

Landscape-scale distribution of nest predators and its relationship with regent honeyeater nest success

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Abstract Overcoming low breeding success is a major challenge for reversing population decline in threatened species. High nest predation rates are a common cause of low productivity in birds, but implementing evidence-based management actions to reduce nest predation is challenging. Targeted breeding management requires a good understanding of where threatened species breed, the identity and distribution of nest predator species and the impact of these nest predators on breeding success. For rare and nomadic species, this information is hard to come by. The breeding success of regent honeyeater *Anthochaera phrygia* has declined over recent decades, and nest predation is the primary cause of breeding failure. We conducted point-count surveys of nine avian and three mammalian nest predator species across 80% of the regent honeyeater's contemporary breeding area in south eastern Australia. We used occupancy models to determine the presence of predator species at survey sites and spatial models to predict predator abundance and species richness across the breeding area. We incorporated predator predictions for regent honeyeater nest locations into nest fate and daily nest survival models. Predator abundance was correlated positively with tree hollow abundance and proximity to water and negatively with shrub cover. Regent honeyeater nest success showed no significant relationship with predator abundance or predator species richness. Given how abundant and widespread avian and mammalian nest predators were throughout the breeding area, improving regent honeyeater nest success is likely to require implementation of simultaneous nest protection measures to avoid potential compensatory nest predation. Further research is required to better understand the relationship between nest predator abundance and regent honeyeater nest success.

Key words: avian ecology, nest predation, nest protection, predator abundance, spatial modelling.

INTRODUCTION

Developing effective management strategies to improve breeding success is a central component of threatened species recovery plans (Lawler *et al.* 2002). For threatened birds, nest predation is a key factor in limiting breeding outcomes (Martin 1993). However, management of nest predation is challenging and requires a good understanding of both the target species' breeding biology and nest predators themselves (Remeš *et al.* 2012). The identity, distribution and abundance of nest predators in breeding areas is important to understand when implementing management to improve breeding success (Ibáñez-Álamo *et al.* 2015).

In cases where a single predator species is the disproportionate cause of nest predation, successful predator management may be achieved by implementing one or two protection measures that are targeted at those species (Robertson *et al.* 1994; Leo & Manley 2018). However, single-species management

can be challenging to sustain if the predator is hyperabundant (Davitt *et al.* 2018; Beggs *et al.* 2019). Where multiple taxa are potential nest predators, successful nest protection requires the implementation of management actions that simultaneously reduce predation risk from the entire predator community (Reitsma *et al.* 1990). Otherwise, compensatory nest predation by other taxa in the local predator community may lead to equivalent, or even increased, nest predation rates (Fulton 2018; Beggs *et al.* 2019). Life-history is also important to consider when implementing management actions to improve breeding outcomes in threatened species (Remeš *et al.* 2012). Multiple life-history traits such as the clutch size, number of broods per season and length of nesting cycle affect species' susceptibility to population decline due to nest predation (Martin 1995). Similarly, management approaches will differ depending on the species' breeding biology. For example, hollow nesting species may better accommodate physical nest protection installations than open cup nesters because they are less prone to disturbance-related nest abandonment (Berris *et al.* 2018).

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One species that could benefit from management of nest predation is the regent honeyeater, a critically endangered songbird endemic to the woodlands of south-eastern Australia (Commonwealth of Australia 2016). In recent decades, the species has undergone severe population decline due to habitat loss and competition from larger honeyeaters (Ford 2011). Population decline may also be underpinned by an Allee effect, given the regent honeyeater's historic tendency to form large flocks and nest in aggregations (Ford *et al.* 1993; Crates *et al.* 2017b). The remaining wild population is a single genetic management unit of approximately 200–400 birds, distributed sparsely and dynamically across over 300 000 km² from northern Victoria to southern Queensland (Kvistad *et al.* 2015; Crates *et al.* 2019b). Contemporary breeding activity is largely restricted to the greater Blue Mountains and the Northern Tablelands in New South Wales, but the annual location of breeding activity is highly variable (Crates *et al.* 2019a).

Regent honeyeaters build small, open-cup nests, typically in the outer forks of large trees near flowering *Eucalyptus* tree species (Oliver *et al.* 1998). Breeding success in wild birds has declined over recent decades, from 35–50% in the 1990s to 9–33% between 2015 and 2017 (Crates *et al.* 2019a). Low breeding success among reintroduced birds (< 20%) is also hindering the capacity of a captive breeding programme to contribute to population recovery (Taylor *et al.* 2018). These estimates are towards the lower end of nest success estimates for other honeyeater species (Crates *et al.* 2019a), but the reasons why nest survival is low for regent honeyeaters relative to many other honeyeater species remains unclear. At the regional scale, regent honeyeater nest survival is spatially variable, but the factors explaining this variation are poorly understood (Crates *et al.* 2019a). Video monitoring revealed predation by a range of birds and marsupials as the primary cause of nest failure (Taylor *et al.* 2018; Crates *et al.* 2019a). Temporal decline in nest success in regent honeyeaters and other threatened woodland birds may be due to concurrent increases in the abundance of nest predators, many of which have responded positively to anthropogenic habitat fragmentation (Remeš *et al.* 2012; Fulton 2018).

Developing effective management strategies to reduce the rate of nest predation in regent honeyeaters will be fundamental to preventing the species' extinction in the wild (Crates *et al.* 2019a). To

inform how best to protect regent honeyeater nests from predation, we conducted point-count surveys of known avian and mammalian nest predators across the species' core remaining breeding range. We developed a survey protocol and modelling framework to achieve two aims. Firstly, we aimed to identify habitat features that predict a) the presence of individual predator species, b) the overall abundance of predators and c) the number of predator species, in a regent honeyeater breeding area. Secondly, we aimed to determine if spatial variation in regent honeyeater breeding success is explained by spatial variation in predator abundance and predator species richness. We predicted that nest success rates over the last five years would be lower in areas of high predator abundance and predator species richness.

