Population viability in data deficient nomadic species: What it will take to save regent honeyeaters from extinction

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ABSTRACT

The long-distance, unpredictable movement patterns of nomadic species make them challenging to monitor and conserve. Critically endangered regent honeyeaters *Anthochaera phrygia* once roamed south-eastern Australia in 'immense flocks' but now number fewer than 300 wild birds over a vast 300,000 km^2 range. Regent honeyeaters are a rare example where extensive monitoring data are now available for a nomadic species, enabling evaluation of the impact of management actions using population viability analysis (PVA). We combined demographic estimates from wild population monitoring in the 1990s, a zoo-based supplementation program and a contemporary range-wide monitoring program to simulate the wild population trajectory under various management and climatic scenarios. Without intervention, our models predicted extinction within 20 years, and showed that management strategies at their current intensity have limited efficacy to prevent extinction. Conservation actions should aim to increase the size and density of the wild population so that Allee effects no longer suppress population growth. Protection of wild regent honeyeater nests is essential as breeding success has declined over recent decades and droughts increasingly reduce breeding opportunities. Our models emphasise the need for zoo-based breeding to bolster the wild population, but show that release of zoo bred birds into the wild only slows the rate of population decline. To recover the wild regent honeyeater population, the next five years will be critical for implementing the most effective conservation strategy. This requires a combination of nest protection and release of zoo-bred birds with improved fitness, predator suppression, habitat protection and increased rates of habitat restoration.

1. Introduction

Given their irregular, long-distance movement patterns, nomadic species pose unique challenges not only for population monitoring but also for effective implementation of conservation actions (Runge et al., 2014, 2016). Obtaining robust estimates of demographic parameters for mobile species typically require long term, species-specific monitoring programs (Lindenmayer et al., 2020). Such monitoring programs are needed to capture often drastic spatio-temporal variation in breeding success and or survival that reflect spatio-temporal variation in environmental conditions, and hence breeding resources (Webb et al., 2014).

Monitoring data available for nomadic species are invariably poor, making nomads under-conserved globally (Cottee-Jones et al., 2015; Scheele et al., 2019).

When available, robust population data can be utilised through Population Viability Analysis (PVA)- simulation models that predict temporal changes in population size and extinction probability given estimates of demographic parameters (Beissinger and Westphal, 1998). PVAs can inform conservation decisions for threatened species (Drechsler and Burgman, 2004), including predicting the outcome of reintroduction efforts (Schaub et al., 2009). For species that are difficult to monitor, PVA is increasingly being used to evaluate their conservation

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status (IUCN, 2019; Heinsohn et al., 2015). PVA can also model the demographic impact of stochastic events on population trajectories (Ward et al., 2020). Even where uncertainties exist around some demographic parameters, which is often the case for endangered nomads (Cottee-Jones et al., 2015), PVA can provide 'best case scenarios' by assigning optimistic values to unknown parameters (Keighley et al., 2021). Future population growth rates are therefore unlikely to be greater than those predicted, but could be substantially lower.

One nomadic species for whom monitoring data have historically proven challenging to acquire is the regent honeyeater (Clarke et al., 2003); a critically endangered songbird endemic to south-eastern Australia (Higgins et al., 2001). The species' original range extended in a broad swathe from Adelaide to central coastal Queensland (Franklin et al., 1989, Fig. 1). There are no reliable estimates of the pre-European population size, but regent honeyeaters were considered common and widespread, roaming the landscape in 'immense flocks' to track nectar resources in flowering eucalyptus tree species (Franklin et al., 1989). Extensive land clearing of the species' preferred habitats (Bradshaw, 2012) has seen the population undergo severe population decline.

Regent honeyeaters are smaller than many other nectar-feeding birds they compete with for access to nectar resources (Ford, 1979). Historically, regent honeyeaters overcame their size disadvantage by feeding in large flocks and nesting in aggregations (Ford et al., 1993). As the population has declined, so too has the average size of flocks and nest aggregations, which is thought to make it more challenging for regent honeyeaters to survive and breed successfully in the wild (Ford et al.,

1993). Such Allee effects occur when components of fitness such as survival and breeding success decline with decreasing population size or density (Berec et al., 2007; Stephens et al., 1999). The regent honeyeater's particular dependence on group living suggests the species is especially vulnerable to population decline driven by an Allee effect (Crates et al., 2017).

It is still unclear which demographic parameters are causing regent honeyeaters to decline much more rapidly than other honeyeater species (Ford et al., 2001). However, decreased breeding output is a possible driver of population decline, caused by the combined effects of increased rates of nest failure, decreased productivity of successful nests (Crates et al., 2019b), severe loss of breeding habitat, Allee effects(Crates et al., 2017) and drought events suppressing breeding opportunities (Commonwealth of Australia, 2016). Expert elicitation predicts the regent honeyeater has a 57% probability of extinction in the wild by 2038 (95% confidence intervals 37–75%), though these predictions were based on limited available monitoring data (Geyle et al., 2018).

In the 1990s, it was estimated that the wild regent honeyeater population comprised 1500–2500 birds (Geering and French, 1998), but numbers have continued to dwindle to the extent that there may well be fewer than 300 mature individuals persisting in the wild (Kvistad et al., 2015, Crates et al., 2021a, Fig. 1). Although birds are occasionally sighted throughout their contemporary range, known breeding activity is now restricted to north-eastern Victoria (estimated population 30 individuals) and two regions of New South Wales; the Northern Tablelands (estimated population 50) and the greater Blue Mountains
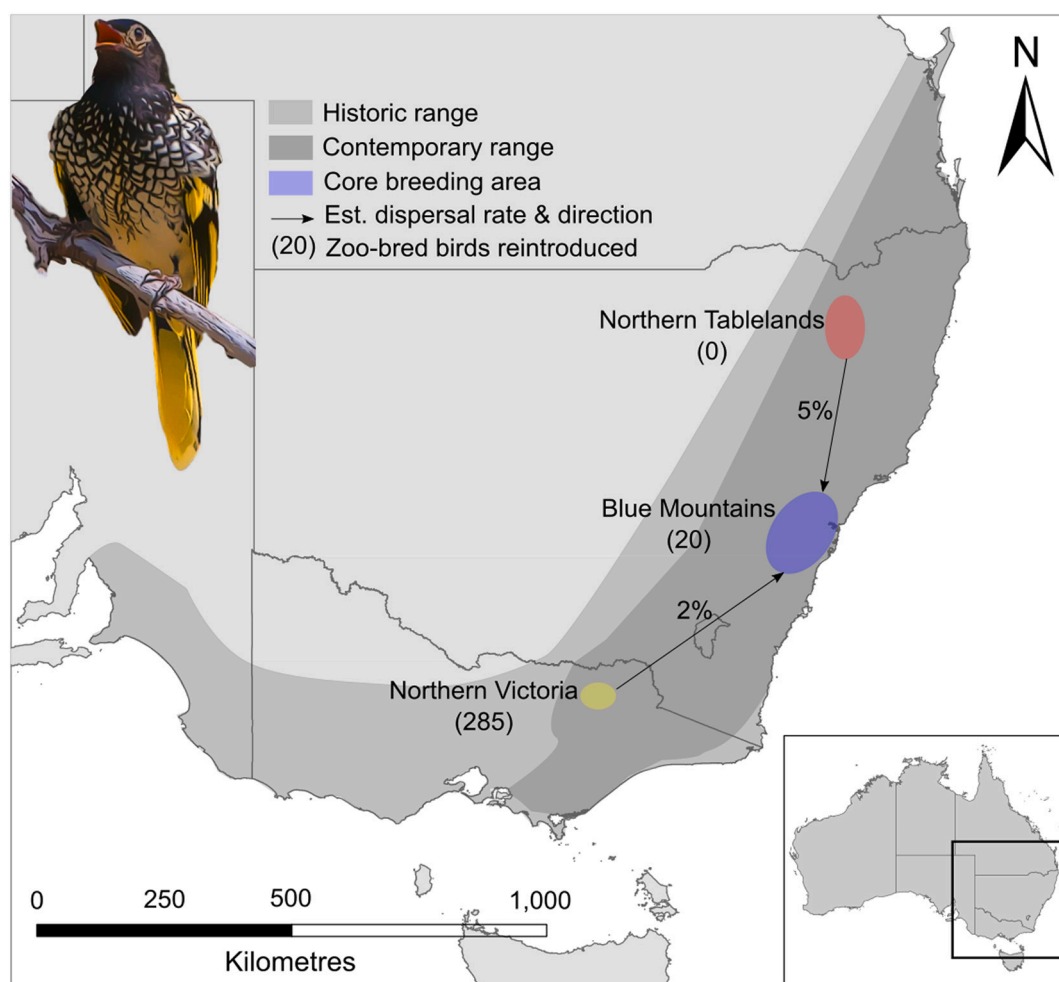

