Using phylogenetics to explore interspecies genetic rescue options for a critically endangered parrot

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Funding information
BirdLife Australia; Linnean Society of NSW

Abstract
As the global biodiversity crisis deepens, with increasing habitat fragmentation and a changing climate, innovative options for conserving species are being explored. One such conservation action is genetic rescue: introduction of new alleles to promote population fitness. However, for critically endangered species where only one viable population remains, options for introducing new alleles are limited. Interspecies hybridization offers a potential solution but requires resolution of evolutionary relationships, a sound understanding of species biology, social license, and permissive legislative frameworks. Here, we show how phylogenetics and species biology can inform genetic rescue options for the orange-bellied parrot (OBP; Neophema chrysogaster), a critically endangered Australian bird with one small remaining wild population. Our phylogenetic analysis of mitochondrial genomes and nuclear loci for all congeneric species provided strong support for OBPs being the sister species to a group comprising elegant, rock, and blue-winged parrots. Accounting for species distribution, behavior, and ecology, a captive trial of interspecific hybridization with the blue-winged parrot is recommended, including assessment of the fitness of hybrid individuals. Introduction of new alleles into the OBP genome would achieve the conservation goal of improving genetic diversity in a critically endangered species. Concurrently, legislative issues will need to be resolved.

KEYWORDS
conservation, interspecies hybridization, Neophema, orange-bellied parrot, phylogenetic analysis, species tree

1 | INTRODUCTION

With each passing year, we move deeper into the biodiversity crisis (Ceballos et al., 2015). As a consequence, there has been an increase in conservation activity, be it through habitat restoration (e.g., Corlett, 2016), translocations (e.g., Corlett, 2016), or captive breeding (e.g., Gilbert & Soorae, 2017). Many conservation actions are based on...
restoring gene flow between small, fragmented populations to improve their sustainability (Frankham et al., 2017). Decision-making tools have been proposed for those species where hybridization (either intra- or interspecific) is a potential solution for improving gene flow or for providing species with adaptive potential in the face of a changing climate (Chan, Hoffmann, & van Oppen, 2019).

Intraspecies hybridization (between conspecific but genetically differentiated populations, sensu Arnold, 1997) has been used in a number of instances to improve the genetic viability of dwindling populations and mitigate inbreeding depression. Notable cases include the Florida panther (Puma concolor coryi; Pimm, Dollar, & Bass Jr, 2006) and the mountain pygmy possum (Burramys parvus; Weeks et al., 2017). Although less common, hybridization between subspecies is being increasingly used to improve genetic diversity, as seen with the helmeted honeyeater (Lichenostomus melanops cassidix) crossed with yellow-tufted honeyeater (L. gippslandicus; Harrison et al., 2016), and with the Norfolk Island boobook owl (Ninox novaeseelandiae undulata) crossed with morepork/ruru (New Zealand subspecies of the boobook owl, N. n. novaseelandiae; Garnett, Olsen, Butchart, & Hoffmann, 2011).

Active hybridization across species boundaries has been the least-used strategy for conservation purposes, but has been trialed in chestnut trees (Clark, Schlarbaum, Saxton, & Hebard, 2016) and corals (Fogarty, 2012). To our knowledge, it has not yet been trialed in vertebrates. Natural cross-species hybridization is common in plants (Soltis & Doyle, 2012), but in vertebrates is often prohibited by biological, physiological, or behavioral barriers to mating or the production of offspring. Even where offspring are produced, hybrids may be nonviable, infertile, or have reduced fitness relative to nonhybrids. Hybrid infertility is predicted in the presence of cytotet genetic differences between species. However, there are instances where cross-species hybridization in vertebrates results in fertile offspring, such as red wolves (Canis lupus rufus), which are hybrids of gray wolves (C. lupus) and coyotes (C. latrans; Pollienger et al., 2011). Where species are closely related, genetically similar, and have comparable biology, the likelihood of natural hybridization increases (Arnold, 1997).

