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Research Article

An Occupancy Approach To Monitoring Regent Honeyeaters

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ABSTRACT Conservation of rare and highly mobile species is frequently limited by a lack of monitoring data. Critically endangered regent honeyeaters (*Anthochaera phrygia*, population 350–400) pose a substantial conservation challenge because of their high mobility and irregular settlement throughout their estimated 600,000-km^2 range. Given an ongoing population decline, enhanced monitoring efforts to inform population management are needed. We conducted an occupancy survey of regent honeyeaters and other nectarivores over 880 km^2 of the species' core range in New South Wales, Australia, during spring 2015. We located approximately 70 regent honeyeaters, potentially representing 20% of the population. Presence of regent honeyeaters was best predicted by high local nectar abundance. Detectability of regent honeyeaters when breeding (0.59) was similar to common, co-occurring nectarivores and was sufficient to distinguish absence from non-detection. For rare and highly mobile species, monitoring approaches that prioritize sampling extent over site visit duration and explicitly accommodate their life-history attributes can provide valuable population data, with subsequent benefits for conservation. © 2017 The Wildlife Society.

KEY WORDS *Anthochaera phrygia*, Australia, bird, conservation, detectability, monitoring, nomadic, spatial simultaneous autoregressive lag model, specialist, species distribution model.

Monitoring is fundamental to identifying trends in population size, evaluating the success of conservation actions, and informing future management (Lovett et al. 2007, Martin et al. 2007, Tulloch et al. 2013). Despite its importance, few threatened species are monitored in a scientifically robust way (Martin et al. 2007). Life-history traits are key determinants of the feasibility of implementing robust monitoring strategies. For instance, species that are sedentary (Olson et al. 2005), highly detectable (Martin et al. 2010), philopatric (Both and Visser 2001), or have a small geographic range (Chambers et al. 2008) provide few logistical challenges to detailed study. In contrast, sampling rare, cryptic, or highly mobile species is problematic (MacKenzie et al. 2005, Wintle et al. 2005, Runge et al. 2014, Hayes and Monfils 2015). Knowledge of the ecological requirements of these species is frequently inadequate (Cottee-Jones et al. 2015), which limits accurate assessments of their population status and the effectiveness of subsequent management actions (Clarke et al. 2003, Cunningham and Lindenmayer 2005).

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Information on species' abundance, demographics, and vital rates is ideally required to establish their conservation status (Bakker et al. 2009). However, for rare and highly mobile species, even estimating their population size, status, or distribution can be challenging, leading to a dependence on data that are not collected using a systematic sampling design (Runge et al. 2014). Because high mobility is frequently linked to habitat specialism (Stojanovic et al. 2015), modeling the distribution of mobile species can also be limited by a lack of data-rich spatial layers that can otherwise provide important information relating to a species' ecological requirements (Osborne et al. 2001). Data paucity means that conservation planning for rare and highly mobile species is usually informed by presence-only modeling techniques or expert opinion (Martin et al. 2012, Morais et al. 2013, Rayner et al. 2014). However, modeling approaches incorporating presence and absence data that also account for imperfect detection perform better than presence-only techniques (Royle et al. 2007, Webb et al. 2014). Such techniques can improve monitoring strategies, assisting conservation planning efforts and avoiding the misallocation of scarce resources (MacKenzie 2005, Martin et al. 2005).

Quantifying detectability (the probability of detection given presence) is of particular importance when monitoring rare and mobile species, for whom occupancy is likely to be low and highly variable over time (Thompson 2002,

MacKenzie et al. 2006). In addition, specialist species that form breeding aggregations often show spatial autocorrelation in their occupancy data, where monitoring sites are not spatially independent in terms of their habitat attributes or probability of occupancy (Webb et al. 2014, Bardos et al. 2015). Modeling approaches must therefore account for imperfect detection and spatial dependence to make robust inferences about a species' ecology from occupancy data (Hui et al. 2006, Rota et al. 2016). Failure to account for either phenomena can bias occupancy estimates (Olson et al. 2005, Banks-Leite et al. 2014) and false absences (failing to detect a species when present) may inhibit capacity to identify changes in the size of small populations (Jones 2011, Ferguson et al. 2015) and compromise understanding of habitat selection (Gu and Swihart 2004), potentially limiting the effectiveness of management actions (Baxter and Possingham 2011, Gilroy et al. 2012).

