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ORIGINAL RESEARCH

Conservation management in the context of unidentified and unmitigated threatening processes

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Abstract

The decision to intervene in endangered species management is often complicated. Migratory species exemplify this difficulty because they experience diverse threats at different times and places that can act cumulatively and synergistically on their populations. We use population viability analysis (PVA) to compare potential conservation interventions on the critically endangered, migratory Orange-bellied Parrot *Neophema chrysogaster*. This species suffers high juvenile mortality, but it is not clear why this is so. Given uncertainty about the best recovery strategy, we compare PVA scenarios that simulate various ways of utilizing captive-bred parrots to support the wild population in the context of unresolved threatening processes. Increasing the number of juveniles entering the population each year had the greatest benefit for population growth rate and size. Directly lowering juvenile mortality rates is difficult given uncertainty about the drivers of mortality in the wild. In lieu of this, releasing 100 juveniles from captivity to the wild population each autumn (either as a stand-alone action, or in combination with other interventions) was the most feasible and straightforward intervention of the options we tested. However, our PVAs also show that unless substantial and sustainable reductions can be made to juvenile mortality rates, Orange-bellied Parrots will remain dependent on intensive conservation management. This study highlights the utility of PVAs for answering practical questions about how to implement species conservation. PVAs provide a way to incorporate the best available information in a replicable modelling framework, and to identify impacts of parameter uncertainty on demographic trends.

Keywords Orange-bellied parrot *Neophema chrysogaster* · Population viability analysis · Conservation · Threatened species · Extinction risk · VORTEX

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Introduction

Conservation management of threatened species can be risky when populations become very small (Gilroy et al. 2012). Decisions about how to intervene must often be made quickly, and often in context of limited or imperfect information (Ng et al. 2014; Norris 2004). Even though decisions may be intended to benefit a species, there is always a chance that interventions aimed at helping may have at best neutral, or at worst perverse outcomes for the target species (Chauvenet et al. 2011) or the ecosystem (Scoleri et al. 2020). Furthermore, some interventions may be most effective in the context of other actions (Sodhi et al. 2011), meaning that practitioners could risk discarding potentially useful approaches simply because they were implemented in a way that diminishes their effectiveness due to knowledge gaps (Ferrière et al. 2021). But the deceptively simple question of when and how to intervene may not have a straightforward answer, especially when threats to the species are multiple or difficult to manage (Heinsohn et al. 2022). This is exemplified by migratory species, where multiple discrete threats at different times and places can act cumulatively and synergistically on a population (Runge et al. 2014). For migrants, correcting any one threat may help the population locally, but this benefit may be undone when the population moves to another area (Runge et al. 2015). These challenges for rare, mobile animals can hinder planning and implementation of recovery projects that aim to reverse population decline, especially for species that move through different jurisdictions (Runge et al. 2015).

Population viability analysis (PVA) is an approach that managers might use to help evaluate the impact of different intervention approaches. PVA enables practitioners to simulate demographic responses of wildlife populations under a range of user defined scenarios (Beissinger and McCullough, 2002, Morris and Doak, 2002) and to model growth rates, size, and extinction risk of populations. PVAs are sensitive to the quality of input data; however, they work well for species where reasonable data on life history and threats are available (Chaudhary and Oli 2020). Where uncertainty exists about particular demographic parameters and threats, the impacts of this uncertainty can be explicitly evaluated within the PVA framework, which offers important insights about how much risk is associated with specific management actions. The flexibility (and repeatability) of PVA thus provides a tool that managers might use to disentangle the individual and interactive impacts of different threats and management options for a given species (Keighley et al. 2021; Heinsohn et al. 2015).

Here we evaluate impacts of different conservation interventions on Orange-bellied Parrots *Neophema chrysogaster*, which are critically endangered and experience diverse threats at different times and places (Stojanovic et al. 2018). During their summer breeding season in south-western Tasmania, Australia, Orange-bellied Parrots suffer from adult sex ratio bias (Troy and Lawrence 2021), competition for limited nesting resources (Stojanovic et al. 2019b), and shortages of natural food (Stojanovic et al. 2020b). However the most damaging problem faced by the species is extremely low juvenile survival during migration to/from south-eastern mainland Australia and over winter (Stojanovic et al. 2020c). The reasons for this are not clear and several untested theories have been proposed. For example, Orange-bellied Parrots (especially naïve juveniles born into the small contemporary population) could experience multiple component Allee effects during autumn/winter that affect dispersal, habitat selection, foraging and anti-predator responses if they are unable to locate conspecifics and learn these critical skills (Crates et al. 2017). Furthermore, loss or degradation of wintering habitats (Menkhorst et al. 2021) may lower the probability of juveniles finding suitable places to overwinter. There is little direct evidence for other anthropogenic threats (e.g. collisions with artificial structures) but these are perceived as risks (Department of Environment Land Water and Planning, 2016). The mechanism by which threats act upon juvenile mortality remain speculative. Unfortunately these knowledge gaps are challenging to address due to the difficulty of gathering statistically robust data on this species when their small population disperses over the large migration/wintering area. These challenges extend to evaluating the effectiveness of recovery actions (Stojanovic et al. 2018, 2020c, d), leaving managers to decide what actions to implement in the context of prevailing uncertainty (Pritchard et al. 2022).