There are some endangered species for which interspecies hybridization may be the only option for conservation. Chan et al. (2019) recently argued that conservation managers and policymakers should move from a species-centric view to a gene-centric view, where management actions should preserve genetic variation that would otherwise go extinct. In this context, we define genetic rescue as an increase in population fitness (growth) owing to the immigration of new alleles by hybridization (Chan et al., 2019; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015). However, the practicalities of interspecies hybridization are complex. These include: obtaining an understanding of current genetic issues (e.g., inbreeding depression and fixation of alleles), the ability to translocate and breed individuals (either in captivity or the wild), differences in species’ ecology and behavior, the social license to undertake such an activity, and the legislative framework to support such action (e.g., Chan et al., 2019; Corlett, 2016; Garnett, Zander, Hagerman, Satterfield, & Meyerhoff, 2018).

Before assessing the biology of species that could be paired for hybridization, or gaining social and legislative license, we need to identify the closest relatives of the species of interest to determine if hybridization is biologically possible. Therefore, an important step is to achieve clear taxonomic and phylogenetic resolution. Subsequent steps after determining taxonomic relationships include developing goals for any genetic rescue attempt, comparing the ecological, behavioral, and phenotypic traits of taxa, and undertaking trials to test whether hybridization produces fertile offspring. Here, we report a case study of a critically endangered species, the Australian orange-bellied parrot (OBP; Neophema chrysogaster). This species has an extremely small population and low immunogenetic diversity and may be a candidate for interspecies hybridization as a form of genetic rescue.

2 | CASE STUDY

The OBP is a small (45 g), critically endangered Australian endemic of the family Psittaculidae. The species has been subject to a national recovery effort since the 1980s (Department of Environment Land Water and Planning, 2016). Its wild population is critically small: the only known wild breeding population, at Melaleuca in south-west Tasmania, has fewer than 30 birds (Stojanovic et al., 2020). OBPs are one of only two migratory parrots, migrating annually to the Australian mainland (predominantly Victoria), but juvenile survival has declined over the past few decades, and between 1995 and 2017, average return rate of juveniles to Melaleuca fell from about 51–20% (Stojanovic et al., 2020). Although there was an increase in the number of returning birds in the 2020/2021 season (S. Troy pers. comm.), this was related primarily to an increase in the number released rather than substantial improvement in return rates. Once found across Tasmania (usually within 30 km of the coast) and habitat along the south-eastern coast of mainland Australia, the species has been in decline for at least the last century for reason(s) that remain unclear (Brown & Wilson, 1980; Higgins, 1999).
A captive insurance population of the OBP was established in 1986 with 10 wild birds (seven of which bred) and, although the population was supplemented intermittently over the years, it suffered from low fecundity in the 2000s (Morrison, Johnson, Grueber, & Hogg, 2020). An additional harvest of 21 juveniles in the summer of 2010/2011, which equated to almost half of the wild juvenile population, improved genetic diversity of the captive population, but had a negative genetic impact on the remaining wild population (Morrison, Johnson, et al., 2020). For any long-term captive breeding program, adaptation to captivity is of concern (Frankham, 2008) and a recent multispecies analysis suggests that such breeding programs limit the number of generations in captivity (Farquharson, Hogg, & Grueber, 2021). For OBPs, there are notable differences in wing shape between captive and wild birds (Stojanovic et al., 2021) and lower fecundity of captive-bred birds than wild-bred birds when released to the wild (Stojanovic et al., 2018). The causes of these differences between captive and wild birds remain unclear. Although there is little genetic differentiation between the populations (see below, Morrison, Johnson, et al., 2020), both are showing signs of low genetic diversity and an accumulation of inbreeding.

Regular releases of birds from the captive population have occurred each year since 2013 to augment the wild population (Morrison, Johnson, et al., 2020; Troy, 2020). Although survival and breeding of translocated individuals have been high during the breeding season, annual returns after winter migrations are low (Troy, 2020).