We considered the case of a highly mobile bird species that poses a substantial challenge to monitoring, making the development of effective conservation actions very difficult (Clarke et al. 2003, Cottee-Jones et al. 2015). The critically endangered regent honeyeater (*Anthochaera phrygia*; International Union for Conservation of Nature 2016) undertakes semi-nomadic movements in response to flowering events in a small but historically widespread number of eucalyptus (*Eucalyptus* spp.) species throughout the species' large geographic range (Franklin et al. 1989, Garnett et al. 2011). The regent honeyeater's small population size ($N = 350$–400) and dynamic movements have severely constrained attempts to accurately determine spatio-temporal changes in population size and distribution (Clarke et al. 2003). The key predictors of regent honeyeater occurrence, the factors influencing population change, and the magnitude of the population decline are poorly understood (Clarke et al. 2003). Consequently, the effectiveness of targeted recovery actions (e.g., to increase nesting success) is unknown and current capacity to undertake adaptive management is limited. Developing a robust population monitoring program is therefore a management priority for the regent honeyeater (Commonwealth of Australia 2016).

Our objective was to develop an effective sampling protocol that allows cost-effective population monitoring at an appropriate sampling scale and intensity. Specifically, we assessed the suitability of a landscape-scale occupancy survey to identify the presence (or absence) of regent honeyeaters in their core range during the breeding season, developed a sampling protocol to maximize the detectability of regent honeyeaters while minimizing the time required for a single site visit, and identified the key environmental predictors of regent honeyeater occurrence. We predicted that nectar abundance would be an important factor determining regent honeyeater occupancy (Franklin et al. 1989, Geering and French 1998, Oliver et al. 1998).

STUDY AREA

We focused on a key region known to be frequently occupied by regent honeyeaters: the Capertee Valley subregion of the New South Wales southwestern slopes bioregion (Australian Department of the Environment and Energy 2016). The study area covered 880 km^2 of the southern Capertee River sub-catchment (bounded by −32.89°, 149.94° and −32.23°, 150.31°) from where regent honeyeaters are most frequently reported (Fig. 1). For further information on the study area, including topography, climate, land uses, and dominant flora, see Geering and French (1998) and Australian Department of the Environment and Energy (2016).

METHODS

Survey Design

We generated 600 random survey points within the study area using ArcMap v10.2 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Survey sites contained ≥1 documented regent honeyeater food tree species (Table S1, available online in Supporting Information). We defined a site as a 50-m radius surrounding each point. We attempted to access as many survey points as possible, subsequently excluding points where land access was not possible. We moved sites up to 200 m from the original random point to locations that supported a higher abundance of food tree species. We ensured a minimum distance of 150 m between sites so that, when individuals were present and nesting, the chances of detecting the same individuals at adjacent sites were minimized. At sites where we detected regent honeyeaters, we used an adaptive sampling approach (Smith et al. 2004) to add further survey sites 150 m from occupied sites or in the closest area with food tree species beyond this distance. Using this approach, we surveyed 321 sites across the study area (Fig. 1).

We conducted repeated 5-minute point-counts to record detection or non-detection data for regent honeyeaters and other nectarivores. To minimize violation of the assumption of closure (a change in the occupancy status of each site during the survey period; MacKenzie et al. 2006), we surveyed each site 3 times (MacKenzie and Royle 2005) in a 1-month window starting on 26 September 2015. We considered a site to be occupied if a bird was present and using the site (i.e., not flying through it). The same observer (RC) conducted surveys at all times throughout the day but not in weather conditions that were likely to compromise detectability (e.g., rain, winds >30 km/hour or temperatures >35°C). Because regent honeyeaters are responsive to song broadcast when breeding (Geering 1998), we broadcast regent honeyeater vocalizations (Pizzey and Knight 2014) using portable speakers for the first minute of each site visit. Based on known nest territory sizes (Geering and French 1998) and speaker volume, we assumed 50 m as a maximum distance that regent honeyeaters, given presence, would initiate a detectable response to playback. We recorded detections as one of a sighting, passive vocal detection, or response to playback. If we located a nest at a site during previous surveys, we specifically did not focus effort on the nest location and relied solely on the detection methods outlined above.