Ideally, conservation action for any species should first identify and mitigate threats in the wild, so that reintroductions are not undertaken prematurely (Snyder et al. 1996). In the case of the Orange-bellied Parrot, an intensive recovery effort for the species has already been underway for decades despite gaps in knowledge (Department of Environment Land Water and Planning, 2016). Although these recovery efforts have occurred in multiple Australian jurisdictions, most intensive conservation actions occur in Tasmania, but these efforts alone may not be enough to recover the species (Stojanovic et al. 2020c; Drechsler et al. 1998; Drechsler 1998). Nevertheless, a central motivation for contemporary interventions is to provide opportunities to identify/mitigate threats by increasing the wild population size enough to delay (and ideally prevent) extinction. Historically, recovery efforts for Orange-bellied Parrots reflected opportunistic and reactionary responses to the emergence of problems (Martin et al. 2012); this is common among conservation programs (Phillis et al. 2013). Fears that undiagnosed threats in the wild would drive Orange-bellied Parrots to extinction resulted in a rush to establish an insurance population (Martin et al. 2012). This had long term implications not just for the species itself (Morrison et al. 2020b) but also for decision making around the types of management interventions applied (Stojanovic et al. 2018). However, simply releasing captive-bred animals to the wild does does not usually lead to effective conservation outcomes unless the key threatening processed have been adequately mitigated (Crates et al. 2022).

As the recent emergencies for Orange-bellied Parrots have subsided (Stojanovic et al. 2018), there have emerged opportunities to explore more proactive approaches to the species' recovery. To this end an expert elicitation procedure was undertaken to identify potential new approaches (Pritchard et al. 2022). This process reflected a shift toward an adaptive response to the species' long-term population trajectory, and resulted in a clearly defined set of individual (and combined) conservation actions whose benefits were assessed based on expert knowledge. Despite the wealth of expertise available within the species' Recovery Team (a group of experts and stakeholders responsible for guiding and implementing the conservation actions for the species), there remains considerable uncertainty about the potential impacts of these actions on the population dynamics of Orange-bellied Parrots (Pritchard et al. 2022). Here, we use PVA to investigate the demographic impacts of the preferred conservation actions proposed by the Orange-bellied Parrot Recovery Team. We test the benefit of different intervention strategies with the aim of informing an adaptive approach to future management, and discuss our results in the context of conservation planning and evaluation of interventions for other migratory species with diverse threats that cannot be directly mitigated.

Materials and methods

Study species life history

Orange-bellied Parrots are critically endangered (Menkhorst et al. 2021) and, unusually for a parrot, are a natal site philopatric north-south migrant. Orange-bellied Parrots breed in southwestern Tasmania, and winter in coastal habitats of southeastern Australia (Higgins, 1999). During their summer breeding season, Orange-bellied Parrots prefer recently burned areas of Buttongrass *Gymnoschoenus sphaerocephalus* moorland near coastal areas, where they eat seeds of regenerating herbs and shrubs (Stojanovic et al. 2020b). The species is dependent on tree cavities for nesting, but the population now breeds only in nest boxes (Stojanovic et al. 2019b). Orange-bellied Parrots are considered socially monogamous; although other similar parrots exhibit a high degree of extra pair paternity at small population sizes (Heinsohn et al. 2019), it is not known whether this is so for Orange-bellied Parrots. The modern population suffers from severely diminished genetic diversity. For example, in a study of Toll-like receptors (which play a crucial role in immune function) three loci were monomorphic, and there was low diversity at six genes (Morrison et al. 2020a). The loss of the species' endemic pathogens (disease fade-out) appears to have increased their vulnerability to disease (Raidal and Peters 2017). There have been multiple outbreaks of beak and feather disease virus (alongside other diseases) in both the captive and wild populations over the last twenty years (Das et al. 2020; Peters et al. 2014; Stojanovic et al. 2018; Sarker et al. 2014; Morrison et al. 2020a). Orange-bellied Parrot siblings have non-independent survival rates, but why this is the case remains uncertain (Stojanovic et al. 2022). We have previously posited that carry over effects of body condition during early life might affect survival on the first migration (Stojanovic et al. 2020a); however, to date this remains untested. Other key life history information is provided in Table 1, including citations to justify the selection of each value.