METHODS

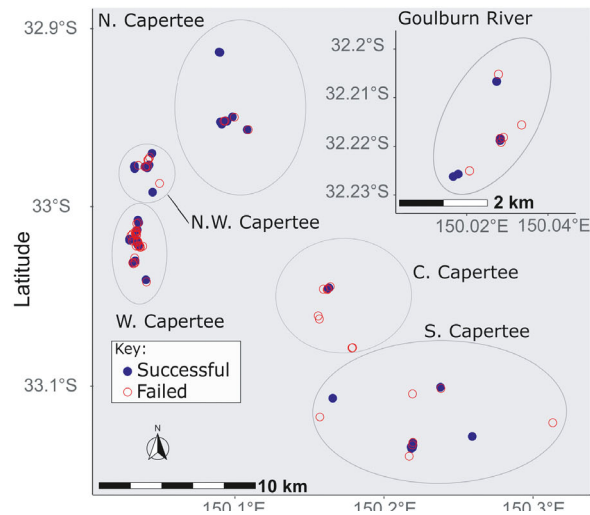
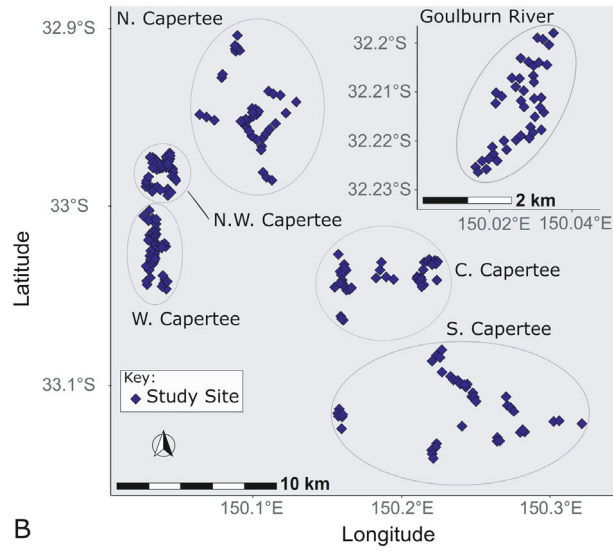
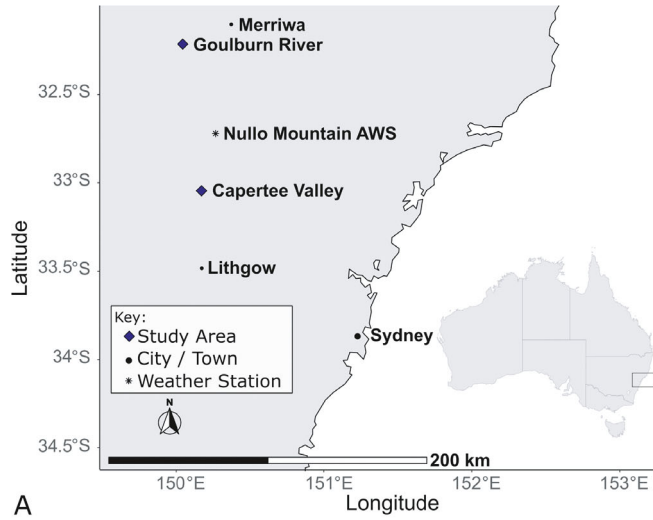
Study area

The study area encompassed 80% of known wild regent honeyeater breeding activity between 2015 and 2019 (Fig. 1, Crates *et al.* 2019a). The Capertee Valley study area covered 460 km² of woodland in the western greater Blue Mountains, NSW, and represents a key breeding area for the regent honeyeater (Crates *et al.* 2019a). Within the Capertee Valley, we defined five regions, based on clusters of nest locations identified by Crates *et al.* (2019a) and differences in daily nest survival within these clusters (Fig. 1). The Goulburn River study area represented a single region and covered 7 km² of largely cleared river flats within the northern greater Blue Mountains, NSW (Fig. 1). Vegetation communities are similar in both valleys, dominated by box-gum-ironbark (*Eucalyptus spp.*) woodland on low-lying slopes and the river-oak (*Casuarina cunninghamiana*) gallery forest along watercourses. Regent honeyeaters are known to move between the Goulburn River and the Capertee Valley, evidenced by re-sightings of colour-banded birds (Crates *et al.* 2019a).

Survey protocol

We defined each survey site as a 50 m radius surrounding a fixed GPS location. We selected 246 sites, with 40–43 sites per region. Most sites ($n = 126$) were pre-selected as part of a national regent honeyeater monitoring program (Crates *et al.* 2019a). We chose additional sites ($n = 79$) based on suitable nesting habitat and varying proximity to contemporary nesting sites in order to increase sampling stratification across habitats and locations.

Fig. 1. (a) Location of the Capertee and Goulburn River valleys in a regional and national context; (b) Distribution of survey sites within regions of the Capertee Valley, as identified by Crates *et al.* (2019a), and (inset) the Goulburn River; (c) Distribution of regent honeyeater nesting activity within the Capertee Valley and (inset) the Goulburn River between 2015 and 2019.