We divided site and visit-level covariates into those affecting occupancy and detectability, respectively (Table 1). To

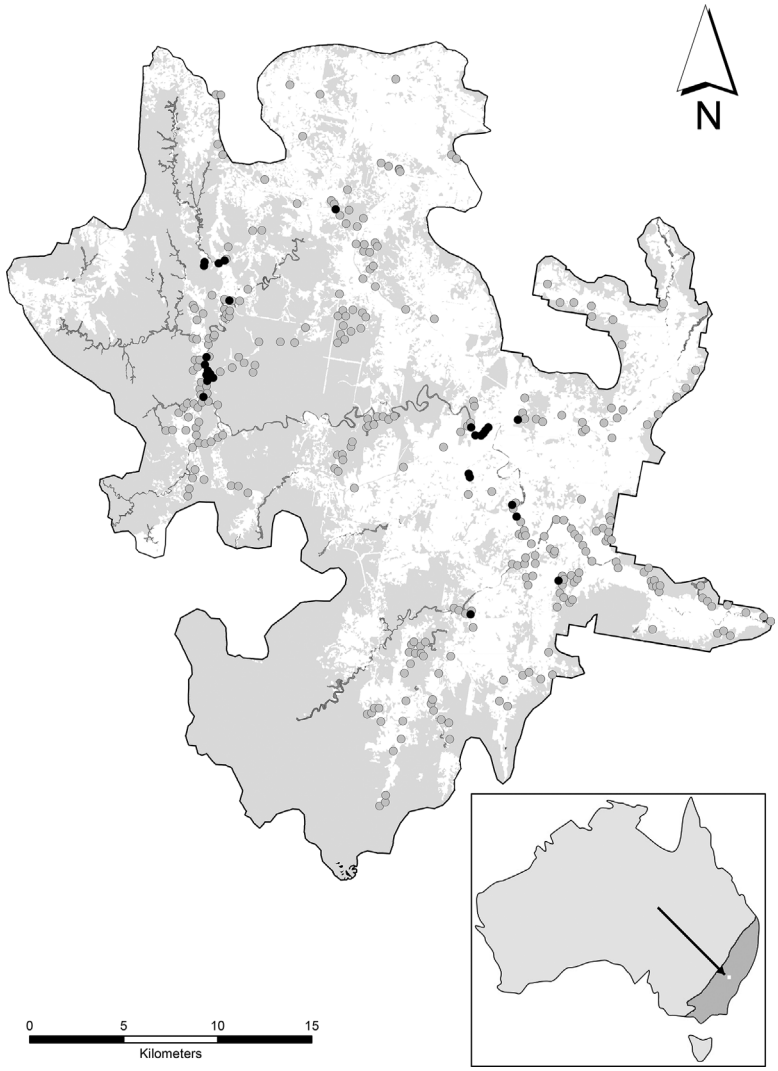

Figure 1. Capertee Valley study area, New South Wales, Australia. Circles represent location of survey sites where regent honeyeaters were (black) and were not (gray) detected in spring 2015. White areas represent cleared or severely disturbed land, shaded areas are vegetated (though not necessarily suitable regent honeyeater habitat). Riparian areas are in dark gray. Inset: location of study area (white square) within the regent honeyeater's 6000,000-km^2 range (dark gray).

calculate an index of estimated nectar abundance at each site (nectar score), we recorded a flowering index at every flowering tree within each site as 1–5, representing <10%, 11–30%, 31–60%, 61–90%, and >90% of crown area in flower, respectively. We scored the crown size of each flowering tree as 1, 3, or 9 to account for the relative crown volume of small (<40 cm trunk diameter at breast height; DBH), medium (40–100 cm DBH), and large (>100 cm DBH) trees, respectively. We accounted for variability in nectar concentration and volume among tree species (Oliver 2000, Law and Chidel 2008) by applying a correction factor to each tree species according to their nectar productivity (Oliver 2000; Table S1). We calculated site-level nectar scores for each visit as the sum of the nectar score (flowering index × crown size score × nectar productivity) for all flowering trees on site and used the mean of these values across the 3 visits as an overall site nectar score. Our nectar score was highly variable across sites and had a highly skewed distribution (range = 0–40.11, $\bar{x} = 3.9$, inter-quartile range = 3.06). To allow the inclusion of the nectar covariate as a factor in the models, we grouped the mean site values into scores from 0 to 4 (0, 0.01–1, 1.01–3, 3.01–10, >10, respectively). We used this coarse index of nectar because of the need to account for variation in nectar productivity across eucalyptus species (and their relative importance to regent honeyeaters). We assumed our index of overall nectar productivity was a more accurate reflection of actual nectar abundance than if we ignored tree species and size (Oliver et al. 1999, Oliver 2000). We conducted research under an Australian National University animal ethics license (no. A2015/28), New South Wales scientific license (no. 101603), and Australian Bird and Bat Banding Service banding licenses (no. 2633, no. 3192).