Conservation challenges and management history

Over the last two decades Orange-bellied Parrots have experienced a population collapse driven primarily by low juvenile survival rates (Stojanovic et al. 2020c). Although the captive insurance population was established in 1986, a collection of founders in 2010/11 for captive breeding may have caused inadvertent harm by further depressing the wild population size (Morrison et al. 2020b). By 2016 the wild population was nearly extinct; only three wild females returned to the breeding ground (Stojanovic et al. 2018), and only one mother produced a surviving lineage (Stojanovic et al. 2022). Since 2013 a range of more intensive conservation interventions than had been previously attempted were implemented to try and reverse their decline. These include: annual soft releases of captive-bred parrots from captivity to correct adult sex ratio biases and maximize breeding output (Troy and Lawrence 2021); provision of veterinary support, supplementary food and nest boxes (Troy and Gales 2016); manipulation of the reproductive success of wild nests (Stojanovic et al. 2018); ecological burning to promote regeneration of natural food sources (Stojanovic et al. 2020b), and; management of nest competitors (Stojanovic et al. 2019b; Troy and Lawrence 2021). The species has also been intensively monitored to quantify individual survival rates (Stojanovic et al. 2020c) and breeding success (Stojanovic et al. 2020a, d), and these data provide important baseline information for our PVAs (Table 1). Disease outbreaks have occurred as a consequence of spillover events both from interactions between the wild Orange-bellied Parrot population with other wild parrots (Peters et al. 2014), and inadvertently through other management actions (Stojanovic et al. 2018). Orange-bellied Parrots have now been bred over several generations in captivity and although over-all body size of captive-bred parrots has not changed (Stojanovic et al. 2019a) their wing shape is different to that of the historical wild population (Stojanovic et al. 2021), which negatively affects their survival after release to the wild (Stojanovic 2022). Recent genetic management has focused on mean kinship minimization between captive and wild genotypes (Morrison et al. 2020b). These efforts have resulted in extensive mixing between these groups and thus, we do not differentiate between captive and wild subpopulations. Historically, released captive-bred birds fared poorly relative to wild conspecifics (Stojanovic et al. 2018) however extensive interbreeding has largely negated previous fitness differences between the groups (Stojanovic et al. 2022). The contemporary population of >400 captive individuals is limited by holding capacity and its flow-on effects for manageable breeding output (Morrison et al. 2020b). Given that managers cannot directly intervene to mitigate most threats faced by wild Orange-bellied Parrots outside the breeding area, reintroductions and associated activities have, by default, become the primary intervention tools for supporting the wild population.

Population viability models

To implement PVAs we used the program VORTEX (Lacy 2000b; Lacy and Pollak 2020) – a widely used software platform that incorporates flexibility over a range of demographic parameters that can be modified to reflect the quirks of a given study species. For example, VORTEX allows users to specify immigration/emigration between discrete populations, supplementation, or harvest schedules, and to account for stochastic events. Based on the available studies of Orange-bellied Parrots outlined above we compiled the demographic variables needed for conducting VORTEX PVAs in Table 1. Most of the parameters we used are the same or similar to those specified in our earlier PVA because that study collated all contemporary life history parameters and used a sensitivity test to explore the impacts of uncertainty around some parameters (Stojanovic et al. 2022). We excluded catastrophes from our simulations because our previous estimates of mortality (Stojanovic et al. 2020c) include several disease outbreaks (Das et al. 2020), which are the main cause of catastrophes in this species. Likewise, we did not include additional inbreeding depression in our models because any realized lethal effects of inbreeding are already accounted for in our estimates of observed mortality rates of wild parrots. The parameters identified in Table 1 were held constant regardless of the scenario being tested.

The Orange-bellied Parrot Recovery Team has identified four main types of intervention that might be implemented using individuals from the captive population (Pritchard et al. 2022):

1. Spring release – involves adult parrots bred in captivity being released to the wild in spring before the breeding season. Spring releases are intended to correct sex ratios in the breeding population and maximize the number of breeding pairs. We incorporated

this action in our simulations using the supplementation option, adding 50 adults of each sex before the ‘breed’ and ‘mortality’ steps.