We surveyed for 12 nest predator species, due to their observed nest predatory behaviour and occurrence within the study region (Taylor *et al.* 2018; Beggs *et al.* 2019; Crates *et al.* 2019a; Fulton 2019a). The predator species were Australian magpie *Gymnorhina tibicen*, Australian raven *Corvus coronoides*, common brushtail possum *Trichosurus vulpecula* (hereafter ‘possum’), grey butcherbird *Cracticus torquatus*, grey shrike-thrush *Colluricincla harmonica*, laughing kookaburra *Dacelo novaeguineae*, noisy miner *Manorina melanocephala*, pied butcherbird *Cracticus nigrogularis*, pied currawong *Strepera graculina*, squirrel glider *Petaurus norfolcensis*, sugar glider *Petaurus breviceps* and white-winged chough *Corcorax melanorhamphos*. We combined sugar glider and squirrel glider as ‘glider sp.’ because rapid identification to species level was not always possible in the field at night.

We conducted three diurnal surveys, two nocturnal surveys and one scat survey at each site during a three-month regent honeyeater nesting season between August and November 2019. Due to the 2019 bushfires, we were unable to undertake 48 of 1476 surveys (3.3% of total surveys including 17 diurnal, 19 nocturnal and 12 scat).

For diurnal surveys, we followed Crates *et al.* (2017a) and surveyed for five minutes, recording the maximum count of each nest predator species detected visually or aurally within 50 m of the site centroid. Nocturnal surveys involved a six-minute point-count, using three complementary methods: spotlighting, thermal imaging and southern boobook *Ninox boobook* call playback to increase sugar glider detectability (Allen *et al.* 2018). Each nocturnal survey required two observers: one spotlighting using a 600-lumen headlamp and the other operating a thermal imaging camera. After five minutes, we broadcast six seconds of southern boobook call playback and listened for responses from sugar gliders for the remainder of the final minute.

We also searched for possum scat at each site as an additional indicator of possum presence (Wayne *et al.* 2005b). To infer possum presence or absence through scat surveys, we modified the spot assessment technique used for koala *Phascolarctos cinereus* detection (Phillips & Callaghan 2011). We searched for possum scat within 1 m of the base of the five most suitable trees within sites, based on largest diameter at breast height, presence of visible hollows and / or food sources (McElhinny *et al.* 2006). We terminated the search when we found possum scat or after unsuccessfully searching the five trees.

Habitat and detectability covariates

A single observer (DG) recorded site-level habitat covariates prior to the first diurnal survey and visit-level habitat covariates and detectability covariates during each site visit (Table 1).

Statistical analysis

Statistical analysis involved three complementary stages: occupancy modelling, spatial modelling and nest survival modelling.

Occupancy models

We used R v3.6.2 (R Core Team 2020) for all data analysis. To determine which habitat features predict the presence of individual nest predator species, whilst accounting for imperfect detection (MacKenzie *et al.* 2005), we fitted single-season, single-species occupancy models using package *unmarked* v0.13.1 (Fiske & Chandler 2011). For each species, we first created a null model and a set of models including single habitat and detectability covariates, with predator species detection / non-detection as a binomial response. We used Akaike Information Criteria (AIC) to estimate the strength of univariate models relative to each other (Burnham *et al.* 2011). We then built a saturated model for each species, including covariates with a smaller univariate AIC than those in the null model. We used *MuMIn* v1.43.15 (Bartoń 2019) to identify the most parsimonious model from the saturated model and ranked the models by AICc (Burnham *et al.* 2011).

Because existing monitoring has shown that no single predator species is the disproportionate cause of regent honeyeater nest predation (Taylor *et al.* 2018; Crates *et al.* 2019a), we calculated predator-community measures for each survey site. We used three predator-community measures:

Predator abundance: sum of the maximum number of each predator species observed across repeat visits to a site, excluding possum scat detections.

Predator species richness: the number of predator species detected across repeat visits to a site, including possum scat detections.

Occupancy-based predator species richness: sum of occupancy probability predictions for each predator species at each site.

Spatial models

To account for spatial autocorrelation in predator-community measures and habitat covariates (Legendre 1993), we used generalised additive models (GAMs) with a smoothed bivariate spatial term $s(Lat, Long)$ in *mgcv* v1.8.31 (Wood 2019). We built two saturated GAMs with predator abundance and predator species richness as the response variables, including habitat covariates and the spatial term (Table 1), and used *MuMIn* to identify the most parsimonious GAMs based on lowest AICc. We tested Poisson and negative binomial error structures for each model and assessed model fit using function ‘gam.check’ in *mgcv* and the degree of residual spatial autocorrelation using package *ncf* v1.2.9 (Bjørnstad 2020). We created smoothed surfaces of predator abundance for the Capertee Valley and Goulburn River using *mgcViz* v0.1.6 (Fasiolo & Nedellec 2020).

Nest success

We monitored regent honeyeater nests during the 2019 breeding season and combined these data with those from

Table 1. Habitat and detection covariates recorded in surveys of regent honeyeater nest predators in the Capertee and Goulburn River Valleys. All covariates are factors, unless otherwise stated. Further details are provided in Appendix S2