Statistical Analysis

For each nectarivore species, we fitted single-season zero-inflated binomial (ZIB) occupancy models based on a robust survey design (MacKenzie et al. 2006) in the program PRESENCE v10.2 (MacKenzie et al. 2002, Hines 2006).

Table 1. Description of covariates tested in single-season occupancy models of the regent honeyeater and other nectarivores in the Capertee Valley, New South Wales, Australia, spring 2015. We grouped covariates by site-level or visit-level and according to their input in the model (i.e., predicted to affect detectability or occupancy).

Level, input[a]	Covariate	Description	Justification
Site, detectability	Canopy	Estimated % canopy cover in survey area (50-m radius around survey point) to nearest 20%.	Detectability of nectarivores likely correlated with vegetation cover (Thompson 2002).
	Density	Vegetation density. Categorical value based on <50%, 51–75%, or >75% density.	Detectability of regent honeyeaters likely negatively correlated with vegetation density (Thompson 2002).
Site, occupancy	Location	X-Y point location. Triangulated as a spatial weights autocovariate.	Explains substantial proportion of variation in occupancy in aggregating species (Webb et al. 2014). Necessary to account for spatial autocorrelation.
	Water	Linear distance to the nearest water source, grouped by <50 m, 51–100 m, 101–300 m, 301–500 m, >500 m.	Regent honeyeaters often associated with riparian zones (Geering and French 1998) and bird baths (BirdLife Australia, unpublished data).
	Mistletoe	No. clumps of live or dead mistletoe in survey area grouped into none (0), 1–5 plants (1), or >5 plants (2).	Mistletoe abundance positively influences local bird diversity (Watson and Herring 2012). Often used by regent honeyeaters as a nesting substrate (Oliver et al. 1998).
	Competitor presence	Detection or non-detection of species larger than regent honeyeaters: noisy miner, noisy friarbird, red wattlebird, and musk lorikeet.	Presence of competitors likely to negatively affect occupancy through interspecific competition or aggressive displacement (Ford 1979, Mac Nally et al. 2012).
	Large flowering trees	No. large flowering trees of the key species (yellow box, mugga ironbark, Blakely's red gum [*E. blakelyi*]) >50 <150 m of survey site.	Large flowering trees likely positively related with regent honeyeater site occupancy (Oliver et al. 1999). Habitat occupancy likely determined by floral attributes at local scale beyond point count area.
	Nectar	Nectar score from 0–4 based on equation (1), averaged across 3 site visits.	Temporal stability of nectar may be important for occupancy related to breeding. Nectar abundance likely to govern occupancy by nectarivores (Mac Nally and McGoldrick 1996, Bennett et al. 2014).
Visit, detectability	Time	2-level factor, early morning-evening or mid-day.	Likely quadratic relationship with detectability, with peaks in morning and evening, and a decrease during mid-day (Field et al. 2002).
	Week	Week of survey season in which each survey was undertaken. Ordinal value from 1–4.	May affect (either positively or negatively) site occupancy or detectability due to change in breeding stage or status. Interval between repeat visits likely to affect closure assumption.
	Noise	Background noise (e.g., wind, other bird species) 3-level categorical, none, low, moderate	Background noise may affect aural detectability.

[a] Some covariates may influence both occupancy and detectability. Because of the limited number of sites where we detected regent honeyeaters, we only tested an effect on either occupancy or detectability, based on our predictions.

We first fitted models with constant occupancy including only detectability covariates (Table 1) to compare the fit of a constant or a site-specific estimate of detectability for each species. Based on lowest quasi Akaike's Information Criterion ($QAIC_c$) scores, we chosen the most parsimonious models as the best models ($\Delta QAIC_c < 2$). We supplemented model assessment with 500 bootstrap simulations, accounting for overdispersion by adjusting c-hat if the model estimate of c-hat was >1 (MacKenzie et al. 2006). Once we established the best covariates for constant occupancy models using this process, we added covariates to the occupancy component of the models and repeated the model selection process, again with the most parsimonious models selected ($\Delta QAIC_c < 2$). Distance from water was highly correlated with large flowering trees ($r = 0.75$), so we did not include both of these covariates in the same model.

