




Contemporary breeding biology of critically endangered Regent Honeyeaters: implications for conservation

ROSS CRATES,*  LAURA RAYNER, DEJAN STOJANOVIC,  MATTHEW WEBB,  ALEKS TERAUDS & ROBERT HEINSOHN

Fenner School of Environment and Society, Linnaeus Way, Acton, Canberra, ACT 2601, Australia

Identifying factors influencing the demographics of threatened species is essential for conservation, but a lack of comprehensive demographic data often impedes the effective conservation of rare and mobile species. We monitored breeding of critically endangered and semi-nomadic Regent Honeyeaters *Anthochaera phrygia* (global population *c.* 100 pairs) over 3 years throughout their range. Overall nest success probability (0.317) was highly spatially variable and considerably lower than previous estimates for this (and many other honeyeater) species, as was productivity of successful nests (mean 1.58 juveniles fledged). Nest surveillance revealed high predation rates by a range of birds and arboreal mammals as the primary cause of nest failure. An estimated 12% of pairs either failed to establish a territory or their nests did not reach the egg stage. We also found a male bias to the adult sex ratio, with an estimated 1.18 males per female. Juvenile survival for the first 2 weeks after fledging was high (86%). Management interventions that aim to increase nest success in areas of low nest survival must be investigated to address an apparent decline in reproductive output and avoid extinction of the Regent Honeyeater. We show that temporal and spatial variation in the breeding success of rare and highly mobile species can be quantified with robust population monitoring using sampling regimens that account for their life histories. Understanding the causes of spatio-temporal variation in breeding success can enhance conservation outcomes for such species through spatially and temporally targeted recovery actions.

Keywords: Allee effect, *Anthochaera phrygia*, juvenile survival, nest predators, nest survival, sex ratio.

Robust modelling of population trajectories requires accurate and precise estimates of demographic parameters (Brook *et al.* 2000) and identification of the factors influencing these parameters is vital for effective conservation (Caughley 1994). For rare and highly mobile species, collecting demographic data can be challenging (Runge *et al.* 2014, Cottee-Jones *et al.* 2015). Consequently, identifying the drivers of population decline in such species is often based on limited data (Rayner *et al.* 2014), reducing the accuracy of estimated demographic parameters. Sampling populations of

widespread species in a subset of their range or over short time periods could lead to biased estimates of breeding success if reproductive parameters vary in space and time (Paradis *et al.* 2000, Stojanovic *et al.* 2014) or are a function of population size or density (Stephens & Sutherland 1999). Thus, data limitations can inhibit detection of limits to population recovery, potentially leading to misallocation of conservation resources (McDonald-Madden *et al.* 2010).

Population growth rates can also be compromised by biased adult sex ratios (the ratio of sexually active males to fertilizable females; Donald 2007) because members of the more abundant sex may be unable to find mates (Gascoigne *et al.* 2009). Biased adult sex ratios are relevant to

*Corresponding author.
Email: ross.crates@gmail.com
Twitter: @CratesRoss

threatened species recovery efforts, via conservation measures to increase numbers of the rarer sex (Ewen *et al.* 2001). Sex ratios are also often spatially variable (Steiffetten & Dale 2006) with implications for determining where recovery effort should be invested (Wedekind 2002). However, robust sex ratio estimates are seldom available for rare and mobile species due to perceived challenges of collecting necessary data (Donald 2007).

We monitored reproduction in the wild population of the critically endangered Regent Honeyeater *Anthochaera phrygia*. The species' estimated population of 350–400 individuals (Kvistad *et al.* 2015) and patchy occurrence across up to 600 000 km² of south-eastern Australia (Commonwealth of Australia 2016) poses challenges for conservation research (Clarke *et al.* 2003a). Historically, Regent Honeyeaters were considered abundant but there has been a rapid population decline since the 1960s (Franklin *et al.* 1989). This decline is primarily attributed to extensive clearing of preferred box-gum-ironbark woodland habitats (Ford *et al.* 1993, 2001), but the demographic factors underlying contemporary population trends are poorly understood (Clarke *et al.* 2003a, Crates *et al.* 2017a).

Regent Honeyeaters build open-cup nests, typically in the outer branches of large trees. They form socially monogamous pairs and nest in loose aggregations in association with the flowering of a select number of *Eucalyptus* tree species (Franklin *et al.* 1989). Parents provision juveniles in separate family groups for 2–3 weeks post-fledging, almost exclusively within 200 m of the nest-site (R. Crates pers. obs). Post-breeding, Regent Honeyeaters form flocks consisting of adults and independent juveniles (Geering & French 1998). Estimates of nesting success (probability of fledging one or more juvenile) in the 1990s were comparable to other Australian honeyeaters (38–47%), leading to the conclusion that low nesting success was not driving population decline (Geering & French 1998, Oliver *et al.* 1998). Current recovery actions focus on biannual releases of captive-bred individuals to the southern edge of the species' contemporary range, and small-scale protection and restoration of habitat (Commonwealth of Australia 2016). No standardized nest monitoring has been undertaken for over 20 years, but given the Regent Honeyeater's conservation status, reassessment of key breeding parameters is a conservation priority (Commonwealth of Australia 2016).

To inform conservation management of the wild Regent Honeyeater population, we aimed to develop a range-wide monitoring programme to locate breeding Regent Honeyeaters. We then aimed to estimate the adult sex ratio and contemporary nesting success and to identify factors affecting these parameters. We also aimed to estimate short-term post-fledging juvenile survival. Lastly, we compared our estimates with historical studies for the Regent Honeyeater and other Australian honeyeaters.

METHODS

Locating Regent Honeyeaters

We searched for Regent Honeyeaters over three breeding seasons. In 2015, we surveyed 321 sites over 880 km² of the Capertee Valley, New South Wales, a known core breeding region for the remaining population (Crates *et al.* 2017b). We then expanded our sampling across the entire contemporary range, surveying 777 and 896 sites in 2016 and 2017, respectively (Supporting Information Table S1 and Fig. S1). Sites were spaced ≥ 150 m apart in Regent Honeyeater breeding habitat (Commonwealth of Australia 2016) and were selected based on a combination of habitat identified as high priority by a species distribution model constructed in 'MaxEnt' (L. Rayner *et al.* unpubl. data), expert advice and extensive field searches for potential breeding habitat.

We visited all sites in the Capertee Valley three times in 2015. In 2016, we visited 777 sites twice, with 371 of those being visited a third time. In 2017, we increased the number of survey sites to 896, of which 610 sites were visited twice (Table S1). In total, 5949 site visits were made over the course of our study. Site visits comprised a 5-min point count within a 50-m radius, with Regent Honeyeater song broadcast (Pizzey & Knight 2014) from portable speakers in the first survey minute (Crates *et al.* 2017b). We also recorded and monitored all Regent Honeyeaters detected (visually or audibly) > 50 m from survey sites or outside the 5-min survey window.

