



Reproductive skew in a Vulnerable bird favors breeders that monopolize nest cavities

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Abstract

Reproductive skew occurs when a few individuals monopolize breeding output, which can act as a mechanism of natural selection. However, when population sizes become small, reproductive skew can depress effective population size and worsen inbreeding. Identifying the cause of reproductive skew is important for mitigating its effect on conservation of small populations. We hypothesized that superb parrots *Polytelis swainsonii*, which strongly select for the morphology of tree cavity nests, may be reproductively skewed toward pairs that monopolize access to nests. We use SNP genotyping to reconstruct a pedigree, estimate molecular relatedness and genetic diversity of wild superb parrot in the Australian Capital Territory. We successfully genotyped 181 nestlings (a census between 2015–2019) and showed they were the progeny of 34 monogamous breeding pairs. There was a strong reproductive skew – 21 pairs bred only once producing 40% of the nestlings, whereas 13 pairs bred two to four times, producing 60% of the total nestlings. Five of these repeat-breeders produced 28% of all nestlings, which was nearly triple the productivity of one-time breeders. Repeat breeders usually monopolized access to their nest cavities, but the few pairs that switched nests did not differ in fecundity from those that stayed. The cause of nest switching was unknown, but uninterrupted access to a suitable nest (not minor variations in morphology between nests) better predicted fitness of breeding superb parrots. Pedigrees offer powerful insights into demographic processes, and identifying reproductive skew early provides opportunities to proactively avoid irreversible loss of genetic diversity via conservation management. We identify new research questions based on our results to clarify the relationship between access to resources and breeding success.

Introduction

Reproductive skew occurs in animal populations when a few individuals monopolize breeding output (Johnstone, 2000). Whereas reproductive skew has been extensively studied in context of animal social behavior and cooperative breeding (Nonacs & Hager, 2011), it also has important implications for conservation. In large populations, reproductive skew is a natural mechanism of selection, whereby traits that optimize individual fecundity are advantageous (Annett & Pierotti, 1999; Fay *et al.*, 2018). However, in species reduced to small population sizes, reproductive skew depresses effective population size (N_e) by curtailing the number of breeders (Anthony & Blumstein, 2000), which in turn worsens inbreeding (Olah *et al.*, 2021a). For small populations, this can become a conservation problem because sometimes these effects are extreme. For example, one male black rhinoceros

Diceros bicornis sired 10 of 19 calves born into a population (Garnier, Bruford, & Goossens, 2001), and only five of 63 cheetah *Acinonyx jubatus* maternal lineages contributed to nearly half of the total population size (Kelly, 2001). Small populations inherently have low genetic diversity (Frankham, 1996). If diversity cannot be replenished by immigration and is further eroded by reproductive skew, this can become a conservation problem (McLennan *et al.*, 2018). High variance in reproductive success among individuals and families may be more common than widely realized (Gompper, Stagey, & Berger, 1997).

By diminishing population-level genetic diversity and elevating inbreeding (Miller *et al.*, 2009), reproductive skew exacerbates extinction risk (Frankham, 2003). Thus, a key conservation strategy is to identify and, where possible, correct reproductive skew (Frankham, Ballou, & Briscoe, 2002). However, correcting reproductive skew depends on

identifying factors that explain variance in breeding success within a population. There are several theories about why variance in reproductive success arises (Nonacs & Hager, 2011). Reproductive skew can be created by unequal access to high quality resources (Heinsohn & Legge, 2003), biased mortality rates (Stojanovic *et al.*, 2022), heritability (Kelly, 2001), social relationships (Dugdale *et al.*, 2008; Ryder *et al.*, 2009; Henry *et al.*, 2013) or other factors like poor intrasexual competitive abilities (Gompper, Stagey, & Berger, 1997). Given the wide range of potential causes of reproductive skew, conservation practitioners must evaluate on a case-by-case basis the factors affecting a given population. Identifying the cause of reproductive skew might empower managers with the information needed to develop and implement effective mitigation measures, for example by protecting against poaching (Harvey Sky *et al.*, 2022) or by equalizing breeding success in managed populations (Wedekind, 2002).