For the remaining analyses, we focused solely on the regent honeyeater, with a primary objective of clarifying factors influencing occupancy for this species. First we assessed the degree of spatial autocorrelation in regent honeyeater detection or non-detection data using correlograms (based on Moran's I statistic; Tiefelsdorf 2000) implemented in R (R Version 3.2.3, https://cran.r-project.org, accessed 27 Apr 2016), using the package ncf (Bjornstad 2015). Because the correlograms indicated significant spatial autocorrelation in the data (see Results section), we explored modeling approaches that complemented the PRESENCE analyses by explicitly accounting for spatial autocorrelation. We first tried fitting models that simultaneously accounted for spatial autocorrelation and imperfect detection using zero-inflated binomial models implemented using the EM Algorithm (Webb et al., 2014). However, the bivariate smooth spatial covariate in the occupancy component of these ZIBs caused overfitting (as indicated by an adjusted R^2 of 1 and 100% of deviance explained in the occupancy component of the model), and was clearly not an appropriate way to deal with the spatial autocorrelation present in these data.

We therefore tried alternative modeling approaches that account for spatial autocorrelation but which assume detection = 1. These approaches were generalized linear mixed models with site or region as random effects, generalized additive models with latitude and longitude as a smooth bivariate term, and spatial simultaneous autoregressive lag models (SARs), including a triangulated weights matrix as a spatial autocovariate. We considered these approaches appropriate and justified for 2 reasons. First, the importance of accounting for spatial autocorrelation in similar studies has been demonstrated (Koenig 1999, Webb et al. 2014). Second, detectability in the PRESENCE models was sufficiently high (and constant) to assume detectability = 1 (see Results section and Fig. S1; Garrard et al. 2008). Of these alternative approaches, model diagnostics indicated SARs were the most appropriate choice. We implemented SARs using the spdep package (Bivand 2014) in R, with the weights matrix calculated using the tri2nb function in the deldir package (Turner 2016). We ranked SARs and chose the best model based on lowest AIC values.

RESULTS

We detected regent honeyeaters at 27 of the 321 sites (Fig. 1); 19% of detections were visual sightings, 50% were passive vocal detections, and 31% were direct responses to song broadcast. The median number of birds detected/visit at occupied sites was 2 (range = 1–7). Thus, reducing abundance data to presence-absence in analyses resulted in minimal loss of information.

Correlograms indicated regent honeyeater detection or non-detection data were positively spatially autocorrelated in the distance classes of 0–1 km and 2–3.5 km (Fig. 2). The variable week was the only covariate that influenced detectability (Table 2), though including week offered only a marginal improvement on constant detectability ($\Delta QAIC_c = 1.43$). Once we added occupancy covariates (Table 1) to the occupancy component of the models, the effect of week on detectability was further reduced ($\Delta QAIC_c = 0.57$; Table 3). We therefore assumed constant detectability to be appropriate for all subsequent analyses. Under this assumption of constant detection, we estimated detectability of regent honeyeaters to be 0.59 ± 0.07 (SE) in the best model. This was in the mid-range of estimates for the wider nectarivore community and considerably higher than estimates for some other common nectarivores (Fig. 3). Given estimated detectability of 0.59 and that sites were visited on 3 occasions, the absence of regent honeyeaters from a site could be inferred with a high degree of confidence (Fig. S1; Garrard et al. 2008).

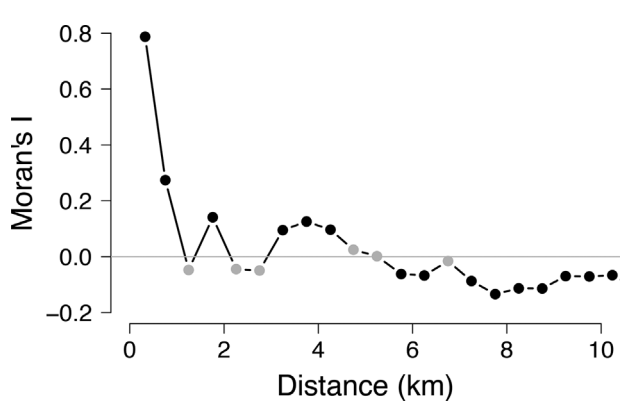

Figure 2. Spatial autocorrelation (Moran's I) of regent honeyeater detection or non-detection during a single-season occupancy survey in the Capertee Valley, New South Wales, Australia, spring 2015. Black points represent significant spatial autocorrelation ($P < 0.05$) and gray points represent non-significant spatial autocorrelation.