Estimating sex ratios

Where Regent Honeyeaters were detected, we undertook repeated adaptive sampling to search for additional birds nearby (Smith *et al.* 2004).

Follow-up searches commenced as soon as possible, and not more than 4 days after the first Regent Honeyeater detection at a site. We marked a sample of individuals (20 females, 48 males) with coloured leg bands using mist-nests and assigned sex based on wing length, plumage and mass (Geering 2010). We then determined the number of individuals present in each aggregation (defined as a group of birds loosely distributed over an area of 2–20 ha), their sex and nesting status. The maximum number of individuals present in each aggregation was estimated during adaptive sampling through combined monitoring of nests, colour-banded individuals and unpaired males. Because aggregations were largely monitored simultaneously within years, movement of individuals between aggregations was minimized. Only two colour-banded individuals were detected in more than one aggregation in the same year; these individuals and their unmarked partners were accounted for in counts. We sexed unmarked birds in the field based on plumage, size and song characteristics, as only males vocalize a full song (R. Crates pers. obs.). We estimated the sex ratio of nesting aggregations by collating data from all Regent Honeyeaters observed at sites (including all colour-marked birds, unmarked pairs and individuals). Unpaired males at nesting aggregations were readily identified by their persistent singing, lack of an accompanying female and the small number of birds in each aggregation. Because nests were invariably inaccessible, we were unable to estimate nestling sex ratios.

Locating and monitoring nests

We located nests by observing bird behaviour (i.e. nest construction, incubating females or parents provisioning young). For nests where egg-laying dates were not known, we estimated initiation date based on a 34-day nesting period with eggs laid on consecutive days, 14 days of incubation and a 19-day nestling period. The nestling period was calculated based on our own observations of 13 successful nests monitored from the date the first egg was laid, which was 2–3 days longer than reported in Geering and French (1998) and Oliver *et al.* (1998). Initiation date could not be estimated to within ± 2 days for two nests, which were excluded from analyses. Because of the small number of pairs at each nesting aggregation ($n = 22$ aggregations, mean n pairs = 6 ± 4.7 sd, range = 1–14), we were

confident that effectively all nesting attempts were located and monitored. We observed nests (mean height = $13 \text{ m} \pm 4.69$ sd, range = 3–25 m) from the ground every 2–7 days using the presence and behaviour of adults to determine whether nests were active. We recorded the nectar sources associated with each nest by observing the tree and mistletoe species in which the adults were foraging.

To identify the causes of nest failure, we deployed wireless infra-red video cameras between 2 and 8 m distant from 14 nests accessible by tree climbing. Where we could not confirm the cause of nest failure, it was assumed where possible: for example, if failed nests were damaged or empty, we assumed that predation had occurred and if intact nests were found on the ground following a period of high winds, we assumed that wind had dislodged the nest.

Post-fledging juvenile survival

At successful nests and where logistically possible, we monitored juvenile survival every 2–4 days for the first 2 weeks after fledging. Juveniles were readily detected by their persistent begging calls (R. Crates pers. obs.). We identified juveniles via the colour bands on the parents provisioning them or because there were no other recently fledged juveniles present concurrently within 200 m.

Data analysis

We modelled the daily survival rate (DSR) of Regent Honeyeater nests in R v3.2.3 (R Core Development Team 2017) using package 'RMark' v2.2.2 (Laake *et al.* 2016), an R-interface for the nest survival model (Dinsmore *et al.* 2002) in the program 'MARK' (White & Burnham 1999, Cooch & White 2001). By calculating daily survival probabilities, these models account for undetected nests in survival estimates (Dinsmore & Dinsmore 2007). We obtained the best-supported nest survival models based on lowest corrected Akaike information criterion (AIC_c) values (Burnham & Anderson 2002). Because it is difficult to assess reliably the goodness of fit of nest survival models (Sturdivant *et al.* 2007), we avoided overfitting by including a maximum of three covariates per model (Table 1).

We assessed spatial autocorrelation in range-wide nesting success (binomial response: fail or

fledge one or more juveniles, sampling distance 50 km) and within the core range of the Capertee Valley (sampling distance 500 m) using correlograms (based on Moran's I, Tiefelsdorf 2000) using the R-package 'ncf' (Bjornstad 2015). To account explicitly for spatial dependence in nest success (which is not possible with nest survival models using RMark), we modelled range-wide nest success including a spatial term. The response metric was daily nest failure probability, calculated using the 'successes per failure' syntax (Aebischer 1999, Shaffer & Thompson 2007). Where the exact day of nest failure was unknown, we assumed nest failure occurred on the median day between visits. We evaluated three spatial modelling approaches: spatial autoregressive lag models, generalized linear models with a spatial autocovariate and generalized additive models (GAMs) with a spatial covariate. Model diagnostics (analysis of residuals and adequacy of basis dimensions of smoothed spatial terms, *sensu* Wood 2017) indicated that GAMs were the most appropriate choice given the distribution of nests throughout the range. We fitted GAMs using the R-package 'mgcv' (Wood 2018), with a binomial link function and nest location (latitude/longitude) as a smoothed spatial covariate. Unlike nest survival models, GAMs also allow the inclusion of random terms. We therefore included Pair ID as a random term because 15% of nests were known to be second attempts by the same pair in the same season. We used MuMIn v1.40.4 (Bartoń 2018) to find the most parsimonious models from the global model, based on the lowest AIC_c value (Burnham & Anderson 2002).

To estimate juvenile survival for the fortnight post-fledging, we fitted constant and age-trend nest survival models using RMark for 56 juveniles from 42 nests in the greater Blue Mountains. Constant nest survival models assume that daily survival does not change during the post-fledging period, whereas age-trend models account for potential temporal changes in daily juvenile survival (Dinsmore & Dinsmore 2007). Thus, each juvenile was 'found' on the first day it fledged, and 'succeeded' if it survived for 14 days post-fledging, regardless of the fate of any siblings. To account for potential non-independence of the fate of siblings ($n = 13$ nests), we ran the models twice more, randomly sampling just one juvenile from each nest.

To compare our Regent Honeyeater nest success and productivity estimates with other studies of Australian honeyeaters, we conducted a

literature search in Google Scholar using the terms 'nest survival', 'nest success', 'honeyeater' and 'Australia'. We included all independent studies of honeyeater species returned by the literature search to accumulate a database of nest success estimates and associated spatio-temporal metadata (see Table 3).

RESULTS

We detected Regent Honeyeaters at 27 monitoring sites in 2015, at 39 sites in 2016, and at 53 sites in 2017 (Table S1). We detected a minimum of 70 adult birds (age ≥ 1 year) in the Capertee Valley in 2015, 73 adult birds range-wide in 2016, and 145 adult birds range-wide in 2017. This represented 30–65% of the estimated effective population each year (Kvistad *et al.* 2015, Commonwealth of Australia 2016). We colour-marked individuals in the Severn River (1 female (F), 7 males (M)), Barraba (2 M), Goulburn River (1 F, 3 M) and Capertee Valley (18 F, 38 M), 94% of which were > 1 year old. The range-wide adult sex ratio was 1.18, but small breeding aggregations in the Northern Tablelands (Barraba and Severn River) were more male-biased (Fig. 1).

