.

Our monitoring objectives focused on regent honeyeater breeding ecology, so we used regent honeyeater occurrence records from the breeding season (September–December), rather than using all available data (see Runge *et al.* 2015; Runge *et al.* 2016). We assumed that rather than responding consistently to environmental conditions through time and within years, the regent honeyeater likely changes its habitat associations between life-history phases (Crates

*et al.* 2017). Our model using the subset of breeding season data achieved higher AUC scores than a single global model using all available occurrence data (test AUC: global model = 0.860; breeding season data = 0.947). We projected breeding season SDMs onto yearly spatial surfaces for the month of October.

Using these breeding season SDMs, we built annual range-wide time-sliced distribution raster layers at  $1 \times 1$  km resolution, matching species occurrence data with environmental conditions over the 12 months preceding each observation. We used this resolution because the long-distance movements of regent honeyeaters call for a trade-off between accounting for fine-scale environmental differences at individual occurrence records and mapping habitat use across very broad spatial extents. The approach produced 11 annual distribution maps for each set of environmental conditions (see Runge *et al.* 2015 for further details of the modelling approach). We implemented MaxEnt with samples with data inputs (Phillips *et al.* 2009). To account for coastal and spring bias in survey effort (Szabo *et al.* 2007), we used the date and geolocation of 10 000 randomly selected 20-min 2-hectare surveys from the BirdLife Australia Bird Atlas database for ‘target group’ background sampling in our models (Phillips & Dudík 2008; Phillips *et al.* 2009). These background points only included surveys conducted between 2000 and 2010 where a regent honeyeater was not detected (i.e. pseudo-absences; Appendix S7). We fitted models with default regularisation parameters (i.e. regularisation coefficient = 1) and using all potential variable response curves in MaxEnt, that is linear, product, quadratic, hinge and threshold features (Elith & Leathwick 2009). We chose these settings based on previously published MaxEnt species distribution modelling of nomadic birds in Australia by the authors, which discovered complex relationships between species occurrence and environmental variables (Runge *et al.* 2015, 2016). Increasing the regularisation coefficient would remove features from the model, potentially over-simplifying the environmental relationships and divorcing predicted values of constraints from empirical values (Merow *et al.* 2013) – this would make it harder to understand the shapes of the relationships between alternative environmental variables and regent honeyeater occurrence.

#### *Habitat suitability mapping*

We used equal sensitivity and specificity threshold values to reclassify the logistic probability outputs of MaxEnt rasters into habitat suitability maps. These maps represented predictions of relative absence and probabilities of presence, a value between 0 (habitat unsuitable) and 1 (100% suitability) as per Runge *et al.* (2015). We summarised habitat suitability maps by averaging cell values of annual habitat suitability across the 11-year sample period. This process identified areas where SDMs indicated suitability was  $>0.5$ , and we refer to this as the ‘priority monitoring range’ map because it showed the refined area within the range of regent honeyeaters where our search effort would be focused. We predicted that this area should represent refugia where, in any given year, some regent honeyeater habitat should occur (Reside *et al.* 2014).

#### **Monitoring programme implementation and evaluation**

The first step of implementing the regent honeyeater monitoring programme involved a six-month site selection phase commencing in July 2016 when we searched areas identified by the ‘priority monitoring range’ map to identify the most suitable regent honeyeater habitat within  $1 \times 1$  km priority grid cells. Additionally, we considered important breeding areas identified in the National Regent Honeyeater Recovery Plan for inclusion in our programme (Appendices S1 and S7).