Level	Covariate	Description	Justifying citations
Habitat Covariates	Vegetation Community	Dominant vegetation community based on value to nesting regent honeyeaters. River-oak <i>Casuarina cunninghamiana</i> (high value); yellow box / mugga ironbark <i>Eucalyptus melliodora</i> / <i>E. sideroxylon</i> (high value); white-box <i>E. albens</i> (medium value); other <i>E. crebra</i> , <i>E. punctata</i> (low value)	Major <i>et al.</i> (2001) Crates <i>et al.</i> (2019a)
	Water Proximity	Linear distance from the site centroid to the nearest water source. On site; 50–200 metres; >200 metres	Palmer and Bennett (2006) Crates <i>et al.</i> (2017a)
	Nest Proximity	Linear distance from the site centroid to nearest-known regent honeyeater nest. On site; 50–200 metres; >200 metres	Ball <i>et al.</i> (2005)
	Blossom Abundance	Maximum blossom abundance level across repeat surveys. None; mild; heavy	McElhinny <i>et al.</i> (2006)
	Mistletoe Abundance	Number of mistletoe clumps on site. None; 1–10 clumps; >10 clumps	Watson and Herring (2012)
	Hollow Abundance	Estimated number of tree hollows on site. None; 1–3 hollows; >3 hollows	McElhinny <i>et al.</i> (2006)
	Woody Debris Abundance	Abundance of woody debris on site. Low; medium; high	Mac Nally <i>et al.</i> (2001)
	Canopy Cover	Percentage of canopy cover on site. 0–15%; 15–30%; >30%	Fulton (2018) Val <i>et al.</i> (2018)
	Shrub Cover	Percentage of shrub cover on site. 0–15%; 15–30%; >30%	Val <i>et al.</i> (2018)
	Ground Cover	Dominant ground cover on site. Bare / leaf litter; short grass; long grass / low shrub	Val <i>et al.</i> (2018)
	Spatial location	Wgs84 latitude / longitude, modelled as a smoothed bivariate term. $s(Lat, Long)$.	Legendre (1993)
Detection Covariates	Visit Number	Visit number. Diurnal (1–3); nocturnal (1–2)	Rota <i>et al.</i> (2009)
	Time of day	Period of the day / night in which survey took place. Diurnal: before 10am; 10am to 4pm; after 4pm Nocturnal: within 2 hours of sunset; >2 hours after sunset	How <i>et al.</i> (2004)
	Wind Speed	Estimated wind speed at the time of survey. None; light; moderate	Allen <i>et al.</i> (2018)
	Temperature	Approximate temperature at the time of survey. Diurnal: <10°C; 10–20°C; >20°C Nocturnal: <15°C; 15–20°C; >20°C	Wayne <i>et al.</i> (2005a)
	Moon Phase	Moon phase observed at the time of nocturnal survey. None; small crescent; large crescent; full	Wayne <i>et al.</i> (2005a)

nests monitored between 2015 and 2018 (Crates *et al.* 2019a), to model nest success in two ways:

Nest fate: A binomial response of whether the nest fledged at least one juvenile (succeed) or not (fail).

Daily nest survival rate (DSR): The probability of an egg or nestling surviving from any given day to the next.

Although nest fate is the ultimate measure of nest success, it does not account for nests that fail prior to detection, creating a potential bias in nest success rate estimates (Johnson *et al.* 2007). We modelled daily nest survival rate to account for this potential bias (Mayfield 1975). We obtained predator abundance and species richness predictions for 115 nest locations from the respective spatial models using ‘predict’ in *mgcv*, with habitat data for nest sites that were included in

the most parsimonious spatial models. We therefore derived predictions of predator abundance and species richness at nest locations from multiple survey sites, weighted through the smoothed term by their distance from the nest. We assumed this approach would help account for the fact that the home ranges of the predator species would differ in size (Smith & Murray 2003). We derived occupancy predictions for each predator species at each nest site, using the habitat covariates included in the most parsimonious occupancy models. We then summed these occupancy probabilities to determine the occupancy-based predator species richness. We did not derive occupancy-based predator species richness from a spatial model to avoid double-analysis of habitat covariates already accounted for in the occupancy modelling process.

To assess the relationship between regent honeyeater nest success and predator-community measures, we created nest fate and daily nest survival rate models. We included nest covariates that were previously found to predict regent honeyeater nest success in our analysis (Crates *et al.* 2019a). These covariates were the nest region, as defined in this study (Fig. 1), position of the nest relative to the edge of the tree crown ('position'), the extent to which the nest was concealed by vegetation ('concealment') and presence / absence of an active regent honeyeater nest within 100m of a focal nest ('conspecifics'). We fitted logistic regressions of nest fate with a binomial response of succeed or fail using *lme4* v1.1.23 (Bates & Maechler 2020). We built a series of logistic regression models, using combinations of nest covariates and one of the predator-community measures, and used *MuMIn* to rank these models by AICc. We modelled daily nest survival rate (DSR) using *RMark* v2.2.7 (Laake 2019), creating multivariate DSR models with combinations of nest variables and one of the predator-community measures. To avoid overfitting, given the relatively small sample of nests ($n = 115$), we included no more than two nest covariates and one predator-community measure in a single DSR model. We identified the most parsimonious models based on AICc. An annotated R-script is provided in the Appendix S1.

RESULTS

Site occupancy

Detection rates for predator species were highly variable, ranging from 8% for pied butcherbirds to 77% for possums (Appendix S7). The most parsimonious occupancy models for individual predator species are shown in Table 2. Hollow abundance, blossom abundance and the extent of shrub cover were the covariates most frequently identified as predicting the presence of individual predator species. Wind speed, visit number, time of day and temperature were the factors most commonly affecting detectability.

Spatial models

Predator abundance, defined as the sum of the maximum number of individuals of each predator species

detected at each site, ranged from 0–14 with a median of 3. The most parsimonious predator abundance model (ΔAICc relative to the second most parsimonious model = 0.31, Akaike weight $w_i = 0.247$) included hollow abundance, water proximity, extent of shrub cover, the type of ground cover, mistletoe abundance and the smoothed spatial term. Predator abundance was correlated positively with hollow abundance ($\beta = 0.40$, $\text{SE} = 0.16$, $P = 0.012$) and water proximity ($\beta = -0.31$, $\text{SE} = 0.11$, $P = 0.007$) and negatively with the extent of shrub cover ($\beta = -0.44$, $\text{SE} = 0.14$, $P = 0.002$). Predator abundance was higher at sites with short grass as the predominant ground cover, relative to other types of ground cover ($\beta = -0.27$, $\text{SE} = 0.10$, $P = 0.008$, Table 3). The predicted predator abundance surface is shown in Fig. 2. The smoothed spatial term accounted for almost all spatial autocorrelation in the predator count data.