Fig. 1. Historic and contemporary range of the regent honeyeater showing reintroduction sites, distribution of contemporary core breeding areas and estimates of dispersal rates and directions between metapopulations (see Table S1 for further information). Inset: Study area on a national scale.

(estimated population 150). Genetic evidence confirms the wild population still represents a single genetic management unit (Kvistad et al., 2015; Crates et al., 2019a), but colour mark resighting data and the existence of distinctive regional song dialects suggest that long-distance movements of individuals between these three subpopulations are rare and non-random (Crates et al., 2021a,b; Powys, 2010).

Other threatening processes may be exacerbating regent honeyeater population decline. Prolonged droughts suppress eucalypt flowering (Law et al., 2000), which causes regent honeyeaters to occupy coastal drought refugia to the east of their typical breeding range (Commonwealth of Australia, 2016; Stojanovic et al., 2021). Droughts may also suppress breeding activity through reducing the proportion of the population attempting to breed, the number of fledglings per brood and/or the number of broods per season (Commonwealth of Australia, 2016). Prolonged droughts can also lead to eucalypt and mistletoe dieback (Hoffmann et al., 2019), making regent honeyeaters particularly susceptible to the increased frequency of drought events predicted for south-eastern Australia under climate change (Collins et al., 2013).

Climate change is also predicted to increase the frequency and severity of catastrophic weather events such as Australia's 2019/20 megafires (Jolly et al., 2015), which affected approximately 40% of contemporary regent honeyeater breeding locations (Crates et al., 2021b). By suppressing eucalypt blossom and killing mistletoe for multiple years after tree crowns are burnt, wildfires reduce the availability of potential breeding habitat and may cause direct mortality of individuals through burning or smoke inhalation (Ward et al., 2020). The proliferation of noisy miners *Manorina melanocephala*; a hyper-aggressive native honeyeater found through many remaining regent honeyeater breeding areas further reduces the availability of potential regent honeyeater breeding sites, because noisy miners aggressively exclude smaller bird species from their colonies once they exceed a threshold density of around 0.6 birds per hectare (Maron et al., 2013). Noisy miners have also been observed destroying regent honeyeater nests (Crates et al., 2019b). Threats from noisy miners can be managed in important breeding areas, but targeting management actions in time and space to benefit a large proportion of the regent honeyeater population is challenging (Crates et al., 2018).

A reintroduction program commencing in 2000 has so far released 315 zoo-bred regent honeyeaters, primarily on the southern edge of the species' contemporary range (Tripovich et al., 2021, Fig. 1). Survival of zoo-bred birds in the 20 weeks post-release is around 70%. Evidence that zoo-bred birds breed successfully in the wild to the extent that they are facilitating population recovery is limited (Taylor et al., 2018; Tripovich et al., 2021). Songs of zoo-bred males are very different from those of their wild counterparts, which may impact their fitness if wild females avoid pairing with zoo-bred males post-release (Crates et al., 2021a). Given high costs of managing and implementing reintroduction programs (Helmstedt and Possingham, 2017), devising methods of enhancing the fitness of zoo-bred bred birds is a conservation priority (Tripovich et al., 2021).

Combining demographic data from the 1990s, the reintroduction program and a new, range-wide monitoring program established in 2015, we used PVA to achieve three aims. First, we identified demographic parameters underpinning the observed rapid population decline in the wild regent honeyeater population. We then aimed to model the potential to facilitate population recovery by (i) increasing breeding output in wild birds via protection of nests from predation; and (ii) reintroducing zoo-bred birds. Finally, we aimed to identify the intensity of combined conservation actions required to facilitate regent honeyeater population recovery.

2. Methods

2.1. Historical population monitoring

Regent honeyeaters were monitored in three regions of New South

Wales in the 1990s. Geering and French (1998) monitored birds in the Blue Mountains between 1994 and 1996, whilst Oliver et al. (1998) monitored birds in the Northern Tablelands between 1993 and 1997. In north-eastern Victoria, breeding activity and surveys were conducted opportunistically in Chiltern-Mount Pilot National Park and surrounds (E. Collins, unpublished data). Between 1998 and 2015, there was no standardised monitoring of breeding activity in the wild population. Monitoring during this period included maintaining a database of public sightings, two range-wide public search weekends in May and August, and annual surveys of 2-hectare, 20-minute bird transects and area searches in the Northern Tablelands and greater Blue Mountains, respectively (BirdLife Australia, unpublished data). The wild population has been opportunistically colour-banded since 1989.

2.2. Zoo-based breeding and reintroduction

Since 1995, a total of 23 regent honeyeaters have been collected from the wild to found a breeding program at Taronga Zoo (Sydney, Australia) which now includes additional zoological partners (Taronga Conservation Society, unpublished data). In 2000 a trial release of eight zoo-bred birds was undertaken in the Blue Mountains (Taronga Conservation Society, unpublished data). Between 2008 and 2017, there were five autumn/winter releases of zoo-bred birds in Chiltern-Mount Pilot National Park in north-eastern Victoria, totalling 287 individuals (Tripovich et al., 2021, Fig. 1). The rationale for releasing zoo-bred birds in Chiltern was to prevent an ongoing range contraction by supplementing the population on its southern range edge (Commonwealth of Australia, 2016). In winter 2020, the approach changed when 20 birds were released in the Lower Hunter Valley to help maximise the density of the remaining core population within the greater Blue Mountains (Fig. 1).