An estimated 12% of potential breeding pairs (exhibiting territorial aggression and male singing) failed either to gain a territory or to lay eggs. In the Capertee Valley, 17 pairs fitted these criteria over 3 years, and in the broader range, six pairs failed to breed in this way.

We found 119 Regent Honeyeater nests reaching the egg stage in five regions of New South Wales: The Capertee and Burragorang Valleys, Goulburn River, Barraba and Severn River (Fig. 1). In total, 51 successful nests produced 82 fledglings. Although nests were associated with a variety of nectar resources, Yellow Box *Eucalyptus melliodora* was disproportionately the most common (Supporting Information Table S3). In all, 34% of nests were found on or before the day the first egg was laid. Median nest age when found was 4 days (mean = 7.5).

The best-supported range-wide nest survival model (Table 2) provided a daily nest survival estimate of 0.967 ± 0.004 (95% confidence interval (CI) 0.959–0.975, effective sample size (N_e) = 1895), giving a nest survival probability over the 34-day nesting period of 0.317 (95% CI 0.24–0.42). DSR models showed high regional variation in nest survival. In the Northern Tablelands

Table 1. Description of covariates included in Regent Honeyeater nest survival models. Further details of covariates are provided in Table S2.

Covariate	Description
Tree cover	Estimated percentage tree cover within 50 m of nest, to nearest 10%.
Edge	Log-transformed distance to (positive) or from (negative) edge of continuous woodland.
Concealment	Four-level factor – concealment of nest by surrounding 2 m ³ vegetation: <i>Low</i> < 25%; <i>Moderate</i> < 50%; <i>High</i> < 75%; <i>Very High</i> > 75%.
Position	Three-level factor – position of nest within tree crown: <i>Outer</i> = outer 10% of crown; <i>Mid</i> = 11–25% of crown; <i>Inner</i> > inner 75% of crown.
Height	Height of nest in metres above ground.
Camera	Presence/absence of nest monitoring camera.
Flower	Five-level factor – relative flower (a proxy for nectar) abundance within 100 m of nest: 0 = none; 1 = light; 2 = moderate; 3 = high; 4 = very high.
Noisy Miner	Detection/non-detection of Noisy Miners within 50 m of each active nest during nest monitoring.
Temperature	Days during nesting period where maximum temperature exceeded 35 °C.
Conspecifics	Number of Regent Honeyeater nests, active synchronously for ≥ 50% of focal nest duration, within 100 m of focal nest.
Region	Two-level factor: 1 = greater Blue Mountains, 2 = Northern Tablelands.
Site	Nine-level factor indicating nest location within regions: 1 = Capertee north; 2 = Capertee north-west; 3 = Capertee west; 4 = Capertee central; 5 = Capertee south; 6 = Goulburn River; 7 = Burragorang 8 = Barraba; 9 = Severn River.
Location	Spatial location (Lat/Long) of nest.
Habitat type	Three-level factor: 1 = box–ironbark woodland; 2 = box–gum woodland; 3 = riparian.
Nest age	Age of nest in days since first egg.
Time	Continuous timing of nest (Julian date) within overall breeding season.
Year	Three-level factor: 1 = 2015 2 = 2016 3 = 2017.

(Barraba and Severn River), nest survival probability was substantially lower (0.093, 95% CI 0.014–0.27, $n = 11$) than in Central NSW (Blue Mountains, 0.337, 95% CI 0.245–0.431, $n = 108$; Figs 1 and 2), with no juveniles fledged from 11 nests found in the Northern Tablelands. Nest survival also differed markedly at the site level between nesting aggregations within the Capertee Valley, ranging from 0.14 in the centre to 0.74 in the north-east (Fig. 2, Supporting Information Tables S4 and S5).

Correlograms of nest success indicated that nests located close to each other tended to share a similar fate (Supporting Information Fig. S2). Nest success was spatially autocorrelated at distances separating discrete breeding sites within the Capertee Valley, and also between regional sub-populations range-wide (Fig. S2). DSR models also identified nest position and the presence of conspecifics as additional factors influencing nest survival. Nests built in the outer canopy and in close proximity to other nesting pairs had the greatest survival probability (Fig. 2, Table S5). Nest survival decreased slightly as nest age increased, but the age-trend model fitted the data no better than constant survival ($\Delta AIC_c = 1.59$). In the Capertee

Valley, nest survival was more than twice as high in 2017 than in other years (Fig. 2, Table S4).

The top-ranked GAMs confirmed that nests positioned in the outer crown of trees had the highest survival rates (Tables 2 and S5). Noisy Miner *Manorina melanocephala* presence was included in two of the four top-ranked models (Table 2) and had a negative but non-significant effect on the probability of Regent Honeyeater nest success (Table S5). The smoothed spatial term of nest location improved the fit of the model (Table 2).

Predation was the main known cause of Regent Honeyeater nest failure, accounting for 89% of nests where the cause of failure was confirmed. Avian predators were Pied Currawongs *Strepera graculina* ($n = 3$), Noisy Miners *Manorina melanocephala* ($n = 2$), a Pied Butcherbird *Cracticus nigrogularis* and a Laughing Kookaburra *Dacelo novaeguineae*. Mammalian predators included a Brush-tailed Possum *Trichosurus vulpecula* and Sugar Glider *Petaurus breviceps*. Inclement weather (high wind, hail, extreme heat) was inferred as the cause of seven additional failures. A second nesting attempt was initiated by eight pairs whose first attempt failed, and by 10 pairs following a successful first attempt.