Since 2012, this species has suffered significant disease outbreaks caused by beak and feather disease virus (Raidal & Peters, 2018) and Pseudomonas aeruginosa (Yang et al., 2019). Initial investigations into immunogenetic diversity, specifically at Toll-like receptor genes, showed the species to have limited diversity compared with other species within the genus, but similar to other critically endangered bird species (Morrison, Hogg, Gales, Johnson, & Grueber, 2020). Genome-wide single nucleotide polymorphism (SNP) analyses revealed an increase in internal relatedness (a measure of homozygosity) in the wild population from 2010 to 2013; but genetic diversity has since increased with the translocation of birds from captivity to the wild from 2013 to the present (Morrison, Johnson, et al., 2020).

Due to the low genetic diversity at the immune genes and low population numbers in the wild, the OBP National Recovery Team, in 2017, sought to better understand the potential of hybridizing the OBP with its most suitable genetic relative to improve overall genetic diversity. Although subspecies crosses have been successful for other birds (helmeted honeyeater, Norfolk Island boobook owl; see Section 1), the OBP has no recognized subspecies. For the OBP, any outcrossing event would therefore need to be between species. However, the genus Neophema consists of birds that are phenotypically similar, and which have at least partially overlapping distributions (Figure 1). These similarities led species managers to ask which of the other Neophema species is the closest relative of the OBP.

There are six species in the genus Neophema with varying distributions across Australia (Figure 1) (Thomas, Thomas, Andrew, & McBride, 2011): N. chrysogaster (OBP); Neophema chrysostoma (blue-winged parrot); Neophema elegans (elegant parrot); Neophema splendida (scarlet-chested parrot); Neophema petrophila (rock parrot); and Neophema pulchella (turquoise parrot). Bourke’s parrot (Neopsephotus bourkii), was formerly included in Neophema but is now placed in the monotypic Neopsephotus as sister genus to Neophema (Christidis & Boles, 2008). Species of Neophema are generally ground feeders, eating seeds and grasses, and usually occur in the wild in small flocks (Higgins, 1999). However, they vary in a number of aspects of their ecology (see Table 1), including movement (sedentary, nomadic, migratory, or some combination of these; Higgins, 1999). Many of the species have attractive plumage and are popular aviary birds (Campagne, 2008, Figure 1).

Some texts have separated the genus Neophema into two subgenera (e.g., Forshaw, 2010; Schodde & Mason, 1997). The subgenus Neonanodes encompasses the coastal-dwelling N. petrophila, N. elegans, N. chrysostoma, and N. chrysogaster: these birds lack red coloration, have a frontal blue band on their faces, and exhibit minimal sexual dimorphism. The subgenus Neophema comprises N. splendida and N. pulchella. Partial molecular phylogenies have been inconsistent in their division of the genus into the two proposed subgenera (Schweizer, Seehausen, Güntert, & Hertwig, 2010). This study aims to resolve the phylogenetic relationships among Neophema using genetic data from all six species, plus the closely related N. bourkii. We estimate the timing of their divergence and investigate any signals of past hybridization and/or gene flow between species.

### 2.1 Methods

Full details of the methods are provided in the Data S1. In summary, samples of frozen tissue were obtained from the Australian National Wildlife Collection and Museums Victoria for all six species of Neophema and its sister species N. bourkii. Genomic DNA was extracted, quantified, and assessed for quality before being used for mitochondrial genome sequencing (using Illumina NextSeq 500) and direct sequencing of nuclear genes (using Applied Biosystems 3730xl DNA Analyzer). For the whole mitochondrial genome, raw reads were filtered for quality, trimmed, and mapped to the OBP...
mitochondrial reference genome (GenBank accession JX133087.1) before gene annotation. The mitochondrial genomes were validated by direct sequencing regions of the genes encoding cytochrome oxidase I (COI) and cytochrome b (CYTB) and using existing data from GenBank (see Data S1). In addition to the mitochondrial genome...
data, we incorporated sequence data from 12 nuclear genes: six Toll-like receptor genes (Morrison, Hogg, et al., 2020), c-mos proto- oncogene (CMOS), recombination- activating gene 1 (RAG1), rhodopsin (RDPSN), transforming growth factor β-2 (TGFB), tropomyosin alpha-subunit (TROP), and zinc-finger-containing transcriptional regulator (ZENK). Sequence alignments of the complete mitochondrial genome and 12 nuclear genes were analyzed individually using maximum likelihood in IQ-TREE 2 (Bui et al., 2020). Whole mitochondrial genomes and nuclear markers are available through GenBank (accession numbers MW587281–MW587322, MW586934–MW586958, MW586981–MW587024, and MW586959–MW586980). We then used IQ-TREE to infer gene trees based on sequence alignments with reduced taxon sampling, such that a single representative was selected from each species. We used a summary-coalescent approach in ASTRAL-III (Zhang, Rabiee, Sayyari, & Mirarab, 2018) to infer the species tree from these gene trees. The evolutionary divergence times among species were inferred using a Bayesian phylogenetic analysis of mitochondrial genomes, with a relaxed molecular clock to account for evolutionary rate variation across lineages. We specified a lognormal prior distribution for the substitution rate based on estimates by Nabholz, Lanfear, and Fuchs (2016) for the OBP with two different calibration sets (mean 0.005 and 0.0034 substitutions/site/million years).