Predator species richness, defined as the number of predator species detected at a site, including detections through scat surveys, ranged from 0–7 with a median of 2. The most parsimonious predator species richness model ($\Delta\text{AICc} = 0.23$, $w_i = 0.084$) included hollow abundance, extent of shrub cover and extent of canopy cover. Predator species richness was correlated positively with hollow abundance ($\beta = 0.51$, $\text{SE} = 0.16$, $P = 0.001$) and negatively with the extent of shrub cover ($\beta = -0.25$, $\text{SE} = 0.12$, $P = 0.037$). Predator species richness was higher at sites with moderate canopy cover ($\beta = -0.52$, $\text{SE} = 0.24$, $P = 0.034$).

Nest success

When controlling for other covariates, the relationships between regent honeyeater nest fate and predator-community measures were non-significant: predator abundance ($\beta = 0.18$, $\text{SE} = 0.14$, $P = 0.200$), predator species richness ($\beta = 0.50$, $\text{SE} = 0.30$, $P = 0.101$) and occupancy-based predator species richness ($\beta = -0.42$, $\text{SE} = 0.34$, $P = 0.217$, Fig. 3, Appendix S3). The most parsimonious nest fate model ($\Delta\text{AICc} = 0.64$, $W_i = 0.261$) included only the presence of conspecifics and nest position. Nest success was higher among nests where conspecifics were present ($\beta = 1.18$, $\text{SE} = 0.41$, $P = 0.004$) relative to those where conspecifics were absent and higher among nests that were located in the outer-crown ($\beta = -1.81$, $\text{SE} = 0.84$, $P = 0.031$) relative to those located in the inner crown (Appendix S4).

The most parsimonious daily nest survival (DSR) model ($\Delta\text{AICc} = 0.15$, $W_i = 0.192$, Fig. 4, Appendix S5 and Appendix S6) included predator abundance, nest position and the presence of conspecifics. The mean probability of regent honeyeater

Table 2. The most parsimonious occupancy model for each nest predator species surveyed. $\Delta AICc$ is relative to the second most parsimonious model for each species

Species	Model	$\Delta AICc$	w_i
Australian magpie	$\Psi(\text{shrub}), p(\text{wind})$	0.52	0.44
Australian raven	$\Psi(\text{wood}), p(\text{visit})$	2.40	0.62
Common brushtail possum	$\Psi(\text{hollows} + \text{blossom} + \text{wood}), p(1)$	1.16	0.36
Glider spp.	$\Psi(\text{blossom}), p(\text{wind})$	0.16	0.30
Grey butcherbird	$\Psi(\text{hollows}), p(\text{temperature} + \text{visit})$	0.41	0.28
Grey shrike-thrush	$\Psi(1), p(\text{time} + \text{visit} + \text{wind})$	0.22	0.25
Laughing kookaburra	$\Psi(\text{ground}), p(1)$	0.12	0.52
Noisy miner	$\Psi(\text{blossom} + \text{shrub}), p(\text{temperature})$	1.76	0.43
Pied butcherbird	$\Psi(\text{shrub}), p(\text{time} + \text{wind})$	0.22	0.25
Pied currawong	$\Psi(\text{vegetation}), p(\text{visit})$	0.39	0.48
White-winged chough	$\Psi(\text{shrub} + \text{vegetation} + \text{wood}), p(\text{wind})$	0.09	0.29

Table 3. Spatial model summaries showing the relationship between predator-community measures and habitat covariates. Significant effects defined as $P < 0.05$ are shown in bold

Measure	Covariate	Relative to	β	SE	z	P
Predator Abundance	Ground Cover (Long grass / low shrub)	Ground (Short grass)	-0.30	0.14	-2.10	0.036
	Ground Cover (Bare / leaf litter)		-0.27	0.10	-2.66	0.008
	Hollow Abundance (1-3)	Hollow Abundance (None)	0.14	0.16	0.86	0.388
	Hollow Abundance (>3)		0.40	0.16	2.50	0.012
	Mistletoe Abundance (1-10)	Mistletoe Abundance (None)	-0.11	0.10	-1.06	0.290
	Mistletoe Abundance (>10)		0.12	0.11	1.08	0.281
	Shrub Cover (15-30%)	Shrub Cover (0-15%)	-0.04	0.10	-0.45	0.655
	Shrub Cover (>30%)		-0.44	0.14	-3.08	0.002
	Water Proximity (50-200 m)	Water Proximity (On site)	-0.27	0.12	-2.22	0.026
	Water Proximity (>200 m)		-0.31	0.11	-2.71	0.007
	<i>s(Lat, Long)</i>		edf	χ^2	P	
			35.01	100.6	< 0.001	
Predator Species Richness	Canopy Cover (15-30%)	Canopy Cover (0-15%)	0.20	0.24	1.13	0.034
	Canopy Cover (>30%)		0.52	0.24	1.74	0.082
	Hollow Abundance (1-3)	Hollow Abundance (None)	0.27	0.16	1.72	0.086
	Hollow Abundance (>3)		0.51	0.16	3.19	0.001
	Shrub Cover (15-30%)	Shrub Cover (0-15%)	0.01	0.10	0.08	0.938
	Shrub Cover (>30%)		-0.25	0.12	-2.09	0.037

nest success between 2015 and 2019 within the Capertee Valley and Goulburn River, assuming a 34-day nesting period from the first egg date to fledging was 31%.