2. Autumn release – involves juvenile captive-bred parrots being released to the wild in the autumn at the end of the breeding season but before migration (referred to as ‘fledgling release’ by Pritchard et al., 2022). Autumn releases are intended to maximize the size of parrot flocks undertaking migration. We incorporated this action into our simulations using the supplementation option, adding 50 juveniles of each sex after the ‘breed’ but before the ‘mortality’ steps.
3. Fostering – involves eggs or nestlings of captive parrots being fostered into the nests of wild parrots that suffer infertility or have small broods (referred to as ‘nest supplementation’ by Pritchard et al., 2022). Fostering is intended to maximize fecundity of wild nests. We incorporated this action into our simulations by increasing the mean (but not maximum) number of offspring reared per brood by one. The limitation on the number of females able to breed in the wild (Table 1) means that no more than 100 eggs/nestlings can be ‘released’ from captivity per year.
4. Juvenile mortality reduction – Although the drivers of juvenile mortality are complex, one approach currently being evaluated involves parrots bred in captivity (mixed ages depending on the availability of captive birds) being released on the Australian mainland during the winter (referred to as ‘mainland release’ by Pritchard et al., 2022). Winter releases are intended to attract wild parrots to areas of high quality wintering habitat to improve their survival. It has not yet been possible to demonstrate that interventions in the migration/wintering habitat of Orange-bellied Parrots can lower mortality rates of juveniles. Here we instead focus simply on the intended outcome of these types of interventions (i.e. improved juvenile mortality rates) in our simulations. We reduce juvenile mortality by 10% to simulate this desired outcome.

The Recovery Team expected that interventions involving n = 100 captive-born parrots per release would be more beneficial (Pritchard et al. 2022), so we used 50 individuals of each sex in all scenarios involving autumn or spring releases. The Recovery Team expected that combining intervention strategies would be more beneficial (because of uncertainty about the efficacy of individual approaches), with combinations involving Autumn and Winter releases considered to be the most beneficial. We ran all scenarios over 50 years so that long term effects of interventions (and their cessation) could be modelled. All interventions were set to occur annually for 20 years – after that the model settings would revert to those of the ‘do nothing’ model for the remaining 30 years, to clarify the effects of intervention when underlying threats remain unmitigated (Table 2). Based on the interventions available to the Recovery Team, we identified two scenario types: (i) basic scenarios – these used rates of juvenile survival recorded in the wild population, including either no intervention, or just one intervention at a time, and (ii) combination scenarios – these were combinations of the better performing basic scenarios. The differences between individual models from each scenario are outlined in detail in Table 2. Although Pritchard et al. (2022) outline the preferred combinations of interventions identified by the Recovery Team, here we used the basic scenarios to guide which combination scenarios to test. We preferred basic scenarios that either had a higher population growth rates and/or larger population sizes. We categorized the achievability of scenarios in Table 2 as: ‘high’ – activities that are known to be deliverable based on existing conservation actions and resourcing; and ‘low’ – activities that

Table 1 Demographic parameters common to all population viability analyses of the wild population of Orange-bellied Parrots

Main Components	Demographic Parameter	Values used	Justification
Inbreeding Depression	Lethal equivalents	0	Excluded because observed mortality rates in the wild population (Stojanovic et al. 2020c) already include potential lethal inbreeding effects.
Carrying capacity	Carrying capacity	1000±0 SD	Optimistic assumption to remove carrying capacity limits.
Reproductive System	Mating system	Monogamy	Social monogamy within a breeding season (Higgins 1999).
	Age range of first offspring and maximum age of reproduction – both sexes	First offspring = 1 year Maximum age = 11 years	Breeds at 1 year old after completing a migration (Higgins, 1999) and optimistic assumption that all birds that survive migration attempt to breed.
	Maximum lifespan	11	Longest-lived wild individual (Stojanovic et al. 2020c).
	Maximum number of broods per year	1	Short breeding season and only one recorded case of double-brooding in the wild (Stojanovic et al. 2018).
	Maximum number of progeny per year	6	Historical (Higgins, 1999) and contemporary sources (Stojanovic et al. 2020a).
	Sex ratio at birth (% males)	50%	Unpublished data from the contemporary population.
Reproductive Rates	Percentage adult females breeding	Formula: MIN(1:100/F)*100. Included 10% SD due to environmental variation	Formula limiting the number of breeding opportunities by the provisioning of 100 nest boxes (Stojanovic et al. 2018).
	Distribution of broods per year	100% have 1 brood	Evidence from the field (Troy and Lawrence 2021). Only one record of double brooding in the wild (Stojanovic et al. 2018).
	Number of offspring per female per brood	Mean of 3.5±1 SD. Scenarios that involved Fostering as an intervention had a mean brood size of 4.5 (Table 2)	Recent and historical data (Stojanovic et al. 2020a, Higgins, 1999). Fostering is possible (Stojanovic et al. 2018) but most broods can only be increased by the addition of one nestling (Stojanovic et al. 2020d).
Mortality Rates	Adult mortality rate	42% ± 2 SD (baseline for all models)	Based on survival estimates (Stojanovic et al. 2020c).
		49% ± 2 SD (only used for the 'Default (Bird et al. 2020)' scenario	Modelled estimate (Bird et al. 2020).
	Baseline juvenile mortality rates	49% ± 10 SD – (used only for the default scenario)	Based on survival estimates (Stojanovic et al. 2020c).
		80% ± 10 SD – (used as the baseline for all scenarios except the two default scenarios)	