In this study, we evaluate evidence for reproductive skew in superb parrots *Polytelis swainsonii*. Superb parrots are medium sized (~145 g) gregarious birds (Higgins, 1999). There remain substantial gaps in knowledge about superb parrots despite studies of their ecology (Manning, Lindenmayer, & Barry, 2004; Manning *et al.*, 2007; Manning *et al.*, 2013). Recent evidence suggests that the species' small breeding population size in Canberra, the Australian Capital Territory, is curtailed by the availability of suitable tree cavities for nesting (Stojanovic *et al.*, 2020c). They are listed as Vulnerable both nationally (Commonwealth of Australia, 2021) and locally in the study area (ACT Government, 2019) due to habitat loss and degradation across southeastern Australian woodlands (which in turn affects nest site availability). This threatened status, and its implications for population size and genetic diversity, mean that reproductive skew (if it exists in this population) may be a potential conservation issue. Superb parrots are social but not cooperative, and whether or not their populations are reproductively skewed is not known. Recent evidence shows that superb parrots in the study area can have high nest success, but that the number and quality of nestlings reared varies among years (Cobden *et al.*, 2023).

Less than one percent of available tree cavities may be suitable as nesting sites for superb parrots in Canberra (Stojanovic *et al.*, 2020c). This resource limitation likely creates intra- and inter-species competition for access to nests. We hypothesize that if this is so, superb parrot populations should be reproductively skewed to individuals that monopolize access to nest sites. Similar patterns have been observed in other parrots that breed in environments with scarce nesting opportunities (Heinsohn & Legge, 2003) – whether this applies more generally is not clear. Evaluating this possibility is important for conservation because, for example, reproductive skew in the critically endangered orange-bellied parrot *Neophema chrysogaster* resulted in the death of 90% of wild family lineages over only three years (Stojanovic *et al.*, 2022) and severely diminished their population genetic diversity over the longer term (Morrison *et al.*, 2020a; Morrison *et al.*, 2020b). We test our hypothesis using genetic techniques to reconstruct a pedigree for Canberra's superb

parrots. We explore whether the characteristics of nest sites explains reproductive success among breeders. We also estimate N_e and compare this important population genetic parameter to the pedigree and estimates of molecular relatedness. Finally, we quantify population genetic spatial structure, diversity and the inbreeding coefficient as a baseline for this population against which future change can be measured. We discuss how the availability of critical nesting resources might contribute to variance in reproductive success among superb parrot pairs and propose new research questions based on our findings.

Materials and methods

Study area and field procedures

We studied superb parrots at their only two known nesting sites in Canberra (details withheld) located ~15 km apart separated by predominantly urban/suburban habitats. This study ran between 2015 and 2019. We identified nest cavities and checked their occupancy each breeding season (October–December) and searched for new nests each year (see Stojanovic *et al.*, 2020c). Our monitoring is effectively a census of all breeding superb parrots in the study area because: (1) nest trees are scattered in open habitat making nest searching straightforward, (2) individual nest cavities are used repeatedly, (3) the species prefers to nest in aggregations, and isolated nesting away from the two main sites is not known to occur, and (4) in any given year only one or two nests are inaccessible for genetic sampling. On average we monitored 10 nests per year (range: 4–17). We checked nests by climbing trees using single rope techniques. We sampled nestlings for DNA (either blood using brachial venipuncture or a pin feather). No genetic samples from adult superb parrots were included in this study.