DISCUSSION

Understanding the processes that limit breeding success in threatened species, and how these threats vary spatially, is critical to informing and implementing effective conservation management (Ibáñez-Álamo *et al.* 2015). We aimed to determine the habitat features influencing nest predator abundance, understand the spatial distribution of nest

predators and explore the relationship between predator abundance and regent honeyeater nest success. A number of habitat features were associated with the presence of individual predator species, as well as the abundance of the predator community as a whole. Predators were found across the study area, with a median of three individuals and two species per survey site. Contrary to our expectations, regent honeyeater nest fate and daily nest survival rates showed no negative relationship with predator-community measures. Instead, we found a non-significant positive relationship between nest success and both predator abundance and predator species richness.

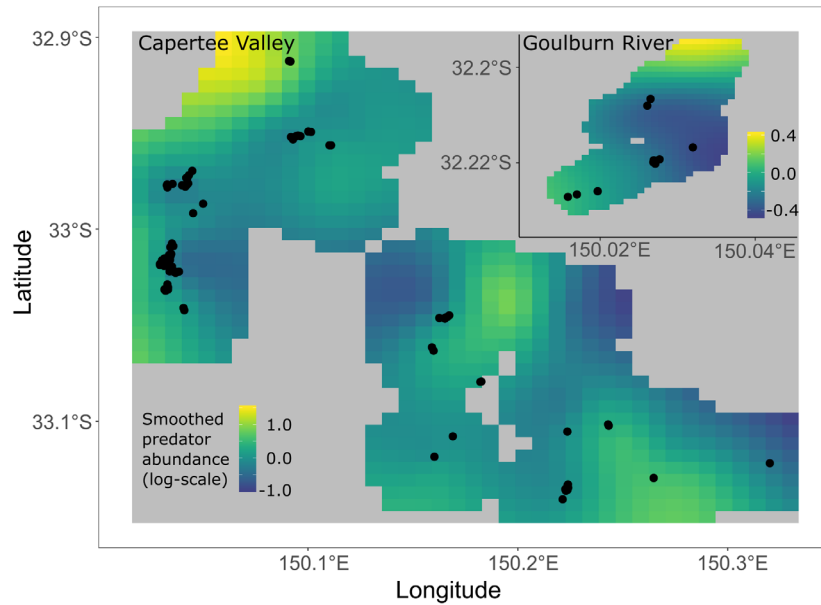


Fig. 2. Smoothed nest predator abundance prediction surface across the Capertee Valley and Goulburn River derived from generalised additive models. Points denote regent honeyeater nest sites located between 2015 and 2019. Note different spatial scales for the Goulburn River (inset).

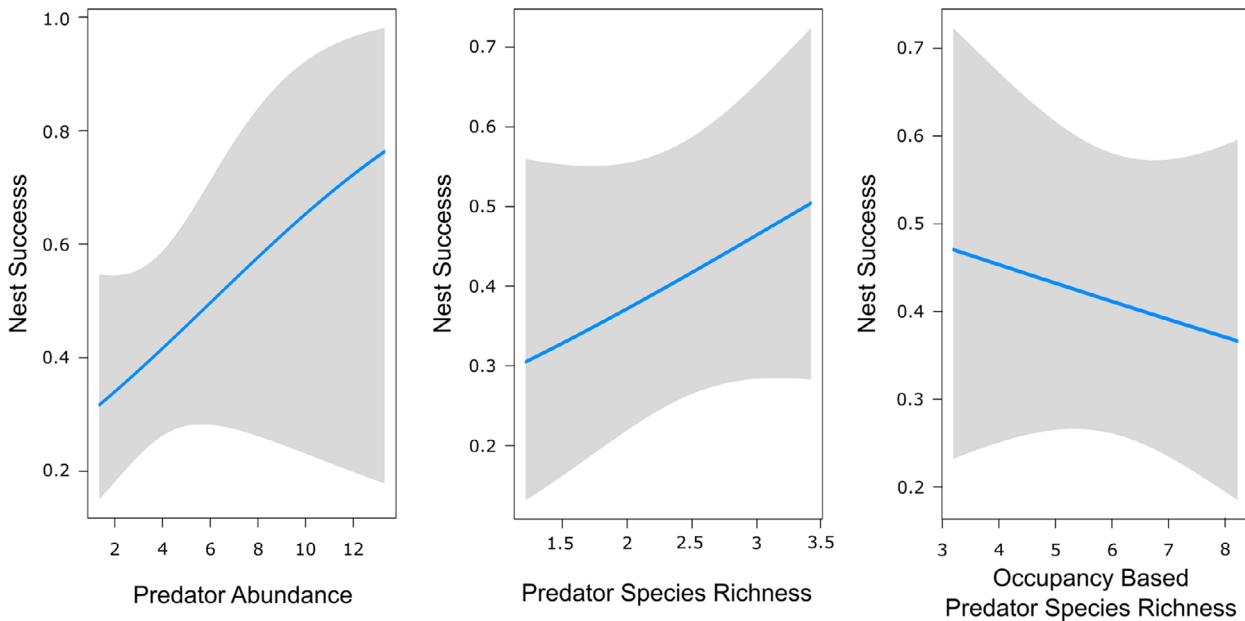


Fig. 3. Logistic regression of the relationship between regent honeyeater nest success in the Capertee Valley and Goulburn River ($n = 115$) and predator-community measures.