Table 1 (continued)

Main Components	Demographic Parameter	Values used	Justification
Mate monopolization	Proportion of males in the breeding population	100%	Management efforts to rectify adult sex ratio biases (Troy and Lawrence 2021).
Initial population size	Initial population size	200	Historical population sizes (Stojanovic et al. 2020c).
	Stable age distribution, based on 100 individuals per sex		Based on automated calculations within VORTEX and set manually for each scenario.

include a 10% reduction in juvenile mortality rates were scored as low achievability because approaches to directly alter this parameter in the real world remain uncertain.

We present the stochastic growth rates and population sizes for each scenario at the 20th and 50th year (i.e. at the end of the periods of conservation intervention and their subsequent withdrawal). Our PVA scenarios ran for 10,000 iterations. This large sample size inherently pushes standard errors and p values toward zero – to account for this when comparing scenarios we used strictly standardised mean differences (SSMD) (Zhang 2007), implemented in vortexR v 1.1.9 (Pacioni and Mayer 2017) using R (R Development Core Team, 2021). We undertook pairwise comparisons of population size (over both extant and extinct populations in each scenario) at the 20th year of simulations (the last year conservation interventions were implemented) using the function *SSMD_matrix*. All figures were produced using the package ggplot2 (Wickham 2016). We focused on population size in this analysis for two reasons. Firstly, population size in the wild is a key metric used to measure success of conservation interventions for Orange-bellied Parrots. Secondly, we assumed that (in line with current practices), the mean kinship minimisation strategy used to manage the captive population of Orange-bellied Parrots (Morrison et al. 2020b) would continue to benefit the wild population, and thus the genetic impacts of the interventions could be ignored for our more general questions in this study.

Results

The default scenarios (which included the optimistic modelled and historical rates of juvenile mortality) both had overall positive population growth rates and resulted in the largest population size at 50 years of any scenario (Fig. 1). This was because of the consistently low juvenile mortality rates of the default scenarios, which were based on the historical wild population (i.e. before population collapse). The 'do nothing' scenario had the worst demographic outcomes, and the results of pairwise SSMD showed that population size was significantly lower than all other scenarios (with the exception of the basic fostering scenario, Table 3). Of the basic scenarios, the largest population size after 20 years was achieved by autumn release, whereas fostering had little benefit (Fig. 1; Table 3). The most effective combined intervention strategies was spring and autumn releases; however, we found no significant difference in the SSMD of population size between the basic autumn release

Table 2 Key life history parameters that were varied in population viability analyses of Orange-bellied Parrots. Basic scenarios either reflected historical (‘default’) or contemporary (‘do nothing’) demographic trajectories, or involved conservation interventions that were implemented one at a time. The combination scenarios are pairings of the basic scenarios with the best population growth rates and sizes. Achievability is the likelihood of success and is scored as high (activities that are known to be deliverable based on existing conservation actions and resourcing) or low (activities where methods to achieve them have not yet been identified)