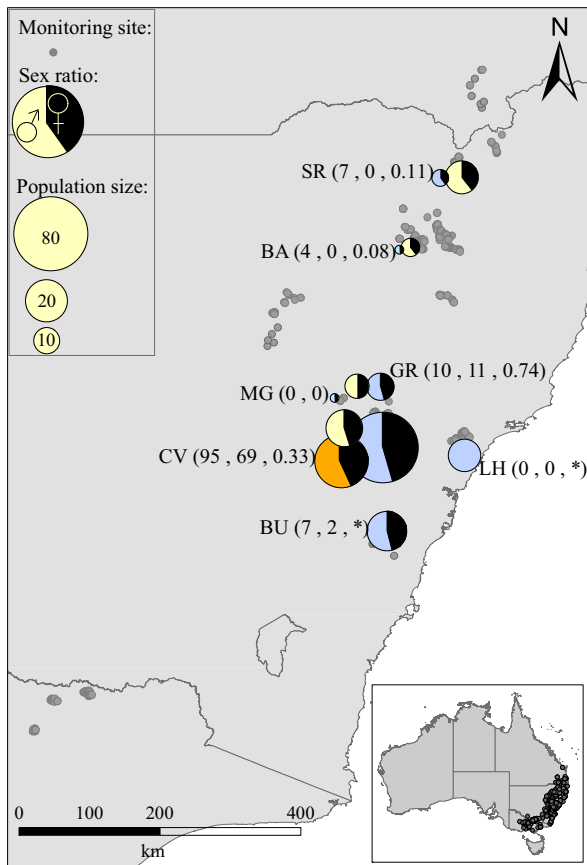


Figure 1. Regional variation in the population size, adult sex ratio and nest success probability of wild Regent Honeyeaters in 2015 (orange), 2016 (yellow) and 2017 (blue). Northern Tablelands: Severn River (SR) and Barraba (BA). Greater Blue Mountains: Goulburn River (GR), Munghom Gap (MG), Capertee Valley (CV), lower Hunter Valley (LH), Burratorang Valley (BU). Figures in parentheses denote, over all years: nests, juveniles, nest success probability. Overlapping population symbols (circles) denote the same regional sites occupied more than 1 year. Inset: Regent Honeyeater range based on 2000–2010 sightings data. *Sex ratio data not available for lower Hunter Valley. Unknown fate of four nests in the Burratorang Valley not included in DSR models.

The mean number of young fledged per nesting attempt was 0.78 ± 0.1 CI. The mean number of juveniles fledged from 59 successful nests was 1.58 ± 0.53 . The age-trend juvenile survival model ($AIC_c = 92.65$, $W_i = 0.86$) fitted the data better than the constant model ($\Delta AIC_c = 3.67$, $W_i = 0.14$), with daily juvenile survival increasing with time since fledging (Fig. 3). Estimated DSR of juveniles ($n = 56$ juveniles, $N_e = 649$) averaged across the fortnight post-fledging was 0.989 ± 0.009 , giving a survival probability of 0.859 (95% CI 0.46–0.97). Models containing only one

Table 2. Top-ranked ($\Delta AIC_c < 2$) nest survival (S) and daily failure probability (F) generalized additive models (GAMs) for 119 Regent Honeyeater nests ($N_e = 1895$) from 2015 to 2017.

Model type	Model	AIC_c	ΔAIC_c	W_i
Nest survival	$S(\text{Site})$	438.88	–	0.40
	$S(\text{Site} + \text{Conspecifics} + \text{Position})$	440.13	1.26	0.21
GAM	$F(\text{Position} + s(\text{Lat}, \text{Long}) + 1 \text{pair ID})$	269.86	0	0.19
	$F(\text{Position} + s(\text{Lat}, \text{Long}) + \text{Noisy Miner} + 1 \text{pair ID})$	270.19	0.33	0.16

juvenile from each nest (i.e. excluding random nest effects) did not substantially alter juvenile survival estimates (Supporting Information Fig. S4).

DISCUSSION

By developing a targeted and spatially stratified sampling design, we consistently located between 30 and 65% of the estimated global population of Regent Honeyeaters. Poor breeding success limits recruitment to the population. High rates of nest predation drive poor reproduction, which is exacerbated by the failure of some pairs to participate in breeding, a decrease in the number of juveniles fledged from successful nests, and a lack of females. Contemporary nesting success (9–34%) was considerably lower than estimates from previous studies (Table 3). Nest success was also highly variable at multiple spatial scales, suggesting that complex factors are suppressing population growth in Regent Honeyeaters.

Approximately one in six males was unable to find a mate. Although our sex ratio estimate is based primarily on the sexing of individuals in the field, we are confident that our estimate is accurate. Unpaired males sang prolifically, which confirmed they were not nesting, as singing ceases prior to egg-laying (R. Crates pers. obs.). Singing males may be more detectable than females, but these males would have facilitated detection of any associated females during follow-up searches (e.g. through courting behaviour) had females been present. Given the very sparse distribution of nesting aggregations throughout the range (Fig. 1), dispersing females may fail to locate other flocks, causing them to become lost from the breeding population (Dale 2001, Gilroy & Lockwood 2012). Alternatively, a male-biased sex ratio could

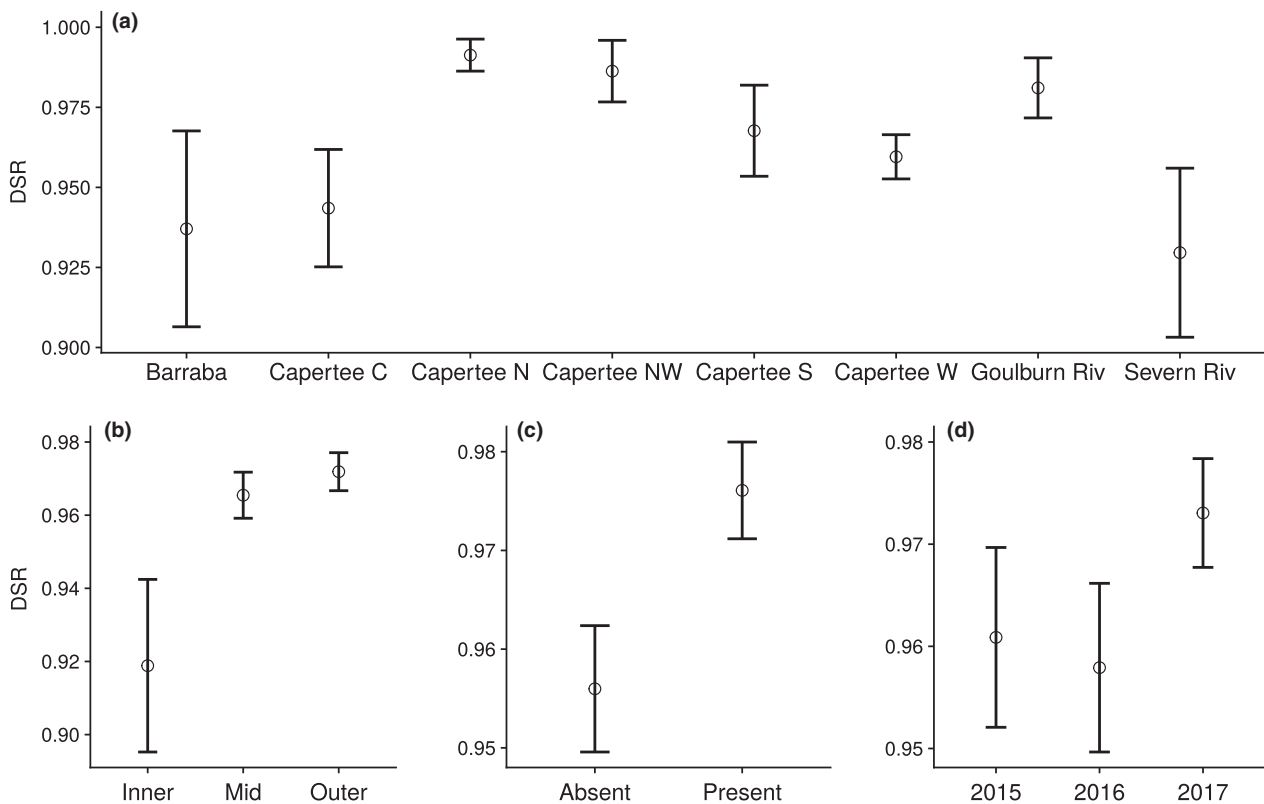


Figure 2. Variation in Regent Honeyeater daily nest survival rate (DSR) \pm se according to factors included in the top ranked nest survival models (Table 2), plus year: (a) breeding site; (b) nest position within tree crown; (c) presence/absence of nesting conspecifics within 100 m; (d) year. Estimates were derived from separate models of each factor. See Tables S4, S5 and Supporting Information Figure S3 for additional information.