Genotyping by sequencing

Genetic samples were sent to Diversity Arrays Technology Pty. Ltd. (DArT; Canberra, Australia) for DNA extraction, molecular sexing, and single-nucleotide polymorphism (SNP) genotyping using DartSeq™ denovo methods (Kilian *et al.*, 2012). They successfully genotyped 188 nestlings including 92 females and 95 males (plus an individual of unassigned sex). We filtered SNPs using the 'dartR' package in R (Gruber *et al.*, 2018; R Development Core Team, 2021), based on a 0.99 reproducibility threshold (calculated via technical replicates performed in-house at DArT), retaining one variant per sequence tag, variants without missing data (call rate threshold of 1), and with minimum minor allele frequency of 3%. For the pedigree analysis (below), we used stricter filtering criteria on sequence depth (between 5 and 20) and minimum minor allele frequency of 5%.

Analytical approach

All analyses were undertaken in R (R Development Core Team, 2021). We used the *Sequoia* v 2.0.7 package to

reconstruct a pedigree by identifying all possible first-, second-, and third- order relationships based on likelihood analysis. *Sequoia* can handle multi-generational, overlapping and inbred pedigrees (Huisman, 2017). All individuals were considered potential breeders by their second year of life (Bird *et al.*, 2020). We included the sex of individuals (determined using sex-linked SNPs) and year of birth as additional life history information in the pedigree. To overcome potential non-assignment of relationships among related individuals by the pedigree, we found putative relatives within our data using the function *GetMaybeRel()* which identifies pairs that are likely to be 1st or 2nd degree relatives conditional on the reconstructed pedigree. Using the function *CalcPairLL()* on the output from *GetMaybeRel()*, we estimated log₁₀-likelihoods for potential relationships of pairs. *CalcPairLL()* quantifies uncertainty about the different possible relationships assigned to pairs, enabling users to evaluate the likelihood that assignments are reasonable.

We quantified the probability that two individuals that share an allele are identical by descent rather than identical by state by estimating molecular relatedness (Hogg *et al.*, 2019). We used simulations in COANCESTRY v 1.0 (Wang, 2011) to determine the most appropriate estimator from five moment and two maximum likelihood estimators (Hogg *et al.*, 2019). We selected TrioML (Wang, 2007) because, it accounts for inbreeding, had the lowest variance and highest Pearson correlation coefficient with the simulated true mean of the estimators considered. We then derived the mean kinship (i.e. TrioML/2) of all pairs and calculated the average relatedness of individuals within/between broods, nest cavities and study sites.

To evaluate whether reproductive success is skewed to individuals that monopolize better quality nesting sites, we used data on the internal morphology of each superb parrot nest cavity from our previous study (Stojanovic *et al.*, 2020c). We focussed on cavity traits that were strongly preferred by parrots: minimum entrance size (cm), depth (cm), and floor diameter (cm). We used these co-varying traits as response variables in a multivariate analysis of variance (MANOVA). Using the pedigree, we identified the occupants of each nest cavity. We created a binary variable that categorized cavities as (i) used repeatedly over time by the same breeding pair (i.e. long term nest site fidelity) or (ii) used either by multiple breeding pairs or just once (i.e. nest switching). We used this as a predictor variable in the MANOVA to evaluate if nests that were monopolized or used temporarily differed in their morphology. We also used a Welch two sample t-test to compare the brood sizes of breeding pairs that stayed in the same nest cavity to those that switched.

We calculated genetic estimates of N_e following recommendations by Olah *et al.* (2021b), using the linkage disequilibrium method (LD; Waples, 2006; Waples and Do, 2010) implemented in the software NEESTIMATOR v2.1 (Do *et al.*, 2014). This approach is robust to the inclusion of siblings and overlapping generations, which exist in our data. We used a threshold frequency of 0.02 for screening out rare alleles, assumed monogamy (based on our pedigree), and calculated 95% confidence intervals for N_e with a jackknife-across-