At the range-wide scale, we undertook monitoring during three 6-week survey rounds: (i) 25 July–7 September, (ii) 25 September–7 November and (iii) 25 November–7 January to sample early-, mid- and late-season food tree flowering events. Our sampling design allowed for survey sites to be added over the course of the monitoring season as we located and gained access to new potentially suitable habitat, since many priority areas were situated on private property. We selected monitoring sites using the priority monitoring range map, by locating wooded habitats within regions identified as high priority. We selected sites if they were both close to access points (to facilitate rapid movement between sites) and contained one or more food tree species. We did not impose any other selection on which habitat types we surveyed, so sites occurred across a wide range of wooded habitats, but always within potentially suitable habitat of regent honeyeaters. Sites were spaced  $\geq 150$  m apart to account for the small size of regent honeyeater breeding territories and the tendency of regent honeyeaters to nest in loose aggregations (Crates *et al.* 2017). Within a given patch of potential habitat, we created a site at the first location that matched our criteria and deployed sites until the potential habitat ran out. Further detail about site selection protocols, particularly for the landscape-scale component of monitoring, is available elsewhere (Crates *et al.* 2017). Our large study area is dominated by patchy habitat so sites were occasionally clustered, such that fine-scale spatial non-independence was problematic, but nevertheless this possibility was accounted for in the modelling process (Crates *et al.* 2017).

Range-wide surveys were brief to maximise spatial coverage and comprised a 5-min point count recording the abundance of regent honeyeaters within a 50 m radius of the site centroid. In the first minute of each survey, we used regent honeyeater song broadcast to improve detection probability (Crates *et al.* 2017). Detections of regent honeyeaters in range-wide surveys triggered follow-up landscape-scale surveys. Landscape-scale surveys followed an adaptive protocol following Crates *et al.* (2017) to target regent honeyeater reproductive behaviour. The methods followed have been reported elsewhere (Crates *et al.* 2019), but we recorded adult breeding participation, sex ratios, nest initiation dates, nest survival, number of fledglings and causes of nest failure. These data aimed to address questions 3 (do population parameters vary across the breeding range) and 4 (what are the contemporary threats to nest success) of our monitoring objectives by providing detailed life-history parameters of regent honeyeaters across the study area. We also recorded key habitat features (including vegetation composition, structure and the availability of

nectar) as well as the occurrence of all other bird species detected. We recorded these data to enable future answering of the second question of our monitoring objectives (what factors drive breeding habitat occupancy) and to understand broader ecological aspects of the study area.

### Species distribution model validation

We validated the predictive performance of SDMs with the results of two years of monitoring data from 2016 and 2017, plus additional data from 2017. We explored the agreement between model predictions and observations using calibration diagrams (Pearce & Ferrier 2000) and the distribution of predicted values for surveyed and unsurveyed cells (Elith & Leathwick 2009). We calculated the AUC of the receiver operating characteristic to evaluate the quality of the predictions. A high AUC value (close to 1) indicates that high predicted scores tend to be areas of known presence and lower model prediction scores tend to be areas in which the target species is known to be absent (or a random point). An AUC score of 0.5 means that the model is as good as a random guess.

## RESULTS

### Species distribution models and priority habitat map

We present the priority habitat map in Fig. 1. Temperature minima, mean maximum temperature and mean precipitation made the strongest contribution to regent honeyeater habitat suitability in the breeding season (Table 1, Appendix S10). The species avoided temperature extremes (which are higher in the west of the study area) and had an approximately quadratic association with distance to streams and rainfall levels. Our models indicated that most of the priority habitat predicted for the regent honeyeater fluctuated in suitability over time (Appendix S8). Thus, only a fraction of the total projected suitable breeding habitat was likely to be suitable in one or more years between 2000 and 2010.

### Survey and monitoring results

During both the pilot year (2016) and implementation year (2017), we added sites to the program as suitable habitat was discovered. This meant that the number of surveys per site ranged from 1 to 3 per season (not every site was surveyed each survey round). At the completion of the present study, our monitoring design comprised 896 sites. Across the area identified by our priority monitoring map, we undertook 1695 surveys in our pilot year (2016), at 777 sites, with 550 sites receiving multiple visits. In

2017, we undertook 1434 surveys, at 896 sites, with 610 sites receiving multiple visits. Data collected in 2015, contributed by Crates *et al.* (2017) to assist in SDM validation, were collected across 321 sites ( $n$  surveys = 963) in the Capertee Valley, NSW.