### 2.2 OBP phylogeny and evolutionary timescale

Our phylogenetic analyses placed the OBP as the sister lineage to a group containing the elegant parrot (N. elegans), rock parrot (N. petrophila), and blue-winged parrot (N. chrysostoma) (Figure 2). Although the
mitochondrial genomes provided strong support for this placement (Figure 2b), the species tree inferred from the combined nuclear and mitochondrial loci did not confidently resolve the relationships among the four species (Figure 2a). The scarlet parrot (Neopsephotus splendida) and the turquoise parrot (Neopsephotus pulchellus) clustered together in both analyses. Our molecular-clock analysis of mitochondrial genomes revealed that the OBP diverged from its congeners between 2.35 million years ago (95% credibility interval 1.85–2.92 million years) and 3.48 million years ago (95% credibility interval 2.76–4.28 million years), depending on the assumed substitution rate.

Our phylogenetic analysis revealed little differentiation among the four species in the subgenus Neonanodes. We found extensive incongruence among gene trees (Figure S1, see Data S1 for details), possibly as a consequence of incomplete lineage sorting, gene flow between species, stochastic estimation error, or some combination of these factors. The results of our phylogenetic analysis do not account for other important genetic factors such as karyotype, which need consideration. It is possible that the land bridges present between Tasmania and mainland Australia during the Pleistocene (Lambeck & Chappell, 2001) facilitated gene flow between two or more of the four species, allowing natural hybridization (sensu Arnold, 1997). Reference genomes of the Neophema species would assist in identifying past hybridization, along with cytogenetic information to confirm genome structure. There are global initiatives that aim to sequence genomes of all forms of eukaryotic life (Lewin et al., 2018), so we are moving toward having the resources to answer these questions. Until then, population-level sampling of genome-wide SNPs would be helpful in determining population structure and rates of gene flow between species.

We also evaluated the morphology and ecology of the Neophema parrots. In our assessment, the blue-winged parrot appears to be a potential candidate to trial hybridization (Table 1 and Table S1). All of the Neophema parrots are similar in size but, consistent with our phylogeny, the OBP is most similar in morphology to the blue-winged, rock, and elegant parrots (Table S1 and Figure 1). Broadly, the Neophema parrots all display similar social behavior, reproductive ecology, and foraging behavior (including diets), although there is variation in distribution, habitat preferences, and movement patterns (Table 1 and Table S1). Determining the most appropriate candidate for a hybridization trial will be dependent on the goals of the genetic rescue, for example, whether the aim is to improve overall genomewide diversity or diversity for specific adaptations; what percentage of mixing OBP genetic ancestry in the offspring is intended; whether there are concerns about hybrid offspring breeding other Neophema species in the wild.

Among the four species in the subgenus Neonanodes, the OBP shares much of its mainland distribution with the blue-winged parrot, but only marginally with the elegant and rock parrots (Figure 1). Indeed, the blue-winged parrot can be observed in all of the mainland coastal habitat types favored by the OBP and OBPs are occasionally reported with groups of blue-winged parrots (Higgins, 1999; Table S1). Furthermore, like the OBP (but unlike the other species of Neophema), some blue-winged parrot populations breed in Tasmania and migrate to the mainland for the non-breeding season (Table S1). Although blue-winged parrots are widespread across Tasmania, they infrequently occur at Melaleuca (<10 records in a decade of observations). Moreover, management intervention to prevent hybridization has been undertaken at Melaleuca in the past and, so the opportunity for hybridization to occur in the wild has been rare, at least in recent decades. Consequently, if crosses were to be considered, there would be a clear need for captive trials to

![Figure 2](image-url)
investigate outcomes in a controlled environment and further examination of blue-winged parrot ecology.