Predictors of predator presence

The habitat features that best predicted occupancy of nest predators varied between species. Noisy miner presence was associated negatively with the extent of shrub cover and blossom abundance; consistent with

findings that noisy miners are associated with fragmented woodland areas where understory vegetation has been cleared (Val *et al.* 2018). The white-winged chough, Australian magpie, pied butcherbird and laughing kookaburra were also associated negatively with the extent of shrub cover and associated

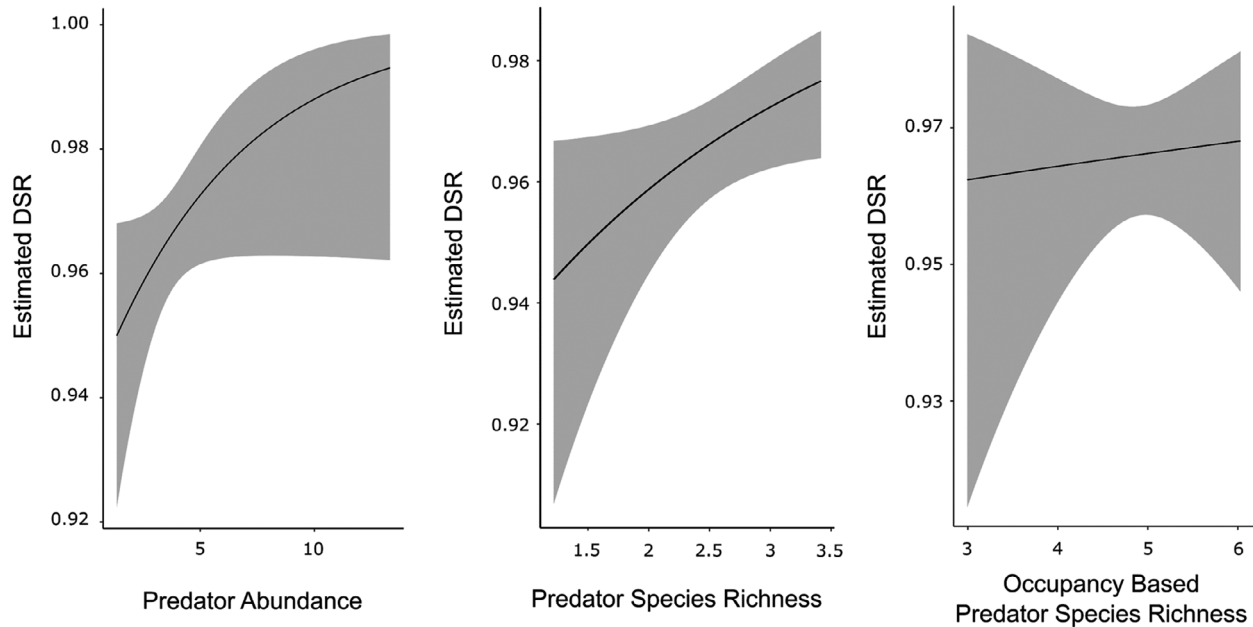


Fig. 4. Modelled relationship between predator-community measures and regent honeyeater daily nest survival rate (DSR) in the Capertee Valley and Goulburn River between 2015 and 2019 ($n = 115$). Predictions are derived from univariate models of each predator-community measure.

positively with short grass as the primary ground cover. These birds primarily forage on the ground (Higgins 2006) and are therefore more likely to avoid areas with extensive shrub cover and / or a dense understory. The common brushtail possum and glider species were associated positively with local blossom abundance; an important food source for arboreal marsupials (Smith & Murray 2003) as well as nesting regent honeyeaters (Crates *et al.* 2017a). Possums were also associated with high estimated hollow abundance; a key habitat feature for arboreal marsupials (McElhinny *et al.* 2006).

For the predator community as a whole, predator abundance and species richness measures were highly variable across both study areas. We detected up to 14 individual predators and up to seven predator species at survey sites, emphasising the high potential predation threat faced by nesting regent honeyeaters. Spatial models revealed that predator abundance and species richness were both higher at sites with more hollows and a lower extent of shrub cover. These habitat features may reflect woodland landscapes that have undergone modification for agricultural purposes, which has been associated with the release of mesopredators (Ford 2011; Fulton 2018). Knowledge of the habitat features impacting nest predator abundance and predator species richness may be helpful in identifying areas with higher potential risk

of nest predation and informing the implementation of targeted predator management.

Nest predator community and regent honeyeater nest success

While our study was not able to find a clear relationship between predator abundance and regent honeyeater nest success, this relationship is well documented among other species. Previous studies have indicated a negative correlation between predator abundance and nest success (e.g. Debus 2006; Heinsohn *et al.* 2015), and removal of predators is often considered an effective strategy in the management of threatened birds (Smith *et al.* 2010). Our results may indicate that a larger sample of nests is required and / or that other factors are obscuring the relationship between predator community measures and regent honeyeater breeding success. One species, or even one individual, may be culpable for a disproportionate amount of nest predation events (Stojanovic *et al.* 2014). For regent honeyeaters, observations of nests being predated by a wide range of species casts doubt on this possibility (Taylor *et al.* 2018; Crates *et al.* 2019a). Less common woodland nest predators, which were not surveyed in our study, could also be responsible for some nest failures (Guppy *et al.* 2017). While nest predation has been shown to account for 89% of contemporary regent honeyeater nest failures where the cause of failure is discernible (Crates *et al.* 2019a), not all nest failures

[Correction added on 12 July 2021, after first online publication: the text 'were associated positively with local blossom abundance' has been removed from the preceding sentence.]

in our database can be attributed to predation events. Other documented causes of nest failure for Australian woodland birds include high winds and disease (Fulton 2019b), and any regent honeyeater nests that failed due to these reasons could further obscure the relationship between predator abundance and nest success.