In total, our range-wide surveys located an estimated 218 adult regent honeyeaters over the 2 years. In 2016, we located 39 regent honeyeaters during range-wide surveys with follow-up landscape-scale surveys locating 34 additional birds. In 2017, we located 53 regent honeyeaters during range-wide surveys with follow-up landscape-scale surveys locating 92 additional birds. Our follow-up landscape-scale surveys yielded 85 regent honeyeaters nests, including 24 at new locations (e.g. Severn River, Goulburn River, Burrigorang Valley) that otherwise would not have received monitoring effort. Additional detail about the types of life-history data we collected and the results of population-wide nest monitoring are reported elsewhere (Crates *et al.* 2019).

We did not detect regent honeyeaters at many breeding areas identified in the National Recovery Plan. Settlement of these locations may be too irregular to influence model predictions, but they may still be important when conditions in other habitats are unfavourable.

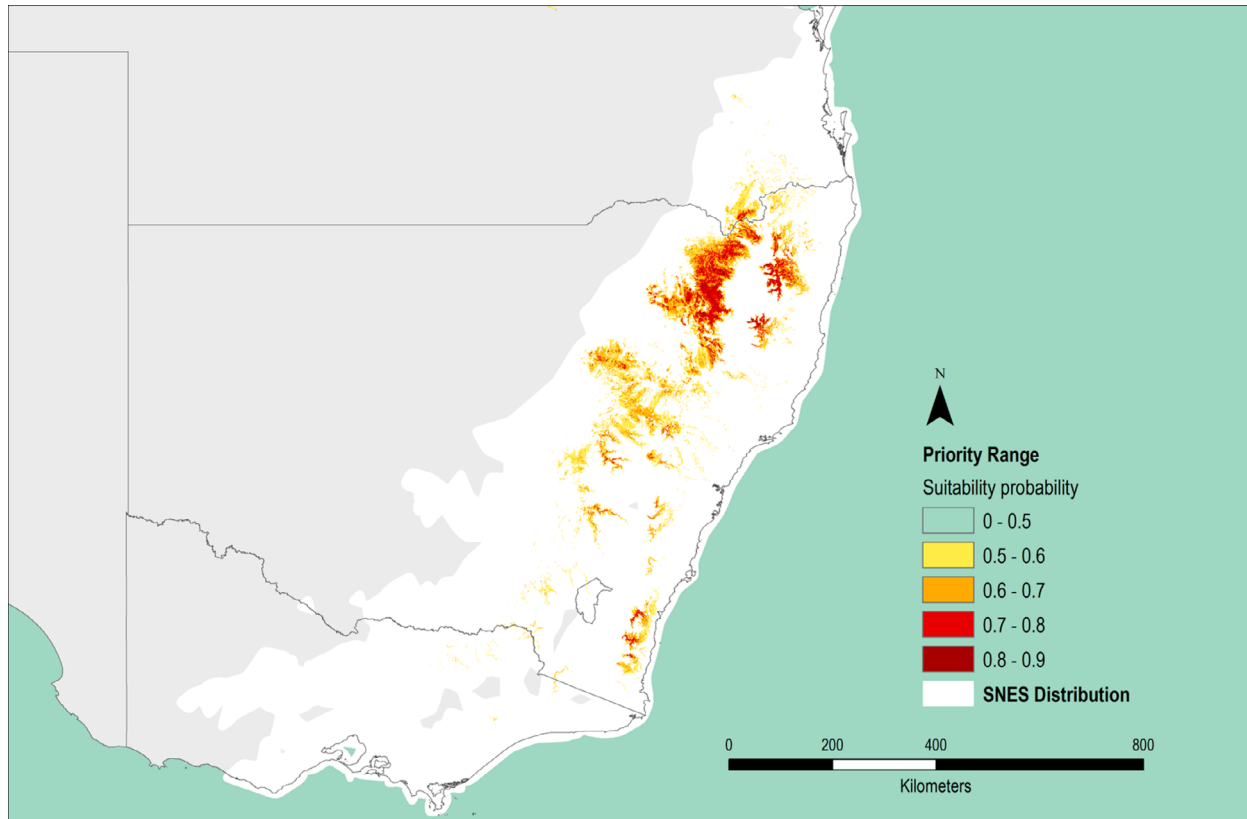
### Model discrimination capacity

The predicted habitat suitability values for cells where regent honeyeaters were located were on average higher than un-surveyed cells, indicating a good discrimination capability of the best model (Appendix S9). Plots of the receiver operating curve had an AUC ranging between 0.51 (breeding models for 2005 and 2008, indicating only slightly higher than random discrimination capacity) and 0.65 (breeding model for 2002, indicating higher discrimination capacity than the models for 2005 and 2008; Appendix S4).