In the two to three months post-release, survival and breeding attempts of zoo-bred regent honeyeaters have been monitored through a combination of sightings of coloured leg bands on released birds, or through radio-tracking within circa 20 km of the release site of a subset of the cohort that wore temporary radio transmitter backpacks (SWIFFT, 2020). After the post-release monitoring period, a significant proportion of survival data on released birds comes from public resightings of colour-banded birds (SWIFFT, 2020). Increased effort to monitor post-release breeding activity in the zoo-bred population commenced from the 2015 release (Taylor et al., 2018).

2.3. Contemporary monitoring data

We derived contemporary parameter estimates of the wild population via the National Regent Honeyeater Monitoring Program (NRHMP). Established in 2015, the NRHMP aims to improve the quality and quantity of regent honeyeater monitoring data, to help inform the implementation of conservation actions to prevent the species' extinction in the wild. The NRHMP surveys approximately 1300 sites twice each Austral spring throughout the species' contemporary breeding range, using a 5-minute survey method that accounts for the species' rarity, large range and specific habitat requirements (Stojanovic et al., 2021, Fig. S1). Where we detected regent honeyeaters at survey sites, we conducted searches of the surrounding area to locate additional birds nearby and monitor breeding activity (Crates et al., 2019b). Data from the NRHMP has shown that breeding success has declined since the 1990s, nest predation is the primary cause of nest failure and the adult sex ratio is male biased (Crates et al., 2019b, Table 1).

2.4. Population viability analysis

We used the software package VORTEX10 v1.3.2 (Lacy et al., 2017a; software available at www.scti.tools/vortex), an individual-based population simulation program, to model regent honeyeater population trajectories over two time periods, 20 years (roughly 6 generations sensu

Table 1
Parameters used for wild regent honeyeaters in all population viability analysis scenarios. Contemporary regional subpopulations: BM = Blue Mountains, NT = Northern Tablelands, VIC = North-eastern Victoria.

Parameter	Value
Population structure	3 weakly connected populations (see Table S1)[a]
Initial population size (carrying capacity)	Historic BM = 1000 (3000), BM = 150 (400), NT = 50 (200), VIC = 30 (200)
Age of first reproduction by males/females	1 year
Maximum age	11
Adult mortality (annual variation)	41.67%, SD = 3.00
Juvenile mortality (annual variation)	41.67%, SD = 10.00
Maximum progeny per year	2 broods (3 nestlings in each)
No. of offspring per female per year	Contemporary (2015–2017)[b]
	0.99 (BM)
	0.38 (NT, Vic)
	Historic (1994–1997)[c,d]
	1.51 (BM)
Proportion males (sex-ratio) at hatching	50:50
Percentage adult females breeding	88
Percentage of males breeding	Historic = 88[d]
	Contemporary = 88[a]
Mating system	Monogamy
Inbreeding	Not included

[a] Crates et al. (2019a).
[b] Crates et al. (2019b).
[c] Geering and French (1998).
[d] Oliver et al. (1998).

Bird et al., 2020, Fig. S2) and 40 years. Vortex has been used for projecting trajectories, assessing threats, and evaluating conservation options for 100 s of species (e.g. Heinsohn et al., 2015; Lacy et al., 2017b, 2021). Vortex uses a discrete-time, age-based demographic model that simulates the demographic events of reproduction, survival, dispersal, carrying capacity limitation, and then censuses on an annual cycle (Lacy, 2000). It includes annual variation in demographic rates ("environmental variation"), demographic stochasticity, breeding system, and the option to specify rates as functions of population density, year, or other environmental, population, or individual variables. We modelled a total of 20 demographic scenarios grouped into three themes: Theme one considered four scenarios of the wild population as it is using starting populations of 1000 (1990s Blue Mountains), 150 (contemporary Blue Mountains) and 230 (contemporary metapopulation comprising Blue Mountains 150 individuals, Northern Tablelands 50 individuals, and Victoria 30 individuals). The contemporary starting populations represent best estimates of the recent and contemporary wild regent honeyeater populations (Fig. 1).

Theme two explored the extent to which the breeding success of wild regent honeyeaters would need to be increased, via nest protection, to restore population growth. Potential measures to protect regent honeyeater nests from predation and restore nest success rates to historical levels (Geering and French, 1998; Oliver et al., 1998) include plastic collaring of nest trees to prevent common brushtail possums *Trichosurus vulpecula* and lace monitors *Varanus varius* accessing them, targeted culling of avian predators, and trapping, temporary housing or translocation of arboreal mammals (Crates et al., 2019a,b). Based on data in Crates et al. (2019b) showing that females currently produce 0.99 fledglings per year, we calculate that approximately 10%–30% of failed nests need to succeed to boost mean productivity to between 1.5 and two fledglings per female per year (Appendix A).

Theme three scenarios explored the impact of releases of zoo-bred birds on growth of the wild population, either (i) within current maximum resourcing capacity, (ii) with double the resourcing capacity, or (iii) in combination with nest protection and increased carrying capacity via habitat restoration and noisy miner suppression. Overall, we therefore aimed to explore the scale of all potential conservation actions that is likely to be required for the wild regent honeyeater population to recover to the extent that it becomes self-sustaining- the ultimate goal of the species' National Recovery Plan (Commonwealth of Australia, 2016, Table 2).

The parameters common to all PVA models in this analysis are given in Table 1 and the additional features of each successive model are given in Table 2. All simulations comprised 1000 iterations. We examined the Blue Mountains population using historic data from the 1990s (Geering and French, 1998, Scenario 1A) and compared the trajectory then to the current trajectory using breeding data from recent studies (Crates et al., 2019b, Scenario 1B). We combined the three extant but weakly-connected populations (Blue Mountains, Northern Tablelands, and Victoria, see Fig. 1 and Table S1) and examined the trajectory of the meta-population (Scenario 1C). We added drought, defined as years where total annual rainfall was greater than one standard deviation lower than the 1900–2020 average as a 'catastrophe' programmed to occur every five years on average (Fig. S3) with reproduction during drought halved and mortality increased by 5% (Scenario 1D). We first used a generation time of 3.4 years (Bird et al., 2020) and age of first reproduction of one year (Crates et al., 2019b) to calculate background adult mortality rates of 41.67% per annum (where Generation time = 1/m + age at first reproduction; m = annual adult mortality rate; Garnett et al., 2011). This mortality rate is calculated from mean life history parameters over the honeyeater family (Meliphagidae) and reflects the generally slow life history of Australian passerines. However, it is likely to be optimistic in the current circumstances and also subject to Allee effects (see below). Our use of optimistic values allows us to state that our models create best case scenarios and that true population trajectories are likely to be worse. We also assumed that juvenile (first year) mortality in the wild population is the same as that of adults. Although there is a lack of data for mortality of juveniles over their entire first year, our field data show that juvenile survival is high (86%) over the first two weeks post-fledging which is a period of typically high mortality for many species (Crates et al., 2019b). Models including zoo-bred birds used higher mortality rates for both adults and juveniles, reflecting the additional mortality these birds suffer in the period immediately after release (see below). We conducted sensitivity tests to examine the impact of variation in reproductive success, adult and juvenile mortality, carrying capacity and initial population size on the stochastic population growth rate (r). The proportion of males able to breed each year in the models was set at 88%, reflecting the male-biased sex ratio. The proportion of females in the breeding pool was independently reduced to 88%, reflecting the proportion of wild pairs observed to initiate nesting but fail to lay eggs (Crates et al., 2019b).