Occupancy models without a spatial autocovariate (ZIB implemented in PRESENCE) indicated that large flowering trees and mean nectar abundance were the strongest predictors of site occupancy by regent honeyeaters (Tables 2 and 3). The best SAR models (as indicated by $\Delta QAIC_c < 2$) also included the covariates large flowering trees ($\beta = 0.057 \pm 0.014$ [SE], $Z = 4.224$, $P < 0.001$) and nectar score ($\beta = 0.034 \pm 0.012$, $Z = 2.822$, $P = 0.005$), similarly indicating their importance as drivers of regent honeyeater occupancy. Site-level occupancy predictions from ZIB and SAR models were significantly correlated (Pearson's 2-sided test $r = 0.57$, 95% CI = 0.46–0.66, $P < 0.001$). However, the SARs predicted many more sites with low occupancy probabilities (i.e., <0.1), and more sites with higher probabilities of being occupied (i.e., 0.6–0.8; Fig. S2).

In addition to insights provided by the modeling analyses, our observations indicated that habitat at monitoring sites occupied by regent honeyeaters were characterized by riparian corridors with adjacent flowering yellow box (*Eucalyptus melliodora*) and high abundance of flowering needle-leaf mistletoe (*Amyaema cambageii*), narrow strips of remnant valley floor vegetation (yellow box and mugga ironbark [*E. sideroxylon*]) on the lower slopes of hillsides, or small clusters of large yellow box paddock trees in highly degraded agricultural land (Fig. 1 and S3). Although regent honeyeaters occupied sites with high estimated nectar abundance, they were not detected at survey sites estimated to have the very highest abundance of nectar at the landscape scale (Fig. 4). Occupancy surveys led to the subsequent identification of 32 nesting attempts, all but one of which were located within 120 m of a survey site at which regent honeyeaters were detected (Fig. S3).

DISCUSSION

Collecting meaningful presence-absence data to estimate the geographic distribution and occupancy rates of regent honeyeaters during their breeding season is possible, despite the challenges posed by their mobile life history and small population size. Even though site occupancy was low, regent honeyeaters were sufficiently detectable when nesting to enable a rapid, regional-scale, intensive survey. By increasing detectability (e.g., use of song broadcast, small area of each individual monitoring site, surveyed early in nesting season) and minimizing the duration of site visits, future monitoring efforts can increase the spatial coverage and intensity of sampling and refine site location based on predictors of occurrence, without introducing bias caused by false absences.

Table 2. Importance of individual covariates in determining regent honeyeater habitat occupancy (Ψ) and detectability (p) in the Capertee Valley, New South Wales, Australia, spring 2015. Covariates are grouped by category and ranked by quasi Akaike's Information Criterion ($QAIC_c$).

Covariate category	Model[a]	$QAIC_c$	$\Delta QAIC_c$	Overall $QAIC_c$ rank
Nectar	Ψ(nectar) · p(constant)	96.34	0.00	1
	Ψ(large FT) · p(constant)	98.03	1.69	2
Habitat	Ψ(NF) · p(constant)	102.74	6.40	3
	Ψ(water) · p(constant)	107.32	10.98	4
	Ψ(RW) · p(constant)	111.99	15.65	6
	Ψ(ML) · p(constant)	113.31	16.97	8
	Ψ(mistletoe) · p(constant)	113.42	17.08	9
	Ψ(density) · p(constant)	113.42	17.08	10
	Ψ(canopy) · p(constant)	113.60	17.26	13
	Ψ(NM) · p(constant)	114.69	18.35	14
Detectability	Ψ(1) · p(week)	110.87	14.53	5
	Ψ(1) · p(constant)	112.30	15.96	7
	Ψ(1) · p(noise)	113.71	17.37	11
	Ψ(1) · p(time)	114.44	18.10	12
	Ψ(1) · p(survey-specific)	116.06	19.72	15

[a] Large FT = large flowering trees; NF = noisy friarbird; RW = red wattlebird; ML = musk lorikeet; density = vegetation density; NM = noisy miner.

Sampling intensively and extensively is critical for monitoring rare and mobile species because it improves capacity to detect spatiotemporal changes in occupancy patterns (Koenig et al. 1996) and population trends (Clarke et al. 2003). These survey attributes are particularly important when a substantial proportion of the population may aggregate in relatively small areas (Smith et al. 2004, Webb et al 2014). For instance, we located approximately 70 regent honeyeaters, potentially representing 20% of the entire population (Garnett et al. 2011, Commonwealth of Australia 2016), through our monitoring efforts in a single season. A significant new breeding site (comprising a third of occupied sites) was also identified in a region that has previously been subject to long-term survey effort (Fig. S3). Furthermore, our sampling design provided a spatially explicit guide to the location of breeding activity; 94% of all wild regent honeyeater nests recorded in 2015 (BirdLife Australia, unpublished data) were subsequently found near occupied sites (Fig. S3).