The 'priority monitoring range' (averaged raster) had increasing observed proportions of positive detections with increasing model estimates up to a value of 0.8 (Fig. 2). The proportion of positive cases declined at values >0.8. This appears to be due to the smaller proportion of model values >0.8, and a smaller number of independent surveys carried out in these very high value locations (due largely to inaccessible terrain; Fig. 2).

## DISCUSSION

There is mounting evidence that question-driven monitoring delivers results that address ecological knowledge gaps and inform conservation planning (Rayner *et al.* 2014). We aimed to compromise



**Fig. 1.** Priority monitoring areas for breeding regent honeyeaters (coloured areas) across their entire contemporary range detailed in the species' recovery plan distribution (i.e. the white area) in south-eastern Australia based on public sighting data obtained between 2000 and 2010. Darker coloured shades from yellow to dark red indicate increasing habitat suitability (displayed for grid cells where the average suitability was  $>0.5$  only) according to time-sliced models implemented in MaxEnt.

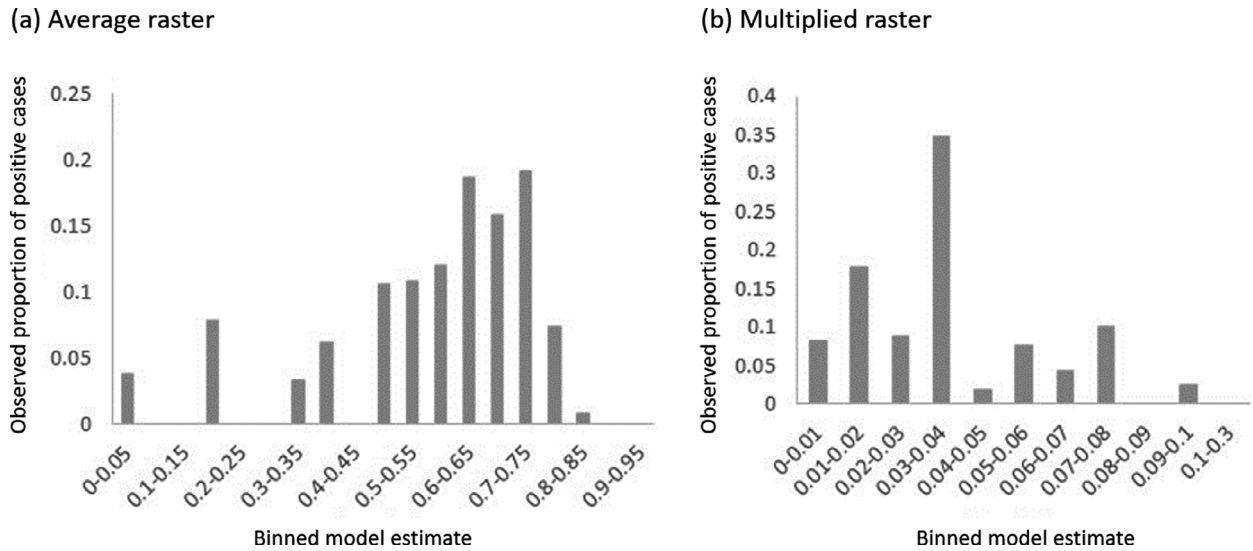
**Table 1.** Variable contributions to regent honeyeater breeding habitat suitability across their contemporary range in south-eastern Australia (see Phillips *et al.* 2006)