All models in theme one included a 'narrow' Allee effect (Stephens et al., 1999), whereby individual breeding success decreased markedly below a population size of 100 but did not improve above that population size(Fig. S4). Although Allee effects are likely to act on both juvenile and adult mortality, we restrict our analysis of Allee effects to those acting on breeding success because of the availability of good field data over more than two decades for that parameter only. Models in themes two & three started with the same narrow Allee effect but later incorporated a 'broad' Allee effect such that individual breeding success continues to improve up to a population size of 2000 (Fig. S4). Overcoming this Allee effect is the mechanism by which managers hope to re-establish population growth. The rationale is that boosting population size through management actions will enable higher reproductive success that will eventually lead to enough population growth so that management interventions are no longer required. The function used for our broad Allee effect (Fig. S4) was chosen because the decelerating curve passes through known breeding success rates at the current population size (0.99 fledglings/female, N = 150 birds), the population size in 1990s (1.50 fledglings/female, N < 1000 birds), and the value determined for the population to reach stability (>2.00 fledglings, N >

Table 2
Population models for the regent honeyeater grouped by three themes. 1. Models exploring the Blue Mountains population and the meta-population without intervention, 2. Models exploring the Blue Mountains population when nests are protected leading to higher reproductive success, and 3. Models with interventions including release of zoo-bred birds and nest protection. The 'Model Characteristics' column highlights key additions to the previous model.

Theme	Scenario	Model characteristics
1: Wild population (no intervention)	A. Blue Mountains (1990s)	Highest annual reproductive success
	B. Blue Mountains (contemporary)	Lower reproductive success
	C. Metapopulation	3 populations Low dispersal (Table S1) Narrow Allee effect (Fig. S3A)
	D. Metapopulation with drought	Mean drought interval = 5 years Reproductive success halved in drought years
2: Wild Blue Mountains population (nest protection)	A. Current conditions including drought, narrow Allee effect	Observed fledglings/female/year = 0.99, narrow Allee effect (Fig. S3A)
	B. Nest protection	Extra 0.5 fledglings/female/year
	C. Higher nest protection	Extra 1.0 fledglings/female/year
	D. Nest protection, broad Allee effect	Extra 0.5 fledglings/female/year, broad Allee effect (Fig. S3B)
	E. Higher nest protection, broad Allee effect	Extra 1.0 fledglings/female/year
	F. Higher nest protection for 20 years	Extra 1.0 fledglings/female/year (stop after year 20), broad Allee effect
3: Wild Blue Mountains population (supplementation with zoo-bred birds 3A–F, supplementation & nest protection 3G–J)	A. Supplementations at current success rate under narrow Allee effect	100 zoo-bred birds released every 2 years. Higher mortality for captive releases Lower breeding participation & breeding success for captive releases
	B. Biennial supplementation under broad Allee effect	Broad Allee effect
	C. Biennial supplementation (last release year 11)	Releases stopped after year 11
	D. Higher (annual) rate of supplementation (last captive release year 11)	100 zoo-bred birds released every year
	E. Annual supplementation, higher carrying capacity (last captive release year 11)	Carrying capacity of environment doubled to 800 birds
	F. Annual supplementation (100/yr), increased carrying capacity (last captive release year 21)	Longer time frame (40 years) with annual captive releases for 20 years
	G. Biennial supplementation, double carrying capacity + nest protection (last release year 11)	100 zoo-bred birds released every 2 years Nests protected (additional 0.5 fledglings per female)
	H. Biennial supplementation (100/2 yrs), increased carrying capacity, nest protection (stop supplementation after year 21)	Longer time frame (40 years) with captive releases for 20 years
	I. Biennial supplementation (100/2 yrs), increased carrying	Increased nest protection (additional 1.0 fledglings per female).

Table 2 (*continued*)

Theme	Scenario	Model characteristics
	capacity, increased nest protection (stop supplementation/nest protection after year 21)	Supplementation and nest protection for 20 years
	J. Biennial supplementation (100/2 yrs), increased carrying capacity, increased nest protection, carrying capacity = 3000 (stop supplementation/nest protection after year 21)	Further increase in carrying capacity to 3000 birds.

2000 birds).

We focused our theme 2 and 3 modelling on the Blue Mountains population because it is the largest remaining subpopulation (Crates et al., 2019b) and is now the focus of reintroduction efforts and other recovery actions. All models in themes two and three include the impact of drought described above. Scenario 2A models the trajectory of the Blue Mountains population under current conditions. Scenarios 2B and 2C increase nest success by 0.5 and 1.0 fledglings per female per year respectively under the assumption of a narrow Allee effect. Scenarios 2D and 2E increase nest success by 0.5 and 1.0 fledglings respectively under the assumption of a broader Allee effect (Table 2). Scenario 2F models the population trajectory over 40 years if nest success is increased by 1.0 nestlings per female per year over the first 20 years but reverts to the current level thereafter.

Scenario 3A assumes 100 zoo-bred birds are released every two years starting in year one of the 20-year period. Zoo-bred released birds were given separate demographic rates using individual state variables. Mortality for released birds in the year of their release was 54.04%. This value reflects field data showing that zoo-bred birds suffered 30% mortality over 20 weeks (Tripovich et al., 2021), representing an additional 12.37% over that period above the background annual rate of 41.67%. We assume that mortality for released birds reverts to the same rate as wild birds after 20 weeks. Participation in breeding for released females was set at 22.2% in their first year (Tripovich et al., 2021), but increased in the models to 55.1% (halfway between first year value and wild bird rate) in their second year, and was assumed equal with wild birds (88%) thereafter. Based on monitoring data, we limited zoo-bred females to one breeding attempt in their release year (BirdLife Australia, unpublished data) and assumed surviving females attempted two broods in each subsequent year. Scenario 3B incorporates the broader Allee effect (Fig. S4) with all other parameters the same as Scenario 3A. Scenario 3C examines the population trajectory when no further releases occur after year 11 in the 20-year period. Scenario 3D doubles the rate of zoo-bred releases to 100 birds every year, but stops after year 11. Scenario 3E examines the impact of the increased number and rate of releases when the carrying capacity is doubled. Scenario 3F examines similar actions over a 40-year time-frame whereby annual releases continue for 20 years. Scenario 3G reverts to releasing 100 birds every two years, but includes a positive management impact from protecting nests improving reproductive success from 0.99 to 1.5 fledglings per female per year. Scenario 3H examines similar actions on a 40-year time-frame whereby biennial releases continue for 20 years before ceasing. Scenario 3I also releases 100 birds biennially, but increases the positive impact of nest protection efforts such that each female fledges on average two juveniles per year. Finally, scenario 3J emulates 3I but further increases the carrying capacity of the Blue Mountains from 800 to 3000.

To gain feedback on parameters we used in the models (Tables 1–3 and S1), we conducted two consultation sessions, each with eight or more experts in various aspects of regent honeyeater conservation such as zoo breeding and monitoring of the reintroduced or wild populations

Table 3

Demographic parameters applied to zoo-bred regent honeyeaters upon release into the wild. Parameter estimates for further years in the wild are equal to those of contemporary wild birds.