Given the survey protocol, the detectability of regent honeyeaters was much higher than expected for such a rare species. Indeed, detectability was similar to or greater than that of some other common nectarivores such as the little (*Glossopsitta pusilla*) and musk lorikeet (*G. concinna*). In contrast, resident and abundant species such as the noisy miner (*Manorina melanocephala*) and white-plumed honeyeater (*Lichenostomus penicillatus*) were highly detectable. We obtained a relatively high detectability estimate for regent honeyeaters by commencing surveys during the early stages of their breeding season. During this period, regent honeyeaters are largely sedentary, highly vocal, and aggressive while establishing and defending small breeding territories (Ford et al. 1993). Thus, difficulties associated

Table 3. Top (Δ quasi Akaike's Information Criterion <2) occupancy (Ψ) models (zero-inflated binomials) of regent honeyeater detection or non-detection data in the Capertee Valley, New South Wales, Australia, spring 2015. Models account for imperfect detection (p) but not spatial autocorrelation and are ranked by Akaike weight (w_i). We present models with difference in quasi Akaike's Information Criterion ($\Delta QAIC_c$) <2.

Model[a]	$QAIC_c$	$\Delta QAIC_c$	w_i
Ψ(nectar) · p(week)	69.86	0.00	0.216
Ψ(nectar) · p(constant)	70.43	0.57	0.201
Ψ(nectar + large FT) · p(week)	70.50	0.64	0.127
Ψ(nectar + large FT) · p(constant)	70.78	0.92	0.098
Ψ(large FT) · p(week)	70.97	1.11	0.097

[a] Large FT = large flowering trees.

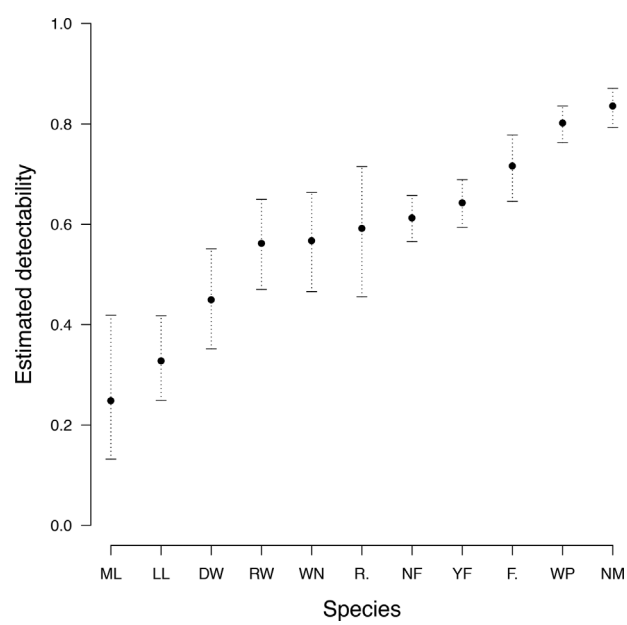

Figure 3. Estimated constant detectability (±95% CI) of nectarivores surveyed in the Capertee Valley, New South Wales, Australia, spring 2015, from zero-inflated binomial models fit in PRESENCE. Species abbreviations (with sample sizes): ML, musk lorikeet (28); LL, little lorikeet (36); DW, dusky woodswallow (*Artamus cyanopterus*, 50); RW, red wattlebird (*Anthochaera carunculata*, 57); WN, white-naped honeyeater (*Melithreptus lunatus*, 46); R., regent honeyeater (27); NF, noisy friarbird (*Philemon corniculatus*, 180); YF, yellow-faced honeyeater (*Lichenostomus chrysops*, 166); F. fuscous honeyeater (*Lichenostomus fuscus*, 71); WP, white-plumed honeyeater (167); NM, noisy miner (126).