be due to predation of some females during nesting (Grüebler *et al.* 2008, Stojanovic *et al.* 2014). Male-biased sex ratios may be common in bird species (Donald 2007), but a lack of females is a clear limit to Regent Honeyeater population recovery, considering the species' estimated effective population of just 100 pairs (Kvistad *et al.* 2015). This effect appears to be greatest at the range edge in northern NSW, indicating the sex ratio bias may increase with population decline (Stojanovic *et al.* 2018). Unpaired males could also reduce breeding success of pairs by attempting to steal mates or increasing nest exposure to predators (Dale 2001).

The failure of 12% of pairs during territory acquisition or nest construction may be a consequence of high attraction to nesting conspecifics in fragmented habitat patches that are too small to support the number of pairs attempting to settle there (Kokko & Sutherland 2001, Schmidt *et al.* 2015). Although some species regularly abandon

nests during construction if concealment is considered to be insufficient (Beckmann & Martin 2016), our observations suggest that the failure of Regent Honeyeater nests during construction was more probably due to competitive displacement by larger honeyeater species. These results emphasize an urgent need for targeted restoration of Yellow Box – Mugga Ironbark *Eucalyptus sideroxylon* habitats (Tulloch *et al.* 2016) to increase the size and availability of breeding habitat and reduce competition for nest-sites.

The best nest survival models included breeding site and nest position as factors influencing nest survival. Given high levels of observed nest predation by an assemblage of species, local predator presence/abundance at breeding sites may explain spatial structure in Regent Honeyeater nest success. Variation in nest position could be explained by the age of nesting pairs, with more experienced pairs selecting less accessible nest positions in trees (Eggers *et al.* 2006). Although the exact age of

Table 3. Published estimates of nest survival probabilities and mean fledglings per successful nest for Australian honeyeaters (Meliphagidae). Estimates are ranked by percentage of nest success. '–', Unavailable data.

Species	Location	Year	% Nest success (nests)	Method ^a	Fledglings per nest (nests) ^b	Citation
White-cheeked Honeyeater	C. NSW	1987–88	68.3 (43)	Binary	–	Armstrong and Pyke (1991)
Bell Miner	S. VIC	1988–1990	57.4 (122)	Binary	–	Poiani (1993)
Regent Honeyeater	C. NSW	1996	46.9 (42)	Mayfield	1.88 (18)	Geering and French (1998)
Brown Honeyeater	NT	1985–1999	42 (75)	Binary	1.74 (19)	Franklin and Noske (2000)
New Holland Honeyeater	C. NSW	1987–88	41	Binary	–	Armstrong and Pyke (1991)
Regent Honeyeater	C. NSW	1995	38.7 (73)	Mayfield	1.78 (50)	Geering and French (1998)
Noisy Friarbird	N. NSW	1990 & 1997	38.4 (224)	Binary	2.07 (85)	Ford (1999)
Regent Honeyeater	N. NSW	1993–1996	38.3 (41)	Mayfield	2.1 (21)	Oliver <i>et al.</i> (1998)
Yellow-faced Honeyeater	C. VIC	1997–2000	37 (69)	DSR	1.73 (50)	Clarke <i>et al.</i> (2003b)
New Holland Honeyeater	W. VIC	–	37 (–)	–	–	Paton (1985)
Regent Honeyeater	C. NSW	2015 – 2017	33.7 (108)	DSR	1.58 (59)	This study
Red Wattlebird	N. NSW	1990 & 1997	33.3 (90)	Binary	1.6 (50)	Ford (1999)
Helmeted Honeyeater	C. VIC	1984–1992	32.9 (257)	Mayfield	1.63 (40)	Franklin <i>et al.</i> (1995)
New Holland Honeyeater	SA	2004	32.2 (–)	Binary	–	Lambert and Kleindorfer (2006)
Fuscous Honeyeater	N. NSW	1984–1988	28.2 (137)	Binary	2 (33)	Dunkerley (1989)
Crescent Honeyeater	S. VIC	1996–1997	20.1 (32)	Mayfield	2.7 (9)	Clarke and Clarke (2000)
Helmeted Honeyeater	C. VIC	1984–1996	17.5 (526)	DSR	–	Smales <i>et al.</i> (2009)
Regent Honeyeater	N.NSW	2016 & 2017	9.3 (11)	DSR	– (0)	This study

^aBinary: percentage of nests that produced one or more fledgling; 'Mayfield': Mayfield (1975) method. 'DSR': method used in this study (see Methods). Parameters presented are from first egg to fledging. We have not provided a comparable Mayfield estimate for our data because Mayfield estimates are prone to inconsistent bias and DSR estimates between the two methods are invariably very similar (Shaffer & Thompson 2007). ^bData presented for successful nests only.

birds was unknown, 94% of colour-marked individuals were adults, suggesting the results were not driven solely by young first-time breeders. The positive effect of the presence of conspecifics may be due to greater probability of attraction to nesting conspecifics at sites with high nest survival (Schmidt *et al.* 2015). Alternatively, nearby nesting conspecifics could facilitate nest survival through antipredator defences, including alarm-calling and predator-mobbing (Serrano *et al.* 2005). Declining nest success over time may therefore reflect a concurrent reduction in the size

and density of breeding aggregations (Crates *et al.* 2017a).

Although only 22% of identified nest predations were attributable to Noisy Miners, their negative impact on Regent Honeyeater nest success, supported by the GAMs, may primarily occur at the settlement phase by excluding Regent Honeyeaters from preferred breeding habitat (Piper & Catterall 2003). Noisy Miners were removed from the north-eastern breeding site in the Capertee Valley in winter 2017 (BirdLife Australia unpubl. data), where 14 Regent Honeyeater pairs subsequently nested.