Parameter	Value
Annual mortality	
- First year in wild	54.04%
- Further years in wild	41.67%
Breeding participation	
- First year in wild	22.2%
- Second year in wild	55.1%
- Further years in wild	88.0%
Nest survival	
- First year in wild	21.0%
- Further years in wild	31.7%

(Appendix A).

3. Results

The results from our regent honeyeater population viability analysis demonstrate severe population decline in most scenarios. Our models show that long term protection of nests from predators, major supplementation from zoo-bred birds, and increased habitat availability, are all essential for restoring population viability of this species. The simulated age structure for the Blue Mountains population is given in Fig. S2.

3.1. Theme 1: regent honeyeater population trajectory without intervention

The population in the Blue Mountains was already in decline in the 1990s (population growth rate $r = -0.061$, Scenario 1A) and this decline has accelerated in contemporary times ($r = -0.222$, Scenario 1B, Table 4). The models show that the rate of decline in the metapopulation including the Northern Tablelands and north-eastern Victorian populations is similarly severe (Scenarios 1C, 1D, Table 4, Fig. 2).

3.2. Theme 2: regent honeyeater population trajectory with intervention via nest protection

Under a narrow Allee effect, the Blue Mountains population continues to decline even if females produce 0.5 and 1.0 extra fledglings per year (Scenarios 2B, 2C, Table 4). When a broad Allee effect is incorporated, the Blue Mountains population shows negative growth when females produce 0.5 extra fledglings (Scenario 2D) but attains positive growth if they produce 1.0 extra fledglings. However, the population goes back into decline if nest protection is halted after 10 or 20 years (Scenarios 2E & 2F, Table 4, Fig. 3).

3.3. Theme 3: regent honeyeater population growth with release of zoo-bred birds

Our models demonstrate that the Blue Mountains population could become self-sustaining under a regime combining supplementation from zoo-bred birds and nest protection if habitat availability (carrying capacity) is also increased (Table 4, Fig. 4). Release of zoo-bred birds at the rate of 100 every two years appears to support the Blue Mountains population to the extent that population decline is much slower whilst the releases are maintained ($r = -0.017$, Scenario 3A), but does not allow the population to grow to a level where it is self-supporting if releases are stopped. This was true even when we allowed a broad Allee effect whereby individual breeding success continues to increase up to relatively large population sizes (Scenario 3B), if the frequency of releases was doubled so that 100 birds were released every year for 11 years (Scenario 3D), and the carrying capacity of the environment was doubled (Scenario 3E). Further, Scenario 3F showed that doubling the time period of releases so they occur every year for 21 years does not lead to a self-sustaining population. Scenarios 3G (20 years) and 3H (40 years) showed that the Blue Mountains population is closer to becoming self-sustaining with a combination of zoo-bred supplementation and protection of nests if nest protection is continued indefinitely. The population decreases again when supplementation stops under both scenarios. Scenario 3I shows that higher nest protection (additional 1.0 fledgling per female) over 21 years does not lead to a self-sustaining population if both nest protection and supplementation stop after 21 years. However, Scenario 3J shows that the population may become self-sustaining under these conditions if carrying capacity is increased
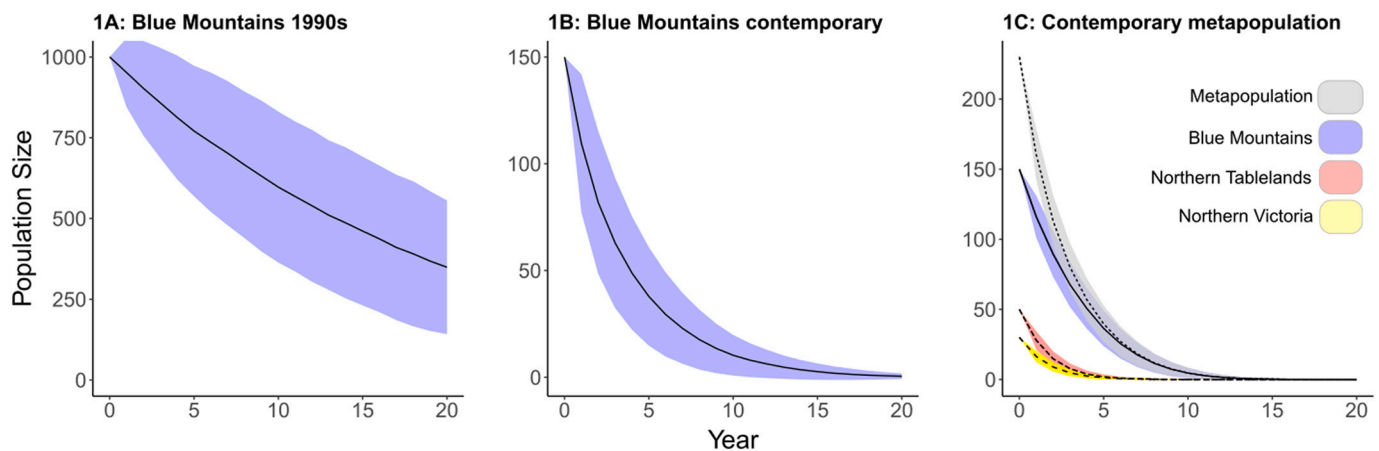
Table 4

Population models for the regent honeyeater. r, stochastic population growth; PE, Probability of Extinction after 20 or 40 years; N_s = starting population size, N_f = final population size.

Theme	Scenario	r	S.D.	PE	N_s	N_f
1. Without conservation intervention	1A. Blue Mountains (1990s)	−0.061	0.120	0	1000	349
	1B. Blue Mountains (contemporary)	−0.222	0.209	0.93	150	4
	1C. Metapopulation	−0.394	0.209	1.00	230	0
	1D. Metapopulation with drought	−0.419	0.218	1.00	230	0
2. Blue Mountains population with nest protection	2A. Narrow Allee effect, no nest protection	−0.360	0.225	1.00	150	0
	2B. Narrow Allee effect, +0.5 fledglings	−0.269	0.235	0.97	150	4
	2C. Narrow Allee effect, +1.0 fledglings	−0.138	0.228	0.45	150	36
	2D. Broad Allee effect, +0.5 fledglings	−0.172	0.216	0.42	150	15
	2E. Broad Allee effect, +1.0 fledglings	0.006	0.198	0.01	150	296
	2F. Broad Allee effect, +1.0 fledglings (stop after year 21)	−0.087	0.242	0.70	150	67
3. Blue Mountains population with captive releases	3A. Biennial supplementation (100/2 yrs), narrow Allee	−0.017	0.494	0	150	109
	3B. Biennial supplementation, broad Allee	−0.005	0.432	0	150	141
	3C. Biennial supplementation (stop after year 11)	−0.122	0.376	0.03	150	17
	3D. Annual supplementation (100/yr, stop after year 11)	−0.063	0.224	0	150	44
	3E. Annual supplementations, increased carrying capacity (stop after year 11)	−0.056	0.219	0	150	77
	3F. Annual supplementation, increased carrying capacity (stop after year 21)	−0.075	0.225	0.47	150	43
	3G. Biennial supplementation, increased carrying capacity, nest protection (stop supplementation after year 11)	0.014	0.286	0	150	277
	3H. Biennial supplementation, increased carrying capacity, nest protection (stop supplementation after year 21)	0.021	0.264	0.04	150	372
	3I. Biennial supplementation, increased carrying capacity, higher (+1.0 fledgling) nest protection (stop supplementation/nest protection after year 21)	0.004	0.279	0.11	150	91
	3J. Biennial supplementation, increased carrying capacity, higher nest protection, carrying capacity = 3000 (stop supplementation/nest protection after year 21)	0.149	0.241	0.01	150	2591