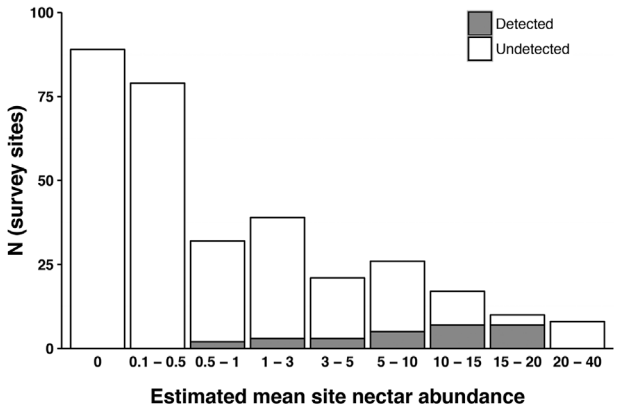

Figure 4. Frequency distribution of mean estimated nectar abundance of survey sites in the Capertee Valley, New South Wales, Australia, spring 2015, that were (gray bars) or were not (white bars) occupied by regent honeyeaters.

with their mobile life history are largely negated during this period as nesting birds become central place foragers. Although detectability may decrease during incubation and the early nestling stage as birds become less vocal, the use of song broadcast serves as a means to maintain high detectability throughout the nesting period. Time of day had no effect on detectability, indicating surveys are viable throughout the day. This not only facilitates increased spatial survey coverage but also allow surveys to be conducted within as short a time window as possible, minimizing closure violations (Rota et al. 2009).

Although some violation of the closure assumption is unavoidable when monitoring highly mobile species (Hayes and Monfils 2015), we attempted to maximize closure with our survey design (i.e., short survey season coinciding with early nesting period, small sites located in core habitat). Regent honeyeaters that are unsuccessful breeders often disperse from nesting sites shortly after nest failure (Geering and French 1998). Because repeated site visits after an initial detection, but following nest failure and dispersal, are likely to decrease detectability estimates, the detectability of nesting regent honeyeaters (excluding transient non-breeders) may well be even higher than our estimate of 0.59. Timing surveys to coincide with the early stages of breeding is also critical because the cumulative probability of nesting failure increases with time (Dinsmore et al. 2002). Failing to locate regent honeyeaters during the early stages of their breeding period may therefore result in underestimated occupancy rates and overestimates of nesting success (Kidd et al. 2015).

The significant positive spatial autocorrelation we found in the distribution of regent honeyeater presence or absence data in the distance classes of 0–1 km and 2–3.5 km represents the distances between small aggregations of nesting regent honeyeaters detected across the study area (Fig. 1 and S3). Despite the low number of sites at which regent honeyeaters were detected, we were able to fit relatively simple occupancy models that accounted for spatial autocorrelation. Although occupancy predictions from these spatial models indicated similar predictors to the zero-inflated models (from PRESENCE), the frequency distribution of site occupancy probabilities differed between the approaches (Fig. S2). This difference highlights the importance of accounting for spatial autocorrelation in species that aggregate and is likely attributable to unmeasured variables or conspecific attraction (Webb et al 2014).

As predicted, regent honeyeater occupancy was largely determined by the abundant flowering of their food trees. However, we did not detect regent honeyeaters at the richest flowering sites in the landscape, possibly because of competitive exclusion by larger nectarivores (Ford 1979, Rota et al. 2016). Throughout the range of the regent honeyeater, negative associations between the noisy miner, a hyper-aggressive native honeyeater, and small-bodied birds have been documented (Piper and Catterall 2003, Mac Nally et al. 2012). However, too few data were available to confidently assess the effect of competitors on regent honeyeater site occupancy. Given their rarity, multiple seasons of monitoring data are likely required to help clarify the influence of aggressive competitors on regent honeyeater settlement decisions. Although there was some evidence that distance to water may also influence regent honeyeater occupancy (Table 2), the best models did not include this variable, most likely attributable to the positive correlation with large flowering trees. Nevertheless, we rarely detected regent honeyeaters more than 150 m from a water source. Gaining a better understanding of the potential importance of distance to water for breeding regent honeyeaters may further increase the efficiency of future monitoring and enable better targeting of conservation actions.

MANAGEMENT IMPLICATIONS

When devising monitoring approaches for rare and highly mobile species, maximizing detectability during short site visits allows much greater spatial coverage without compromising data quality (e.g., false absences). Spatial autoregressive lag models offer a promising means of accounting for spatial autocorrelation when modeling the occurrence of rare species with sparse data, providing more realistic occurrence probabilities. Such an approach provides spatially comprehensive estimates of population distributions that can greatly enhance the efficiency of conservation planning and future population monitoring. Our findings reinforce that mobility and scarcity do not necessarily impede the collection of highly valuable data for species that might otherwise be dismissed as too challenging to study in detail.

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