	Intervention Strategy	Juvenile mortality rate	Adult mortality rate	Model features	Achievability
Basic Scenarios	default	49%	42%	Based on estimates of mortality in the wild from 1995 before population size collapsed (Stojanovic et al., 2020c), i.e. an optimistic scenario.	-
	default (Bird et al. 2020)	49%	42.6%	Based on modelled generation length of 3.35 years (Bird et al., 2020).	-
	do nothing	80%	42%	Based on the wild population in 2017, but with no conservation intervention.	High
	spring release	80%	42%	Supplementation: 100 adults (50 per sex) released before the ‘breed’ event for the first 20 years.	High
	autumn release	80%	42%	Supplementation: 100 juveniles (50 per sex) released after the ‘breed’ event for the first 20 years.	High
	fostering	80%	42%	Mean brood size increased to 4.5 for the first 20 years. Due to nest box availability no more than 100 breeding opportunities are available, so a maximum of 100 individuals could be added to the wild population by fostering.	High
	juvenile mortality reduction	70%	42%	10% reduction in juvenile mortality rates for the first 20 years.	Low
Combination Scenarios	spring & autumn releases	80%	42%	Supplementation: two supplements both with 25 adult and 25 juveniles of each sex. Supplement 1 is before the ‘breed’ event and supplement 2 is afterward. Both are before the ‘mortality’ event, and included for the first 20 years.	High
	juvenile mortality reduction & autumn release	70%	42%	Supplementation: 100 juveniles (50 each sex) released after the ‘breed’ event, plus a 10% reduction of juvenile mortality rates. Both included for the first 20 years.	Low

Table 3 Matrix of strictly standardized mean differences (below diagonal) and p values (above diagonal – bold if significant) for population size of Orange-bellied Parrots after 20 years of simulated conservation interventions using population viability analysis

	default	default (bird et al. 2020)	do nothing	spring release	autumn release	fostering	juvenile mortality reduction	spring and autumn release	juvenile mortality reduction and autumn release
default		0.48	**0.00**	0.11	0.42	**0.00**	**0.02**	0.12	0.27
default (Bird et al. 2020)	-0.05		**0.00**	0.12	0.44	**0.00**	**0.03**	0.11	0.25
do nothing	-5.01	-4.93		**0.00**	**0.00**	0.17	**0.00**	**0.00**	**0.00**
spring release	-1.25	-1.19	4.32		0.12	**0.02**	0.18	**0.00**	**0.02**
autumn release	-0.21	-0.15	5.84	1.19		**0.00**	**0.02**	0.06	0.18
fostering	-2.87	-2.81	0.96	-1.98	-2.96		0.14	**0.00**	**0.00**
juvenile mortality reduction	-1.99	-1.93	2.61	-0.93	-2.01	1.06		**0.00**	**0.00**
spring and autumn release	1.16	1.22	7.05	2.63	1.53	4.10	3.29		0.28
juvenile mortality reduction and autumn release	0.62	0.68	6.38	2.04	0.92	3.60	2.75	-0.58	

scenario and either of the combined scenarios (Table 3). Thus, comparable results could be attained between basic autumn releases and the best performing combined interventions.

Regardless of the interventions implemented, population sizes all collapsed to zero by 50 years due to reversion of PVAs to the high background rates of juvenile mortality from year 21 onward (Fig. 1).

Discussion

Identifying which conservation interventions to implement can be difficult, especially when there are multiple threats that act on a population at different times and places. PVAs provide an empirical and repeatable framework for evaluating the impacts of conservation interventions (Heinsohn et al. 2022), as well as an approach for identifying which threats are most impactful on overall population growth (Heinsohn et al. 2015). We have previously shown that juvenile mortality strongly influences the population growth of Orange-bellied Parrots (Stojanovic et al. 2022). In lieu of mitigating the threats that have elevated wild juvenile mortality rates, the most impactful and achievable conservation interventions for Orange-bellied Parrots involve increasing the number of juveniles entering the population each year. Autumn releases of juvenile parrots born in captivity (either as a stand-alone action, or in combination with other actions) had the greatest benefit of the interventions we tested. The highest population sizes were reached when autumn and spring releases were combined, likely because the latter action increases the breeding population size, and thus, further boosts the number of juveniles entering the population each year. This particular combination of recovery actions is already being implemented, and as predicted by our PVA, the wild population size has grown recently (Troy and Lawrence 2021). Interestingly, we found no significant difference using SSMD between the combination scenarios and the basic autumn release scenario (Table 4). This suggests that the simpler (and cheaper) basic autumn release scenario may still yield comparable outcomes to the combined approaches. This information provides managers with a clear pathway for adaptive management of future recovery actions.