Fig. 2. Population trajectories (±S.D. at each time point shown as a ribbon) over three scenarios for the wild regent honeyeater population over 20 years without conservation intervention. Scenario 1A: Blue Mountains using historical breeding data; Scenario 1B: Blue Mountains using contemporary breeding data; Scenario 1C: Contemporary meta-population (top line) comprising the three sub-populations. Note variable scale of the y-axes. See Fig. S5 for population trajectory under scenario 1D.
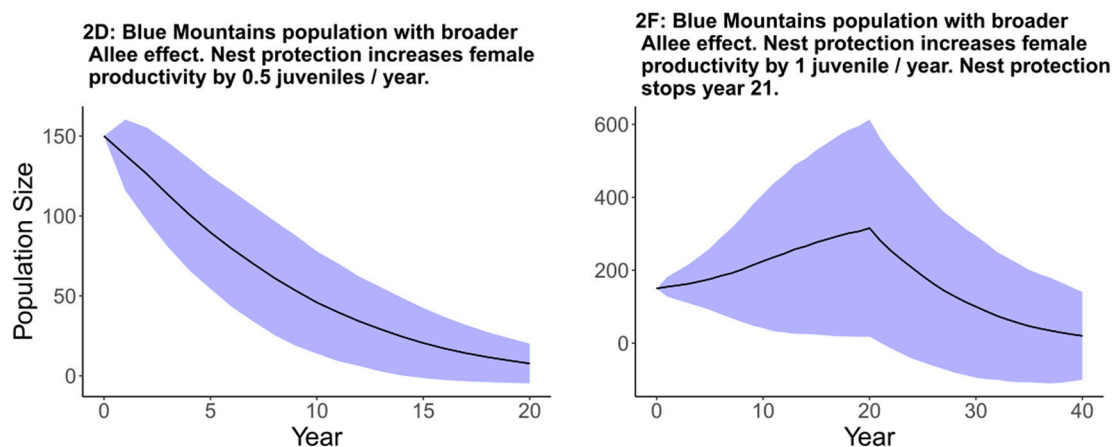

Fig. 3. Population trajectories (±S.D. at each time point shown as a ribbon) over two scenarios for the wild Blue Mountains regent honeyeater population over 20–40 years with two levels of nest protection. Scenario 2D: Blue Mountains with broad Allee effect and females producing 0.5 extra fledglings per year; Scenario 2F: Blue Mountains with broad Allee effect and females producing 1.0 extra fledglings per year, but nest protection is stopped after year 21. Note variable scale of x and y-axes. See Fig. S5 for population trajectory under scenario 2E.

substantially so that the population can grow to a larger size whilst being supplemented by zoo-bred birds and nests are protected.

Sensitivity analyses showed that uncertainty in adult and juvenile mortality accounted for the highest proportion of variance in two baseline models, one showing steep population decline and the other with stable population size. Uncertainty in reproductive rates was also important but accounted for a smaller proportion of the variance when the population was in decline than when the population was stable (Table S3). Correlations among variables are shown in Table S4.

4. Discussion

Our population viability analysis emphasises the difficulties of providing effective conservation action for threatened data-deficient nomadic species, and the value of range-wide population monitoring programs for gaining crucial data on breeding locations and success (Crates et al., 2019b; Stojanovic et al., 2021). Such data allowed analyses of the dynamics of past and present regent honeyeater populations, and present a bleak picture of the species' current population trajectories and the limited efficacy of conservation measures at their current intensity to halt population decline. However, our models demonstrate that the largest of the remaining populations could overcome likely

Allee effects and become self-sustaining under a management regime including protection of nests from predators, habitat restoration and supplementation from zoo-bred birds. Here we evaluate the efficacy of our models to forecast the regent honeyeater population trajectory, including the validity of key assumptions, and the conservation actions required to prevent the species' extinction in the wild.

Historical data from the Blue Mountains support evidence that the population was already suffering rapid decline in the 1990s (Franklin et al., 1989, Table 4, Fig. 2a). Although the exact size of the Blue Mountains regent honeyeater population was unknown in the 1990s, the rate of decline from 1000 birds to fewer than 500 over 20 years is commensurate with population estimates from the 2010s (Garnett et al., 2011). The breeding rate in the 1990s (1.51 juveniles per female) was considerably higher than it is now (0.99) and in that case, the observed population decline fits well with our estimates. The worsening trajectory in the contemporary population (Scenarios 1B, 1C, and 1D, Table 4) is cause for major concern and justifies strong conservation interventions. However, available data on the fitness attributes of released birds (higher mortality, lower breeding participation and lower nest success than wild birds) indicate that the current rate of their release can only buffer the population without enabling it to become self-sustaining.

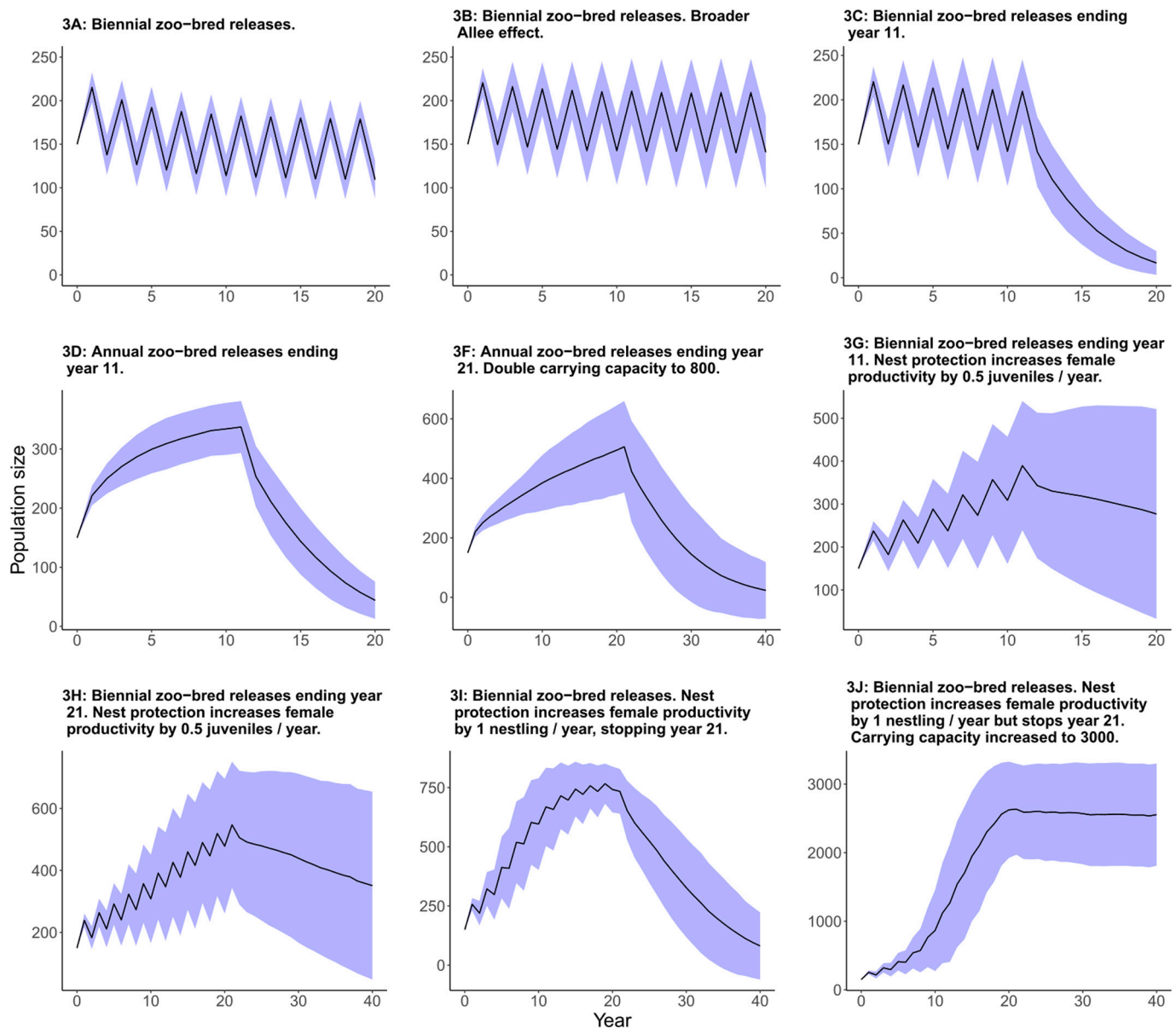The next five years will be critical for implementing every possible