Variable	Permutation importance (% contribution)
Temperature minima	30.1 (25.4)
Mean maximum temperature	20.1 (29.6)
Mean precipitation	16.4 (15.1)
Temperature maxima	8.7 (12.7)
Mean minimum temperature	12.0 (11.0)
Stream distance	9.8 (4.7)
Vegetation class	1.8 (0.7)
Total precipitation	0.1 (0.1)
Landscape position	1.0 (0.7)
Cleared land	0.0 (0.0)

between the need to account for the unpredictable annual settlement patterns of regent honeyeaters and the need to develop a practical and deliverable monitoring strategy at an ecologically relevant scale. Our approach generated more detections of breeding

regent honeyeaters than had been achieved in the preceding decade. Using time-lagged SDMs to model the habitat of nomadic regent honeyeaters enabled us to prioritise habitat where the species was most likely to occur. Prioritising survey effort in areas of high occurrence probability was critical given the vast size of the potential study area. Furthermore, objectively targeted survey effort showed that it is possible to compromise between the need to account for dynamic distributions of nomads over time and the practical limitations on project delivery. Similar approaches have been used across smaller areas than the range of our target species (Webb *et al.* 2014b; Stojanovic *et al.* 2019), but we show with this study how to 'scale up' monitoring by refining the search area.

By averaging multiple discrete models that account for the effects of spatiotemporal variation on regent honeyeater occurrence, we produced a static map of habitat refugia for the species. A fully dynamic approach (e.g. where the search area might be identified each year via a new modelling process) might be more flexible, but would pose potentially insurmountable feasibility challenges if the survey area



**Fig. 2.** Comparison of MaxEnt species distribution model estimates with the observed proportion of positive detections by an independent survey for regent honeyeaters across their entire contemporary range in south-eastern Australia between 2016 and 2017. (a) The averaged breeding model (see Appendix S5) and (b) the multiplied breeding model (see Appendix S6). Each point represents a binned sample of the surveys.

changed each year. By identifying the areas most likely to be used on average, fixed sites can be annually surveyed. This eliminates need for repeated annual SDMs and improves the odds that citizen scientists can help deliver well-designed projects with clear aims (and identified limitations).

After only two years, we discovered new breeding habitat in the north of the species range (per Research Question 1). These areas were previously unknown, and our results provide new opportunities to deliver local on-ground conservation actions such as nest protection. Monitoring also yielded opportunities for intensive research into reproductive parameters and applied management interventions in scattered contemporary breeding populations separated by hundreds of kilometres (Crates *et al.* 2018; Crates *et al.* 2019; Crates *et al.* 2020), addressing Research Questions 3 and 4. Extensive sampling coupled with follow-up searches overcame the challenge of low encounter rates of rare, sparsely distributed species, which can hinder collection of enough data for analysis for some aspects of life history.

If details of the ecology of nomads are ignored, SDMs can substantially overestimate habitat availability (Webb *et al.* 2017). Regional habitat suitability within the range of regent honeyeaters varied dramatically among years. Inclusion of other covariates, particularly *Eucalyptus* flower availability, could further refine our model predictions. Although these data are not currently available for our study area, we expect that tree flowering data collected during range-wide monitoring will serve this purpose. Concurrent collection of flowering data at monitoring sites also provides a large-

scale flowering phenology data set of relevance to many native taxa, including non-target threatened and nomadic species. Factors that drive variation in the phenology of tree flowering at large scales remain uncertain (Law *et al.* 2000), so it is not possible to evaluate the links between bioclimatic variation, tree flowering and the occurrence of regent honeyeaters using data available from previous monitoring attempts. Even if regent honeyeater encounter rates are low, our monitoring program therefore has substantial ‘added value,’ given the potential to answer broader ecological questions an unprecedented spatial scale.

We encountered some issues with the performance of our priority maps for monitoring that illustrate important considerations for practitioners seeking to utilise our approach. Looking at individual breeding models, the best linear fits for the observed proportions of positive cases from data in 2017 and model estimates were for the breeding 2002 model ( $R^2 = 0.439$ ) and breeding 2005 model ( $R^2 = 0.428$ ). The ability of the models to predict occupied sites for static monitoring varied dramatically depending on how the time-sliced models were aggregated. Our study reiterates the importance of ground-truthing model estimates of habitat suitability for SDMs undertaken at large scales (Rapacciuolo *et al.* 2012; Smith *et al.* 2013; Hertzog *et al.* 2014). Predictive performance of the ‘priority monitoring range’ map peaked at approximately 0.8 and declined at higher values. Limited spatial resolution and specificity of our modelling covariates may explain this result, and this could have been overlooked without ground-truthing. For example, even though regent