Lowering juvenile mortality rates by 10% was less effective at increasing population sizes than interventions that increased the number of juveniles that entered the population. In reality, directly and permanently manipulating juvenile mortality rates of wild juvenile Orange-bellied Parrots may be impossible because most threats during migration/winter remain unidentified, let alone mitigated. Although our results starkly support earlier studies that identify the need for lower juvenile mortality rates (Drechsler 2000; Drechsler et al. 1998), we also show that existing interventions should grow the wild population size regardless of juvenile mortality rates during winter/migration. Although this population growth is contingent on maintaining intensive conservation interventions, we argue that ‘buying time’ is in itself a worthwhile conservation goal. Together, our PVAs suggest that two concurrent strategies may benefit Orange-bellied Parrots. First, spring and autumn release should be continued as a combined action for the foreseeable future to (i) maximize population growth, (ii) reduce extinction risk and (iii) encourage reoccupation of the historical breeding range as the local area around the contemporary breeding population becomes saturated. Based on our results, managers may consider whether withdrawing spring releases could free up resources that could be redirected toward autumn releases. Second, continuing eval-

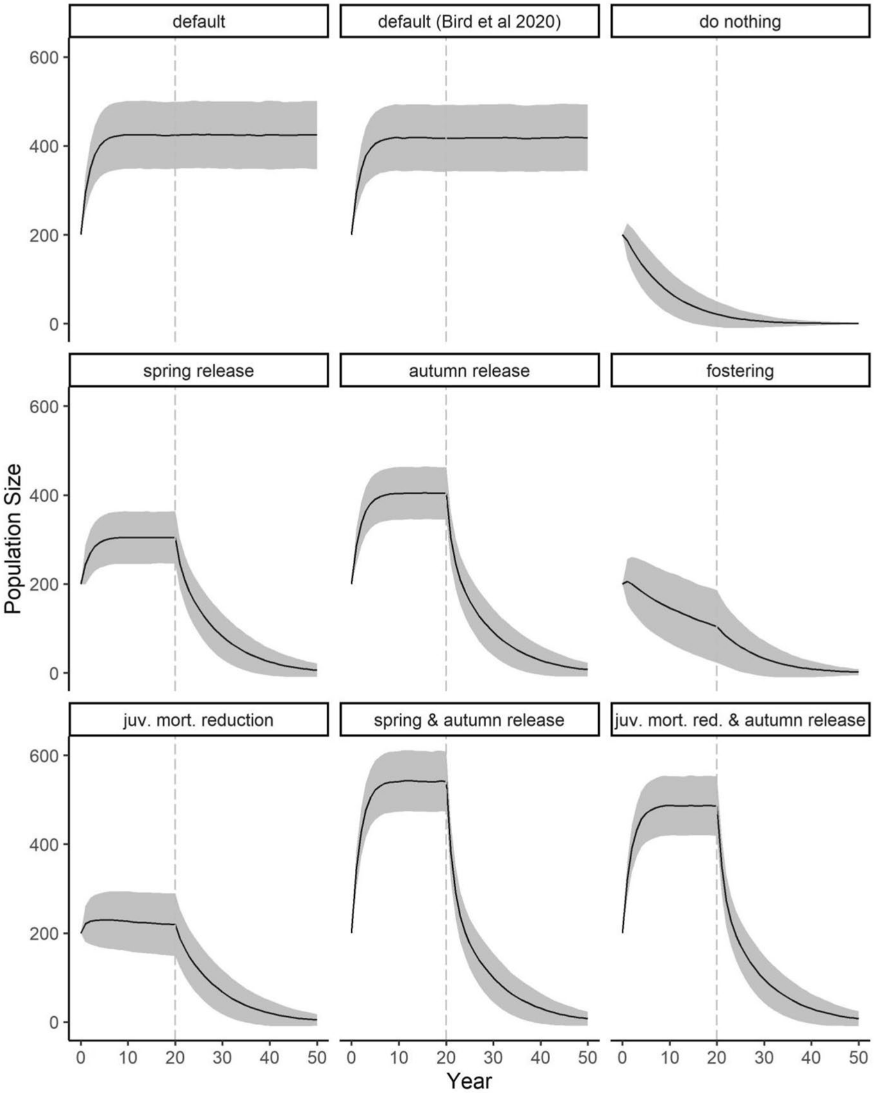

Fig. 1 Population sizes over time for each of the conservation intervention scenarios for Orange-bellied Parrots tested using population viability analysis. Interventions (if included) were withdrawn after 20 years (indicated by the vertical dashed lines). Each panel shows the mean (black lines) and standard deviation (grey ribbons) for the named scenario

uation of juvenile mortality rates and options to mitigate threats during migration/winter should be a priority.