Fig. 4. Population trajectories (±S.D. at each time point shown as a ribbon) incorporating impact of zoo-bred regent honeyeaters released into the wild Blue Mountains population. Scenario 3A: 100 birds released every 2 years into the Blue Mountains population, narrow Allee effect. Scenario 3B: 100 birds released every 2 years, broad Allee effect; Scenario 3C: 100 birds released every 2 years until year 11, broad Allee effect; Scenario 3D: 100 birds released *every* year until year 11, broad Allee effect; Scenario 3F: 100 birds released *every* year until year 21, time-scale = 40 years, broad Allee effect, carrying capacity increased; Scenario 3G: 100 birds released every 2 years until year 11, broad Allee effect, carrying capacity increased, nests protected (reproductive success increased by 0.5 fledglings per year per female); Scenario 3H: 100 birds released every 2 years until year 21, time-scale = 40 years, broad Allee effect, carrying capacity increased, nests protected (reproductive success increased by 0.5 fledglings per year per female). Scenario 3I:100 birds released every 2 years, time-scale = 40 years, broad Allee effect, carrying capacity increased, nests protected (reproductive success increased by 1.0 fledglings per year per female) but nest protection and supplementation stop after year 21. Scenario 3J: 100 birds released every 2 years until year 21, time-scale = 40 years, broad Allee effect, carrying capacity increased, nests protected (reproductive success increased by 1.0 fledglings per year per female) but nest protection and supplementation stop year 21. Carrying capacity increased to 3000. Note variable scale of both figure axes across scenarios. See Fig. S4 for population trajectory under scenario 3E.

conservation action and escalating the intensity of conservation actions already being implemented to save the wild regent honeyeater population from extinction. Our metapopulation models predict breeding subpopulations in north-eastern Victoria and the NSW Northern Tablelands are likely to become extinct by the end of this period, if enhanced conservation action of these populations is not undertaken. There is limited evidence that a decade of reintroductions has improved the outlook for the north-eastern Victoria population, whilst contemporary breeding success in the NSW Northern Tablelands is very low. Recruiting wild birds to the zoo population may be best achieved by targeting the

small number of birds persisting in these areas. Recruiting from north-eastern Victoria and the Northern Tablelands will minimise the impact of harvesting on the wild population growth rate centred on the largest of the three remaining subpopulations in the Blue Mountains. Given low estimated dispersal rates between subpopulations (Table S1), our models suggest remaining birds occupying north-eastern Victoria and the Northern Tablelands are otherwise unlikely to contribute to population recovery in the wild. If as predicted, regent honeyeater population decline is underpinned by an Allee effect, conservation actions should do everything possible to maximise the density of the remaining wild

population in the Blue Mountains (Crates et al., 2017). The Blue Mountains population itself functions as a smaller-scale metapopulation, with colour-marked birds known to move tens or hundreds of kilometres between distinct breeding areas within the Blue Mountains (Commonwealth of Australia, 2016). Therefore, the risk of creating an 'all eggs in one basket' scenario (Webb et al., 2019) by focussing recovery efforts on the Blue Mountains population is considered low, relative to the risk of not maximising population density to address the Allee effect.

Our models emphasise the important role reintroducing zoo-bred birds could play in stabilising the Blue Mountains population over coming decades. However, in line with modelling 'best case' scenarios, our parameter estimates for post-release survival, breeding participation and nest success for zoo-bred birds in the years after release were somewhat higher than those derived from field studies (Taylor et al., 2018; Tripovich et al., 2021). This emphasises the importance of increasing the phenotypic quality of zoo-bred birds, such that their post-release fitness is closer to their wild counterparts. Current husbandry strategies include promoting 'silver spoon effects' by reducing the annual number of broods each zoo-based female produces (Spagopoulou et al., 2020; Tripovich et al., 2021), pre-exposing zoo-bred birds to interspecific competition they will face in the wild by housing them in mixed-species aviaries (Tripovich et al., 2021), and song tutoring (Crates et al., 2021a; Tripovich et al., 2021). Importantly, our models do not account for potential inbreeding. Measures to maintain the long-term genetic integrity of zoo-bred stock (Farquharson et al., 2021), should consider that opportunities to recruit wild birds to the zoo population will diminish. Calculations using *PMx* software (Ballou et al., 2020 show that genetic diversity (GD), currently estimated at 95.4% ($n = 151$ birds) can be maintained at $\geq90\%$ for a further 17 years without further recruitment of wild birds into the captive population, suggesting that further recruitment of wild founders will be required if supplementation of zoo-bred birds is continued for 21 years (M. Van Sluys, unpublished).

Modifying release protocols could also help increase the fitness of zoo-bred birds (Armstrong and Seddon, 2009). Recent evidence from orange-bellied parrots *Neophema chrysogaster* suggests that releasing juvenile birds instead of birds that have spent one to two years in captivity could be an efficient way of increasing the fitness of zoo-bred birds (Pritchard et al., 2021). Many culturally-acquired behaviours such as songs, anti-predator behaviours and dispersal routes are learned in early life (Brakes et al., 2019; Teitelbaum et al., 2018). Releasing zoo-bred juveniles into post-breeding wild regent honeyeater flocks could help released birds acquire these important behaviours.