Other factors showed a stronger correlation with regent honeyeater nest success than predator abundance. Nest success was significantly higher among nests located in the outer crown, relative to nests located in the mid or inner sections of the crown. This relationship suggests that a nest's position in the outer crown reduces its susceptibility to nest predation, possibly due to dense foliage on outer tree limbs reducing visual detectability. A similar pattern has been recorded in other species, with nest concealment reducing predation by visual predators (e.g. Flaspohler *et al.* 2000; Colombelli-Négrel & Kleindorfer 2009). The presence of another active regent honeyeater nest within 100m was associated with higher rates of nest success. Improved nest success rates near other active nests may reflect superior resource availability at these sites or result from the decreased individual effort expended on excluding competitor species when other regent honeyeaters are present (Ford *et al.* 1993). Further monitoring of regent honeyeater breeding activity, localised breeding conditions and predator abundance at active nests may help in understanding the processes at play.

Study limitations

Due to the sparsity of contemporary regent honeyeater nest sites and the large number of known nest predator species, some limitations to our survey approach were unavoidable. In order to achieve a sufficient sample of nests, we required data from five breeding seasons (2015–2019). Only 10% of the nests were active in 2019, meaning predator levels may have changed between survey year and nesting year. In addition, the home ranges of many of the predator species are likely to exceed the 50 m site radius used in our survey design (Cox & Bauer 1997), violating the closure assumption which assumes that occupancy does not change between survey visits (Rota *et al.* 2009). However, we attempted to minimise closure violation by conducting all repeat surveys in as short a time period as possible (Rota *et al.* 2009). Furthermore, the use of a 50 m site radius has been shown to be ecologically relevant for breeding regent honeyeaters, which typically occupy small breeding territories during nesting (Crates *et al.* 2017a). Whilst our inferences would be more robust if we were able to survey

nest predators in real time at active nest sites, the rarity of the regent honeyeater prevented us from doing so.

Management and research recommendations

Provided a sufficient sample size can be obtained, future studies would benefit from the collection of predator data from active regent honeyeater nest sites, potentially at larger and more widely stratified spatial scales. The abundance and widespread occurrence of nest predators in regent honeyeater breeding areas emphasises the threat of nest predation facing the species and has management implications for future nest protection efforts. Of particular note were the high site-occupancy rates for nest predators such as the Australian magpie and glider species, for which no nest protection measures are currently implemented. To date, attempts to protect regent honeyeater nests have involved the suppression of noisy miners and the deployment of trunk collars to prevent possums and monitor lizards from accessing nest trees (Regent honeyeater recovery team, unpublished data). Our findings suggest that even if current nest protection measures help reduce predation rates by these species, there is a real risk of compensatory nest predation by other known predator species, as shown by Beggs *et al.* (2019). Nest protection measures that account for threats posed by the entire predator community would most effectively mitigate this risk (Smith *et al.* 2010). Such measures may include temporary removal of gliders that cannot otherwise be prevented from accessing nests (Stojanovic *et al.* in press) or implementing deterrents to keep avian predators away from nest sites (Peterson & Colwell 2014). Large-scale habitat management that aims to reduce habitat suitability for predators presents another potential avenue for controlling elevated rates of nest predation (Laidlaw *et al.* 2017). For regent honeyeaters, our results suggest this could be achieved through restoration of shrubby understory vegetation and reducing grazing pressure from livestock. Whether such large-scale habitat change can occur, and successfully suppress nest predation rates, in a time scale that can help prevent extinction of regent honeyeaters is questionable (Bedward *et al.* 2009).

Although regent honeyeater numbers have been declining for decades, only recently has increased emphasis been placed on developing standardised monitoring, locating breeding sites and establishing a robust understanding of the causes of nesting failure (Crates *et al.* 2019b). To inform management of threatened species, there is a need to obtain high-quality monitoring data, and enigmatic threats call for ongoing investment in monitoring and research (Robinson *et al.*, 2018; Scheele *et al.* 2018). Our study provides a pertinent

warning that, if targeted monitoring and conservation efforts are left too late, threatened species can decline to the extent that it becomes challenging to obtain robust evidence to help inform effective adaptive management to facilitate population recovery.

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AUTHOR CONTRIBUTION

Daniel Gautschi: Conceptualization (supporting); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing—original draft (lead). **Robert Heinsohn:** Conceptualization (supporting); Supervision (supporting); Validation (lead); Writing—review & editing (supporting). **Liam Murphy:** Data curation (supporting); Investigation (supporting). **Ross Crates:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Supervision (lead); Visualization (supporting); Writing—review & editing (lead).

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CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data are available upon request from the author. Data are sensitive because they involve regent honeyeater breeding locations. R Scripts are provided in supporting documentation.

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SUPPORTING INFORMATION

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

Appendix S1. R Script used for statistical analysis.

Appendix S2. Habitat and detection covariates recorded in surveys of regent honeyeater nest predators in the Capertee and Goulburn River Valleys.

Appendix S3. Logistic regression of the relationship between predator-community measures and regent honeyeater nest fate within the Capertee Valley and Goulburn River from 2015 to 2019 ($n = 115$).

Appendix S4. Summary of the most parsimonious logistic regression model of regent honeyeater nest fate within the Capertee Valley and Goulburn River from 2015 to 2019 ($n = 115$). Significant effects defined as $P < 0.05$ are shown in bold.

Appendix S5. The five most parsimonious models of regent honeyeater daily nest survival rate (DSR) ranked by AICc. The model we considered to be most parsimonious, based on delta AICc and number of terms, is highlighted in bold. Akaike weight (w_i) refers to the weight of each model within the (5) most parsimonious models.

Appendix S6. Summary of the most parsimonious model of regent honeyeater daily nest survival rate (DSR). Covariates / factor levels where $\beta \pm 2 \times \text{SE}$ does not overlap 0 are shown in bold. N/A indicates that a value is not applicable as the covariate is not a factor.

Appendix S7. Detection rates of nest predator species at survey sites in regent honeyeater breeding areas within the Capertee Valley and Goulburn River.