Unless juvenile mortality rates can be sustainably and substantially lowered, Orange-bellied Parrots will remain dependent on conservation management interventions. Across all the scenarios, when interventions were withdrawn at 20 years the populations collapsed to extinction. This result may be somewhat simplistic, especially if higher population sizes arising from management action have unforeseen long term benefits (e.g. recolonization of historical habitat and establishment of new subpopulations). Nevertheless, these results reinforce the need to balance short and longer term management objectives and highlight important ethical considerations if the underlying threats are not able to be mitigated. We have previously shown that neutral/positive population growth rates in this species can only be achieved when juvenile mortality is around 60% or less (Stojanovic et al. 2022). If threats to Orange-bellied Parrot remain elusive and unresolved, is it ethical to continue releasing captive bred parrots to the wild? Into the future, these considerations, and others such as the perpetuation of 'wild' culture (Crates et al. 2021), should be carefully balanced in long-term planning for Orange-bellied Parrot recovery.

Migratory species are difficult to protect because intervention at one place and time can only temporarily benefit the population before animals move away and succumb to other threats elsewhere (Runge et al. 2014). Conservation of mobile species should focus on identifying (i) times and places where aggregation of animals means that a larger proportion of the population can benefit from intervention, and (ii) interventions that exert the greatest positive influence on population growth regardless of whether or not other threats remain unaddressed. The diverse and spatiotemporally variable threats faced by juvenile Orange-bellied Parrots on their first migration/winter means that, away from their breeding ground, corrective actions for local threats at any one time and place may only ever impact a fraction of the population. But this does not necessarily mean that small-scale conservation action for the species is not worthwhile. Even intervention-dependent population growth may empower experimental evaluation of different management options for Orange-bellied Parrots because small population sizes (which to date have hindered research on the species) may be at least temporarily alleviated. Other programs faced with similar problems show that this approach can be important for delaying extinction in the wild and providing a large enough population size to facilitate further research (Oppel et al. 2021).

This study highlights the utility of PVAs for answering practical questions about how to implement species conservation. Management interventions for threatened species typically are resource limited and tend to operate in context of high uncertainty about what course of action to take (Ferrière et al. 2021; Gerber and Kendall 2018; Meek et al. 2015). Coupled with the inherent difficulties of measuring success due to small population sizes, this can leave conservation managers with low confidence when making high stakes decisions (Webb et al. 2019). PVAs provide a way to incorporate the best available information in a replicable modelling framework, and to explicitly identify the impacts of parameter uncertainty on demographic trends (Manlik et al. 2018). Ideally, PVAs should utilize reliable real world data on life history parameters of the study species (Lacy 2000a), and in this regard the Orange-bellied Parrot is a good example of how intensive monitoring of multiple aspects of life history can yield critical details to inform simulations. Most of our input parameters were derived from published sources or reliable unpublished data from the species' recovery project. Thus there was minimal parameter uncertainty in our study, and of the inputs based on assumptions, sensitivity testing in our earlier work demonstrated relatively small impacts on simulations (Stojanovic et al. 2022). Furthermore, our mortality rates included impacts of a range of different factors (including disease outbreaks, age class and captive/wild provenance). Testing of expert opinions around possible interventions using theoretical techniques, like those outlined here, that are validated and refined using field data is the first step. Continuing to refine interventions by updating simulations using information gained from ongoing research into the impacts of those interventions should be the critical next steps. This approach is fundamental for developing an adaptive management framework for Orange-bellied Parrots, where expert opinions (Pritchard et al. 2022) are tested using PVAs that are validated and refined using new field data. Explicitly accounting for uncertainty around the long term resourcing of conservation activities (Ferrière et al. 2021) may be a useful next step in planning for the recovery of the Orange-bellied Parrot in the wild over coming decades.

Migratory species embody the challenges faced by conservationists in a world where protecting populations from threats is extremely challenging. Our study shows the benefit of combining detailed ecological information, targeted solicitation of expert opinion, and PVA for planning conservation interventions. However, our approach can be more broadly applied beyond migrants to other species where the impacts of conservation interventions are uncertain. We hope that conservation practitioners embrace the use of PVA to evaluate the impacts of intervention options in an adaptive management framework. Implementing conservation action can be extremely difficult to resource, and in context of the global extinction crisis, we have a responsibility to ensure that available resources are put to good use and that captive-bred animals are utilized as ethically as possible. PVAs provide a low risk but highly informative approach for evaluating different conservation approaches and offer the security of a defensible, empirical and repeatable way of making decisions in context of high uncertainty and extinction risk.

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Author Contribution DS conceived the study, analysed the data and drafted the manuscript. ST provided the data and reviewed the manuscript. DS, CJH, and RH analysed the data and reviewed the manuscript. All authors reviewed the manuscript. All authors contributed to the manuscript and conceptualisation of the study.

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Declarations

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