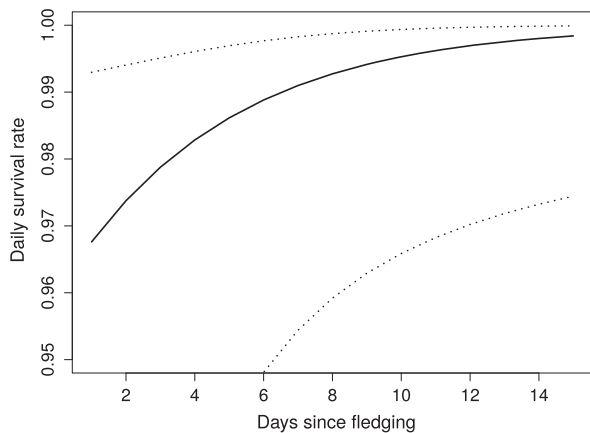


Figure 3. Effect of days since fledging on short-term post-fledging survival of juvenile Regent Honeyeaters from 2015 to 2017 ($n = 56$). The full line is the model estimate of daily juvenile survival and the dotted lines are the 95% upper and lower confidence intervals.

Nest success at this site was the highest observed during the study, which is reflected by the importance of 'site' (and in association with 'year') in nest survival models. Although adverse effects of Noisy Miners are understood to be a function of their local abundance (Piper & Catterall 2003), our observations indicate that the presence of a single pair of Noisy Miners poses a risk to Regent Honeyeater nest survival. As some pairs fledged young despite the presence of Noisy Miners, however, the nature of interspecific interactions between the two species appears to be highly context-specific, representing an area for future study.

Our contemporary estimates of Regent Honeyeater nest success and productivity were lower than historical estimates for the Regent Honeyeater and many other honeyeater species (Table 5). Declining nest success, particularly in the Northern Tablelands, may be explained by a concurrent increase in the abundance of nest predators (Bayly & Blumstein 2001, Remes *et al.* 2012). Reporting rates for Pied Currawongs and Noisy Miners have increased substantially since the 1980s (Barrett *et al.* 2003). Unlike some species (Schmidt *et al.* 2006), Regent Honeyeaters rarely avoid nesting at sites with high perceived predator abundance, probably because a severe lack of breeding habitat makes settlement at high predation risk sites unavoidable (Gilroy & Sutherland 2007). Compounding the effects of decreased nest success, productivity of successful nests (1.58 ± 0.58 juveniles) was also lower than historical estimates

(1.78–2.1, Table 5). Reduced nest productivity could be explained by a reduction in nectar abundance due to senescence of food trees or mistletoe, or increased interference competition from competitors such as the Noisy Miner (Ford *et al.* 1993). The decrease in the size and density of nesting aggregations could also reduce nest productivity, forcing pairs to invest more time defending nests and less time provisioning young (Ford *et al.* 1993).

Recent work by Taylor *et al.* (2018) shows that captive-bred Regent Honeyeaters have a 48% lower rate of nest success than our estimate for wild conspecifics. Given substantial funds invested in the breeding and release of captive birds (Canessa *et al.* 2014), spatial variation in nest success and adult sex ratios have implications for the management of reintroduction efforts (Armstrong & Wittmer 2011). For instance, captive-bred females could be released strategically to stabilize sex ratios at nesting aggregations (Wedekind 2002, Derebec & Courchamp 2007). Captive birds could also be released early in the breeding season at sites known to have high nest success that are occupied by wild birds. Intensive management intervention aimed at reducing nest predation at high-risk breeding sites and stabilizing sex ratios may be more effective at facilitating population recovery than releasing captive-bred birds alone.

Detailed demographic data are seldom available for rare and mobile species but are potentially vital for their conservation (Heinsohn *et al.* 2015). We show that it is possible consistently to locate and monitor a substantial proportion of breeding Regent Honeyeaters from the early stages of nesting. Consequently, implementation of rapid conservation actions including nest protection (Major *et al.* 2014), competitor suppression (Debus 2006, Fletcher *et al.* 2010) and complementary release of captive-bred birds is more achievable and necessary than previously thought (Clarke *et al.* 2003a). Our study highlights the need for vigilance against deteriorating demographic parameters in declining populations. Comprehensive spatially explicit demographic data facilitate more effective investment of conservation resources, allowing high-risk areas to be identified and thus maximizing the likelihood of population recovery.

S. Debus, A. Ley, C. Probeta, M. Roderick and N. Sherwood assisted with surveys and nest monitoring. H. Evans and D. Ingwersen provided valuable logistical

support. Many landowners allowed access to their properties, especially B. and D. Upton, R. and S. Hill, and C. and J. Goodreid. The project was supported financially by a Commonwealth environmental offset (paid by Cumnock Pty), grants from the Mohamed Bin Zayed species conservation fund, Holsworth research endowment, BirdLife Australia, Hunter Bird Observers, Birding New South Wales and Oatley Flora and Fauna. Research was conducted under Australian National University Animal Ethics protocols #A2015/28 and A2015/55, New South Wales scientific licences #SL101603 and SL101556, Victorian wildlife research permit #10008014 and ABBS banding licences #3192. D. Chamberlain and two anonymous reviewers provided comments that greatly improved the manuscript.