An additional research priority should be to assess the efficacy of nest protection as a means of increasing recruitment to the wild population. Regent honeyeater breeding success has declined over recent decades and predation of nests by a range of avian and mammalian predator species is the predominant cause of nest predation (Crates et al., 2019b; Taylor et al., 2018). Range-wide monitoring through the NRHMP means we now have a much-improved picture of the location of contemporary breeding activity in the wild population. Managing predation risk from a despotic competitor- the noisy miner- is achievable in some known regent honeyeater breeding areas (Crates et al., 2018, 2020). Removing noisy miners from key breeding areas also helps to increase the carrying capacity of the regent honeyeater population by allowing them access to breeding habitat from which they would otherwise be excluded by noisy miners (Maron et al., 2013).

Our models predict that increasing carrying capacity of the wild population through actions such as effective noisy miner suppression could nearly halve the rate of population decline over the next 20 years (Model 3E compared to Model 3D). Considering the very small size of the remaining wild regent honeyeater population, displacement by larger competitor species to access breeding habitat is a substantial threatening process (Ford et al., 1993). Noisy miner management is ethically contentious, however (Beggs et al., 2019), and will only ever benefit a proportion of breeding regent honeyeaters in any given year.

Preserving regent honeyeater breeding habitat in areas where noisy miner impacts are currently minimal, such as the Burragorang Valley, is therefore crucial.

To stabilise the regent honeyeater population trajectory, breeding rates of all birds in the wild need to approximately double, with the breeding rate continuing to increase as zoo-based releases swell the population and thereby reduce the Allee effect on breeding success (Scenario 3J). To achieve such increases in breeding output will require protection of nests not just against noisy miners, but an entire suite of mammalian and avian predators to avoid compensatory nest predation (Beggs et al., 2019; Gautschi et al., 2021). Our calculations suggest this is a major task, though possibly feasible, as roughly 30% of failed nests would need to be protected (Table S2).

Short term intervention measures to save regent honeyeaters from extinction will be futile in the longer term, unless the declining population paradigm of severe habitat loss is addressed (Caughley, 1994; Bradshaw, 2012). Given their specialist habitat requirements, an associated decline in regent honeyeater breeding output is most likely underpinned by a drastic decline in the amount and accessibility of functional breeding habitat limiting breeding opportunities. Importantly, model 3J emphasises these higher breeding rates will only lead to a self-sustaining population when carrying capacity is greatly increased and the population can be increased to over 2000 birds (Fig. 4). Current woodland restoration rates in fertile riparian zones that support highest woodland bird diversity (Watson, 2011) are far below what is required to increase the carrying capacity for habitat specialist like the regent honeyeater. Threats to core breeding habitat from proposed infrastructure projects (Department of Primary Industries, 2014), megafires (Wintle et al., 2020; Crates et al., 2021b) and drought-induced eucalypt dieback, mean it is likely that the regent honeyeater is suffering a net loss of breeding habitat at present.

When working with rare nomadic species with life-history traits that challenge the traditional population monitoring paradigm, modelling approaches will always have limitations (Coulson et al., 2001). For regent honeyeaters, sensitivity analyses revealed that uncertainty around juvenile and adult mortality rates may impact population trajectories. We note that the mortality rates we use present a 'best case' scenario as they were derived from modelled values across the honeyeater family. Mortality rates may in fact be higher in current circumstances and also subject to Allee effects. Within the broad ranges tested for each parameter, there was also considerable but somewhat lower impact of varying reproductive success, but the priorities for management need to be based on which demographic rates can be most effectively addressed through management actions (Manlik et al., 2018). Initial population size, carrying capacity, and demographic stochasticity contributed much less to variation in population growth than did the mortality and breeding rates, in line with the view that the deterministic causes of decline need to be addressed before worrying about the stochastic processes that also beset populations that have been reduced to very low numbers.

There is also uncertainty around the impacts of drought events on breeding output as the extent to which regent honeyeaters breed in alternative areas when blossom is in short supply is poorly understood. Whilst we may have overestimated the impact of droughts by halving breeding output and increasing mortality by 5% during drought years, the millennium drought in south-eastern Australia is thought to have been a major driver of regent honeyeater population decline during that period and high breeding output has never been observed during drought years (Crates et al., 2021c). Nonetheless, accounting for increased frequency of drought events in model 1C had a negligible impact on the population growth rate relative to the already severe decline predicted in model 1B where increasing drought frequency was not accounted for. We also assumed that survival of zoo-bred birds was equal to wild birds in the second year after release, and that breeding participation was equal two years after release. Current data to support these assumptions are lacking. Since the performance of reintroduced

animals is highly variable relative to wild conspecifics (Berger-Tal et al., 2020), assessing the long-term performance of zoo-bred regent honeyeaters in the wild is an important research priority for optimising future recovery strategies.

We assume that regent honeyeaters are subject to Allee effects and although very likely (Crates et al., 2017), this has not been proven. Uncertainty also exists around the nature of Allee effects (i.e. the shape of the Allee curve) in the wild regent honeyeater population (Crates et al., 2017) although the function we used was constructed to fit with available data (Fig. S4B). We assumed Allee effects concerning breeding success would increase population growth rates up to a population size of 2000. Whilst this represents an 'optimistically achievable' population size given the 20–40 year timescale of our models, it remains well below the species' historic population size. Since population size does not necessarily correlate with population density (especially in sparsely-distributed, nomadic species), our models may underestimate both the strength of a likely Allee effect and the population sizes at which an Allee effect impacts regent honeyeater population growth rates (Berec et al., 2007). It is also likely that Allee effects act on both juvenile and adult mortality (Berec et al., 2007) but we have no reliable field data to suggest the nature of the relationship. We restricted our analysis to breeding success because of the availability of good field data over time for that parameter, but note that higher population density, if achieved via higher reproduction and captive releases, may help alleviate Allee effects on other parameters.

Our study reinforces the need for better monitoring of threatened species and particularly of nomadic species more broadly (Runge et al., 2014; Scheele et al., 2019). Where good quality monitoring data are unavailable, assessments of extinction risk in threatened species invariably rely on expert elicitation (Geyle et al., 2018). Whilst expert elicitation processes have clear value in conservation prioritisation, they could be prone to systematic bias (Roy et al., 2020), which risks underestimation of extinction threat and delayed implementation of potentially crucial recovery actions for data-sparse species. Asking experts to estimate key population parameters and running PVAs on these estimates could be a useful way of overcoming some potential biases in the expert elicitation process. Even with uncertainty around some parameters we were able to determine that release of zoo-bred birds is unlikely in itself to save regent honeyeaters from extinction. Instead, our approach using PVA has shown that substantial increases in the intensity of interventions to protect the nests of wild birds are necessary alongside the release of zoo-bred regent honeyeaters if the population is to reach the critical mass necessary so that the population becomes self-sustaining. Crucially, the models show the population can only become self-sustaining if the carrying capacity is increased via habitat protection and restoration. Other interventions will have limited efficacy unless this occurs.

CRediT authorship contribution statement

Robert Heinsohn: Conceptualization, Methodology, Writing. Robert Lacy: Methodology, Writing. Andrew Elphinstone: Methodology. Dean Ingwersen: Methodology. Ben Pitcher: Methodology. Mick Roderick: Methodology. Emily Schmelitschec: Methodology. Monique Van Sluys: Methodology. Dejan Stojanovic: Methodology. Joy Tripovich: Methodology. Ross Crates: Conceptualization, Methodology, Writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109430.

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