Despite the similarities between the orange-bellied and blue-winged parrots, there must remain considerable uncertainty about the outcome of hybridization between these species. Although some blue-winged parrots undertake migration, others do not, so a key question is the potential effect of hybridization on typical OBP migratory behavior. Even within migratory species, migratory behavior can be altered through conservation breeding and reintroductions. One example of this is the whooping crane (Grus americana), which naturally breeds in Canada during the summer months and migrates to the southern United States over the winter months (Folk et al., 2010). Due to critically low numbers in the wild, a non-migratory population was established in Florida between 1999 and 2002 because of a reintroduction program (Folk et al., 2010). There are now two migratory populations and several non-migratory populations, resulting in two distinct behavioral phenotypes in this species (Folk et al., 2010).

Although Chan et al. (2019) advocate for hybridization as a conservation tool, the reality of using it is neither simple nor clear-cut. For example, based on our findings, we suggest that the next step would be to undertake a cytogenetic analysis of the OBP and blue-winged parrot to further ascertain whether the species are likely to be genetically compatible. Assuming compatibility, it would be prudent to communicate and consult with the broader community to obtain the social license to undertake captive hybridization trials between these two species. A study by Garnett et al. (2018) showed that more than 80% of Australians wish to avoid the extinction of species, but this study did not specifically address genetic mixing or interspecies hybridization. Many members of the public were willing to follow the advice of experts, and also wished to support existing wild populations (Garnett et al., 2018). This brings us back to discussions about what we are aiming to conserve: individual species as we have currently defined them, or their genes and the evolutionary potential that they represent (Chan et al., 2019).

Trialing interspecies hybridization of a critically endangered parrot not only requires social license but also legislative changes (see below) as well as a comprehensive operational plan and experimental design that sets out the target genetic composition of hybrids, and the measures of success. We are not proposing the creation of a new hybrid species that lies between an OBP and a blue-winged parrot, but rather the controlled introduction of genetic variation from the blue-winged parrot into the OBP population through breeding and backcrossing to form the basis for future adaptation. This type of integration requires time and multiple generations to produce offspring with a significantly greater percentage of OBP genome than blue-winged parrot genome in the offspring. An alternative way to integrate new genetic variation could be to use new gene-editing technology such as clustered regularly interspaced short palindromic repeats (CRISPR) (Novak, Maloney, & Phelan, 2018), noting that this technology is designed for editing targeted genes which may be difficult if there are multiple genes involved in complex traits (e.g., immune function), or for reducing inbreeding depression (which likely involves many genes). Either method would require characterization of whole genome diversity so that changes in hybrid offspring could be compared with non-hybrids, and an assessment of changes in fitness measures such as immune response, individual reproductive success, sperm quality, and/or eggshell thickness. At this time, without a reference genome for either species, it is difficult to predict the number of generations and backcrosses that will be needed to improve genetic diversity at key gene regions for OBPs. Future research requires the development of a reference genome, characterization of gene families, and comparison between historical and current samples to determine where diversity has been lost over the past 30–50 years (timeframe of current museum samples). Concurrent with this genomic research, there needs to be consultation and communication with the broader community regarding the plight of the OBP genetically and requirements to ensure support for future captive hybridization trials—should they be undertaken.