REFERENCES

- Aebischer, N.J.** 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46**: s22–s31.
- Armstrong, D.P. & Pyke, G.H.** 1991. Seasonal patterns of reproduction in heathland honeyeaters are not responses to changing nectar availability. *Auk* **108**: 99–107.
- Armstrong, D.P. & Wittmer, H.U.** 2011. Incorporating Allee effects into reintroduction strategies. *Ecol. Res.* **26**: 687–695.
- Barrett, G., Silcocks, A., Barry, S., Cunningham, R. & Poulter, R.** 2003. *The New Atlas of Australian Birds*. Melbourne: BirdLife Australia.
- Bartoń, K.** 2018. *Package MuMIN v1.40.4. Multi-model inference*.
- Bayly, K.L. & Blumstein, D.T.** 2001. Pied Currawongs and the decline of native birds. *Emu* **101**: 199–204.
- Beckmann, C. & Martin, K.** 2016. Testing hypotheses about the function of repeated nest abandonment as a life history strategy in a passerine bird. *The Ibis* **158**: 335–342.
- Bjornstad, O.** 2015. *Ncf: spatial nonparametric covariance functions. R package version 0.5-92*. Available at: <https://cran.r-project.org/web/packages/ncf/ncf.pdf>.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Resit Akçakaya, H. & Frankham, R.** 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**: 385–387.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Berlin: Springer Science & Business Media.
- Canessa, S., Hunter, D., McFadden, M., Marantelli, G. & McCarthy, M.A.** 2014. Optimal release strategies for cost-effective reintroductions. *J. Appl. Ecol.* **51**: 1107–1115.
- Caughley, G.** 1994. Directions in conservation biology. *J. Anim. Ecol.* **63**: 215–224.
- Clarke, R.H. & Clarke, M.F.** 2000. The breeding biology of the crescent honeyeater *Phylidonyris pyrrhoptera* at Wilson's Promontory, Victoria. *Emu* **100**: 115–124.
- Clarke, R.H., Oliver, D.L., Boulton, R.L., Cassey, M. & Clarke, M.F.** 2003a. Assessing programs for monitoring threatened species – A tale of three honeyeaters (Meliphagidae). *Wild. Res.* **30**: 427–435.
- Clarke, M.F., Schipper, C., Boulton, R. & Ewen, J.** 2003b. The social organization and breeding behaviour of the Yellow-faced Honeyeater *Lichenostomus chrysops* – a migratory passerine from the Southern Hemisphere. *Ibis* **145**: 611–623.
- Commonwealth of Australia.** 2016. *National recovery plan for the Regent Honeyeater (Anthochaera phrygia)*. Department of Environment, Commonwealth of Australia. Available at: <http://www.environment.gov.au/biodiversity/threatened/recovery-plans/national-recovery-plan-regent-honeyeateranthochaera-phrygia-2016>.
- Cooch, E. & White, G.** 2001. *Program Mark. A Gentle Introduction*. Available at: <http://www.phidot.org/software/mark/docs/book>.
- Cottee-Jones, H., Matthews, T.J. & Whittaker, R.J.** 2015. The movement shortfall in bird conservation: accounting for nomadic, dispersive and irruptive species. *Anim. Cons.* **19**: 227–234.
- Crates, R., Rayner, L., Stojanovic, D., Webb, M. & Heinsohn, R.** 2017a. Undetected Allee effects in Australia's threatened birds: implications for conservation. *Emu* **117**: 207–221.
- Crates, R., Terauds, A., Rayner, L., Stojanovic, D., Heinsohn, R., Ingwersen, D. & Webb, M.** 2017b. An occupancy approach to monitoring regent honeyeaters. *J. Wild. Man.* **81**: 669–677.
- Dale, S.** 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* **92**: 344–356.
- Debus, S.J.** 2006. The role of intense nest predation in the decline of Scarlet Robins and Eastern Yellow Robins in remnant woodland near Armidale, New South Wales. *Pac. Cons. Biol.* **12**: 279–287.
- Derebec, A. & Courchamp, F.** 2007. Importance of the Allee effect for reintroductions. *Ecoscience* **14**: 440–451.
- Dinsmore, S.J. & Dinsmore, J.J.** 2007. Modeling avian nest survival in program MARK. *Stud. Avian Biol.* **34**: 73–83.
- Dinsmore, S.J., White, G.C. & Knopf, F.L.** 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**: 3476–3488.
- Donald, P.** 2007. Adult sex ratios in wild bird populations. *Ibis* **149**: 671–692.
- Dunkerley, G.** 1989. *The fuscous honeyeater: food resources and the bird community*. Unpublished PhD thesis, University of New England, Armidale.
- Eggers, S., Griesser, M., Nystrand, M. & Ekman, J.** 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian Jay. *Proc. R. Soc. B* **273**: 701–706.
- Ewen, J.G., Clarke, R.H., Moysey, E., Boulton, R.L., Crozier, R.H. & Clarke, M.F.** 2001. Primary sex ratio bias in an endangered cooperatively breeding bird, the black-eared miner, and its implications for conservation. *Biol. Cons.* **101**: 137–145.
- Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N.** 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *J. Appl. Ecol.* **47**: 263–272.
- Ford, H.A.** 1999. Nest site selection and breeding success in large Australian honeyeaters: are there benefits from being different? *Emu* **99**: 91–99.
- Ford, H.A., Davis, W.E., Debus, S., Ley, A., Recher, H. & Williams, B.** 1993. Foraging and aggressive behaviour of

- the Regent Honeyeater *Xanthomyza phrygia* in northern New South Wales. *Emu* **93**: 277–281.
- Ford, H.A., Barrett, G.W., Saunders, D.A. & Recher, H.F. 2001. Why have birds in the woodland of Southern Australia declined? *Biol. Cons.* **97**: 71–88.
- Franklin, D.C. & Noske, R.A. 2000. The nesting biology of the Brown Honeyeater *Lichmera indistincta* in the Darwin region of northern Australia, with notes on tidal flooding of nests. *Corella* **24**: 38–44.
- Franklin, D.C., Menkhorst, P.W. & Robinson, J. 1989. Ecology of the Regent Honeyeater *Xanthomyza phrygia*. *Emu* **89**: 140–154.
- Franklin, D.C., Smales, I.J., Miller, M.A. & Menkhorst, P.W. 1995. The reproductive biology of the Helmeted Honeyeater, *Lichenostomus melanops cassidix*. *Wild. Res.* **22**: 173–191.
- Gascoigne, J., Berec, L., Gregory, S. & Courchamp, F. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Pop. Ecol.* **51**: 355–372.
- Geering, D. 2010. Ageing and sexing of the Regent Honeyeater *Anthochaera phrygia*. *Corella* **34**: 53–59.
- Geering, D. & French, K. 1998. Breeding biology of the Regent Honeyeater *Xanthomyza phrygia* in the Capertee Valley, New South Wales. *Emu* **98**: 104–116.
- Gilroy, J.J. & Lockwood, J.L. 2012. Mate-finding as an overlooked critical determinant of dispersal variation in sexually-reproducing animals. *PLoS ONE* **7**: e38091.
- Gilroy, J.J. & Sutherland, W.J. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends Ecol. Evol.* **22**: 351–356.
- Grüebler, M.U., Schuler, H., Müller, M., Spaar, R., Horch, P. & Naef-Denzer, B. 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biol. Cons.* **141**: 3040–3049.
- Heinsohn, R., Webb, M., Lacy, R., Terauds, A., Alderman, R. & Stojanovic, D. 2015. A severe predator-induced population decline predicted for endangered, migratory Swift Parrots (*Lathamus discolor*). *Biol. Cons.* **186**: 75–82.
- Kokko, H. & Sutherland, W.J. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behavioural mediated Allee effect. *Evol. Ecol. Res.* **3**: 537–610.
- Kvistad, L., Ingwersen, D., Pavlova, A., Bull, J.K. & Sunnucks, P. 2015. Very low population structure in a highly mobile and wide-ranging endangered bird species. *PLoS ONE* **10**: e0143746.
- Laake, J., Rakimberdiev, E., Collier, B., Rotella, J. & Paul, A. 2016. *RMark: R Code for MARK Analysis. R package version 2.2.2*. Available at: <https://cran.r-project.org/web/packages/RMark/index.html>
- Lambert, S. & Kleindorfer, S. 2006. Nest concealment but not human visitation predicts predation of New Holland Honeyeater nests. *Emu* **106**: 63–68.
- Major, R.E., Ashcroft, M.B. & Davis, A. 2014. Nest caging as a conservation tool for threatened songbirds. *Wild. Res.* **41**: 598–605.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- McDonald-Madden, E., Probert, W., Hauser, C.E., Runge, M.C., Possingham, H.P., Jones, M.E., Moore, J.L., Rout, T.M., Vesk, P.A. & Wintle, B.A. 2010. Active adaptive conservation of threatened species in the face of uncertainty. *Ecol. App.* **20**: 1476–1489.
- Oliver, D.L., Ley, A.J. & Williams, B. 1998. Breeding success and nest site selection of the Regent Honeyeater *Xanthomyza phrygia* near Armidale, New South Wales. *Emu* **98**: 97–103.
- Paradis, E., Baillie, S.R., Sutherland, W.J., Dudley, C., Crick, H. & Gregory, R.D. 2000. Large-scale spatial variation in the breeding performance of Song Thrushes *Turdus philomelos* and Blackbirds *T. merula* in Britain. *J. Appl. Ecol.* **37**: 73–87.
- Paton, D.C. 1985. Do New Holland Honeyeaters *Phylidonyris novaehollandiae* breed regularly in spring and autumn? *Emu* **85**: 130–133.
- Piper, S.D. & Catterall, C.P. 2003. A particular case and a general pattern: hyperaggressive behaviour by one species may mediate avifaunal decreases in fragmented Australian forests. *Oikos* **101**: 602–614.
- Pizzey, G. & Knight, F. 2014. *Birds of Australia Digital Edition for iPad, Version 1.1*. Melbourne: Gibbon Multimedia.
- Poiani, A. 1993. Effects of clutch size manipulations on reproductive behaviour and nesting success in the cooperatively breeding Bell Miner (*Manorina melanophrys*). *Evol. Ecol.* **7**: 329–356.
- R Core Team. 2017. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rayner, L., Lindenmayer, D.B., Gibbons, P. & Manning, A.P. 2014. Evaluating empirical evidence for decline in temperate woodland birds: a nationally threatened assemblage of species. *Biol. Cons.* **171**: 145–155.
- Remes, V., Matysiokova, B. & Cockburn, A. 2012. Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. *J. Avian Biol.* **43**: 435–444.
- Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G. & Fuller, R.A. 2014. Conserving mobile species. *Front. Ecol. Env.* **12**: 395–402.
- Schmidt, K.A., Ostfeld, R.S. & Smyth, K.N. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* **148**: 22–29.
- Schmidt, K.A., Johansson, J. & Betts, M.G. 2015. Information-mediated Allee effects in breeding habitat selection. *Am. Nat.* **186**: e162–e171.
- Serrano, D., Oro, D. & Ursu, E. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *Am. Nat.* **166**: e22–e31.
- Shaffer, T.L. & Thompson, F.R. 2007. Making meaningful estimates of nest survival with model-based methods. *Stud. Avian Biol.* **34**: 84.
- Smales, I.J., Quin, P., Menkhorst, P.W. & Franklin, D.C. 2009. Demography of the Helmeted Honeyeater (*Lichenostomus melanops cassidix*). *Emu* **109**: 352–359.
- Smith, D.R., Brown, J.A. & Lo, N.C.H. 2004. Application of adaptive cluster sampling to biological populations. In Thompson, W.L. (ed.) *Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters*: 77–122. Covelo: Island Press.
- Steiffetten, Ø. & Dale, S. 2006. Viability of an endangered population of Ortolan Buntings: the effect of a skewed operational sex ratio. *Biol. Cons.* **132**: 88–97.