honeyeaters are dependent on nearby water availability (Crates *et al.* 2017), our linear ‘distance to water’ covariate was unable to downplay the importance of large water bodies such as lakes, dams and river gorges (which regent honeyeaters are unlikely to utilise) relative to the importance of smaller rivers, creeks, livestock dams and ephemeral water bodies (which regent honeyeaters are much more likely to utilise). We predict that in fact this relationship is quadratic, with the species selecting for low-flat productive soils along smaller streams and rivers in wide valleys. Furthermore, water availability is highly variable across the Australian continent, and this could create opportunities for error when using bioclimatic data. For instance, at places mapped as distant from water, temporary pools or streams that briefly appear after rain are not recorded by static maps of water availability, but may nevertheless influence regent honeyeater occurrence. Finer scale mapping of ephemeral water sources may be important to improving model performance for species such as regent honeyeaters, but would be very challenging to incorporate into time-lagged models such as ours. Given the likelihood of Australia becoming hotter and drier with global heating (CSIRO & Bureau of Meteorology 2015), future studies should consider how habitat suitability for nomads such as regent honeyeaters might change in extent and location.

Regent honeyeaters are typical of many nomadic species in that most data on occurrence are collected incidentally by citizen scientists outside of structured, targeted monitoring. Utilising presence-only records in time-sliced models enabled us to prioritise habitat using the best available data, while accounting for environmental variations that may explain settlement patterns. This substantially refined our search area and enabled the implementation of a spatially stratified monitoring design that could be further refined with field validation. However, while habitat suitability estimation must occur at large scales to be useful for nomads, in practice, fine-scale habitat features are critical for predicting occurrence of nomads at a given site. We caution that time-sliced SDMs must be validated, for both habitat suitability and presence/absence of the target species, before their results are applied to the real world. This is particularly crucial for site-specific management prioritisation. Without field validation, the decline in predictive capacity of our priority habitat models at high habitat suitability values could have resulted in misdirected allocation of monitoring effort towards areas where the target species was unlikely to occur.

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## AUTHOR CONTRIBUTIONS

**Dejan Stojanovic:** Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (equal); Supervision (lead); Writing-original draft (lead); Writing-review & editing (lead). **Laura Rayner:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Ayesha Tulloch:** Formal analysis (equal); Methodology (equal); Writing-review & editing (equal). **Ross Crates:** Methodology (equal); Writing-review & editing (equal). **Matthew H Webb:** Methodology (supporting); Writing-review & editing (supporting). **Dean Ingwersen:** Funding acquisition (supporting); Writing-review & editing (supporting). **Claire Alice Runge:** Methodology (equal); Software (equal); Writing-review & editing (equal). **Robert Heinsohn:** Conceptualization (equal); Funding acquisition (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal).

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## CONFLICTS OF INTEREST

The authors have no conflicts to declare.



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## SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

**Appendix S1.** List of 'regularly used' breeding areas identified in the Regent Honeyeater National Recovery Plan (Commonwealth of Australia 2016) included in the range-wide monitoring program.

**Appendix S2.** Variable contributions and how they differ between four periods of interest.

**Appendix S3.** Comparison of Test AUC scores when applying different lag periods (3, 6, 9 and 12 months) in a global model using all occurrence data.

**Appendix S4.** Area under the curve results with number of regent honeyeater occurrences ( $n$ ).

**Appendix S5.** Results of independent survey compared with the average breeding model predictions.

**Appendix S6.** Results of independent survey compared with the multiplied breeding model predictions.

**Appendix S7.** Location of regent honeyeater sightings (red dots) and pseudo-absences (black dots) between 2000 and 2010 included in regent honeyeater MaxEnt models.

**Appendix S8.** Annual regent honeyeater priority areas derived from MaxEnt models exemplifying temporal variation in the quantity and distribution of regent honeyeater breeding habitat.

**Appendix S9.** Boxplot showing distribution and average of predicted model values for the aggregated average raster associated with either detection (blue) or non-detection (red) cells in the independent survey.

**Appendix S10.** Output curves from MaxEnt for each variable.