The OBP is listed as critically endangered under both the Australian Environment Protection and Biodiversity Conservation Act (EPBC Act) and the IUCN Red List. The National Recovery Plan for the species currently lists “Hybridization with Blue-winged Parrots” as a potential threat to the species (Department of Environment Land Water and Planning, 2016), which will need to be addressed prior to any captive trials being undertaken. The threat status of intentional interspecies hybrids for conservation purposes is currently unclear in both international (e.g., IUCN, Convention of Biological Diversity) and national legislation. Section 13A 186(3) of the Australian EPBC Act does allow for protection of species similar to a species that is eligible for protection under the Act, provided that the former closely resembles the listed species. This provision may afford some scope to provide OBP hybrids with the same threat status as the critically endangered OBP, but at this time, it is unclear what protection the legislative framework will afford hybrids. If
hybridization is to be used as a conservation action, then international and national legislation needs to clarify how offspring from the intentional hybridization of a threatened and non-threatened species will be classified.

Unfortunately for many threatened species like the OBP, where ongoing declines have led to the loss of genetic diversity and there are few wild populations remaining, radical alternatives such as interspecies hybridization, gene editing technology (CRISPR, Novak et al., 2018), or cloning (Holt, Pickard, & Prather, 2004) may be our only options of introducing new genetic variation. Future research into addressing these technical challenges should not be undertaken in a sequential manner (one after the other), nor in the absence of consultation with the broader community (Kohl, Brossard, Scheufele, & Xenos, 2019) and legislative agencies, but rather as a multipronged, multifaceted approach. For many species, there is simply not time to waste.

3 | CONCLUSION

One of the questions that conservation managers and policymakers need to ask when deciding to carry out hybridization, whether it is within species, between subspecies, or between species, is what they are aiming to conserve. At a global level, we designate threat status primarily based on species, but the unresolved taxonomy of many species limits our ability to undertake conservation action. Through ongoing, global, genome sequencing initiatives, many of our concerns about unresolved taxonomy and chromosomal and genomic differences will be ameliorated. This does not preclude timely action on genetic rescue of critically endangered species, as alternative assessment pathways exist. If using interspecies hybridization to introduce genetic variation is becoming our only option to conserve species in the face of a changing world, we need the science, legislation, and society to keep pace with these challenges.

ACKNOWLEDGMENTS

We thank the Orange-bellied Parrot Recovery Team for their contributions to this project, as well as DPIPWE Tasmania for OBP opportunistic tissue collection, and Museums Victoria and the Australian National Wildlife Collection for loan of frozen tissue samples. We acknowledge BirdLife Australia, the Linnean Society New South Wales, and the University of Sydney for financial support of our research. CEG acknowledges the support of San Diego Zoo Global; CJH acknowledges the support of Toledo Zoo and Aquarium and JSD is supported from a University of Sydney Robinson Fellowship to CEG.

CONFLICT OF INTERESTS

Carolyn J. Hogg and Michael J. L. Magrath are both members of the OBP National Recovery Team. No other conflicts of interest are declared.

AUTHOR CONTRIBUTIONS

The study was conceived and funded by Carolyn J. Hogg, Rebecca N. Johnson, and Catherine E. Grueber, lab work and sequence analysis was undertaken by Caitlin Morrison, Jessica S. Dudley, Catherine E. Grueber, and David E. Alquezar-Planas, phylogenetic analysis was undertaken by Perry G. Beasley-Hall, Simon Y. W. Ho, and Nathan Lo, interspecies ecology & biology was collated by Michael J. L Magrath, manuscript was drafted by Carolyn J. Hogg, Catherine E. Grueber, and Caitlin Morrison, all authors revised and contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

Sequence data are accessible through GenBank (accession numbers MW587281–MW587322, MW586934–MW586958, MW586981–MW587024, and MW586959–MW586980) for all species presented in this article and in Table S4.

ETHICS STATEMENT

All samples used in this study were from the Australian National Wildlife Collection and Museums Victoria.

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**SUPPORTING INFORMATION**

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

**How to cite this article:** Hogg, C. J., Morrison, C., Dudley, J. S., Alquezar-Planas, D. E., Beasley-Hall, P. G., Magrath, M. J. L., Ho, S. Y. W., Lo, N., Johnson, R. N., & Grueber, C. E. (2021). Using phylogenetics to explore interspecies genetic rescue options for a critically endangered parrot. *Conservation Science and Practice*, e483. [https://doi.org/10.1111/csp2.483](https://doi.org/10.1111/csp2.483)