- Stephens, P. & Sutherland, W.J.** 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**: 401–405.
- Stojanovic, D., Webb, M., Alderman, R., Porfirio, L.L. & Heinsohn, R.** 2014. Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. *Divers. Distrib.* **20**: 1200–1207.
- Stojanovic, D., Alves, F., Cook, H., Crates, R., Heinsohn, R., Peters, A., Rayner, L., Troy, S. & Webb, M.** 2018. Further knowledge and urgent action required to save Orange-bellied Parrots from extinction. *Emu* **118**: 126–134.
- Sturdivant, R.X., Rotella, J.J. & Russell, R.E.** 2007. A smoothed residual based goodness of fit statistic for nest survival models. *Stud. Avian Biol.* **34**: 45.
- Taylor, G., Ewen, J.G., Clarke, R.H., Blackburn, T., Johnson, G. & Ingwersen, D.** 2018. Video monitoring reveals novel threat to critically endangered captive-bred and released Regent Honeyeaters. *Emu* **118**: 304–310.
- Tiefelsdorf, M.** 2000. *Modeling Spatial Processes: The Identification and Analysis of Spatial Relationships in Regression Residuals by Means of Morans' I*. Cambridge: Cambridge, University Press.
- Tulloch, A., Barnes, M.D., Ringma, J., Fuller, R.A. & Watson, J.** 2016. Understanding the importance of small patches of habitat for conservation. *J. Appl. Ecol.* **53**: 418–429.
- Wedekind, C.** 2002. Manipulating sex ratios for conservation: short-term risks and long-term benefits. *Anim. Cons.* **5**: 13–20.
- White, G.C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: s120–s139.
- Wood, S.** 2017. *Generalized Additive Models: An Introduction with R*, 2nd edn. Boca Raton, FL: Chapman and Hall/CRC Press.
- Wood, S.** 2018. *mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. R-package version 1.8-24*. Available at: <https://cran.r-project.org/web/packages/mgcv>

Received 11 March 2018;

revision accepted 7 August 2018.

Associate Editor: Jose Antonio Sanchez-Zapata.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Location of range-wide Regent Honeyeater monitoring sites. Ellipses and numbers delineate survey regions as described in Table S1. Inset, study area in a national context.

Figure S2. Spatial autocorrelation in Regent Honeyeater nest success between (a) regional aggregations range-wide (sampling distance = 50 km, $n = 119$ nests, see Figure 1) and (b) breeding sites within the Capertee Valley (sampling distance = 0.5 km, $n = 95$ nests). Shaded area denotes $p > 0.05$, black points denote $p < 0.05$, grey points outside the shaded area are due lack of data at those distance classes.

Figure S3. Spatial distribution of Regent Honeyeater nests within the Capertee Valley in 2015–2017.

Figure S4. Post-fledging survival ($\pm 95\%$ CI) of all monitored juveniles (black, $n = 56$) and excluding random duplicate juveniles from the same nests (red and blue, $n = 42$).

Table S1. Breakdown of range-wide Regent Honeyeater monitoring sites by region and number of sites where Regent Honeyeaters were detected in 2016 and 17.

Table S2. Covariates included in models of Regent Honeyeater nest survival.

Table S3. Nectar sources with which Regent Honeyeater nesting attempts were associated throughout the species' range from 2015 to 2017.

Table S4. Site-level and annual variation in Regent Honeyeater nest survival within the Capertee Valley, New South Wales, between 2015 and 2017, $N_e = 1562$.

Table S5. Beta coefficients of covariates included in top-ranked Regent Honeyeater nest survival models and generalized additive model (GAM), using data from 119 nests ($N_e = 1895$) monitored throughout the species' range from 2015 to 2017.