samples method (Jones, Ovenden, & Wang, 2016). In order to adjust the estimates of contemporary N_e and interpolate the real world total/adult census population sizes (N) based on the genetic data, we used the software AgeNe (Waples, Do, & Chopelet, 2011). Where possible we used our own data to inform the life history parameters needed to estimate N . The demographic parameters we used were: (1) 24 age classes (Bird *et al.*, 2020), (2) age at first reproduction is two years old (Bird *et al.*, 2020), (3) average clutch size of 3.8 (from our own data, automatically rescaled with Poisson factor = 1), (4) 50% estimated juvenile survival (based on the highest juvenile survival rates of orange-bellied parrots, Stojanovic *et al.*, 2020b), (5) 62% observed adult survival for both sexes (Bird *et al.*, 2020), and (6) 50% sex ratio. We calculated three adjusted values of N_e (Waples, Antao, & Luikart, 2014) using (1) true N_b/N_e from AgeNe, (2) adult life span (AL) = 23.7 and age at maturity (α) = 1.3, and (3) AL, α , and coefficient of variation of mean number of offspring for adult life span (CVf) = 0. We then repeated these calculations by incorporating the results from our pedigree and accounting for the detected reproductive skew. Specifically, we (1) changed the male sex ratio to 51%, (2) used average clutch sizes of 3.5 for age class #2 (one-time breeders), 3.55 for age class #3, and 3.4 for age classes #4–24, (3) calculated the reproductive variance parameters (Poisson factor) for each age class as the corresponding clutch size variance divided by its mean, and (4) the CVf = 0.175 (Waples *et al.*, 2013). We report the pedigree-adjusted N values to highlight the degree to which reproductive skew is impacting the population.

To support the results of the pedigree and identify potential gene flow among the subpopulations in the study area, we calculated the pairwise fixation index (F_{ST}) for the two subpopulations and looked for spatial genetic structure. We conducted exploratory principal coordinates analysis (PCoA) using the *adeigenet* package (Jombart & Ahmed, 2011), and then implemented discriminant analysis of principal components (DAPC). This approach is sensitive to fine genetic differences among populations but does not make any assumptions about Hardy–Weinberg equilibrium (HWE) or linkage disequilibrium (LD). This enabled us to include all samples and evaluate whether there were differentiable groupings within the data without making any *a priori* assumptions. We allowed the package first to infer the number of clusters with the *find.clusters* function. We used the optimal *a*-score and cross-validation (Jombart & Ahmed, 2011) to retain principal components (PCs).

Finally, to provide baseline information about the population, we quantified genetic diversity and inbreeding by calculating observed – (H_o), expected – (H_e), and unbiased expected heterozygosity (uH_e), and the inbreeding coefficient (F_{IS}) using GenAIEx 6.5 (Peakall & Smouse, 2012) on a subset of the data where – based on the results of the pedigree – only one individual per family was included.

Results

We obtained a total of 43,201 binary SNPs for 188 individuals. The mean read depth was 14.3 per individual (2.5–

188.8) and the mean call rate was 89%. The initial filtering left us with 5,698 SNPs with a mean read depth of 25.5 per individual (median = 23). For the pedigree analysis, the dataset contained 3290 SNPs.

We assigned parentage in the reconstructed pedigree for 181 of 188 superb parrot nestlings. Pairwise contrasts among individuals likely to have a potential kin relationship (i.e. within, not between sites) resulted in 543 full sibling pairs assigned, and 17,035 unrelated pairs. We found strong evidence of prevailing monogamy because 268/282 pairs within the same brood were assigned confidently as full siblings (LLR = 27.54) and the remaining 14 pairs were assigned with low confidence as half siblings (LLR = 1.34). We also found strong evidence that most individuals born in the same tree cavity (regardless of birth year) were full siblings, with 268/363 pairs assigned as full siblings (LLR = 27.54). The remaining pairs from the same tree cavity were confidently assigned as half avuncular ($n = 4$, LLR = 71.83) or parent-offspring ($n = 21$, LLR = 11.62), or tentatively assigned as grandparent ($n = 56$, LLR 5.53) or half siblings ($n = 14$, LLR = 1.34) but support for the latter categorisations was weak. This suggests we did not observe breeding recruitment over the five years of this study.

Estimates using molecular relatedness supported the pedigree. Over the 17,578 pairwise contrasts in the full sample, mean kinship among brood-mates was 0.25 ± 0.22 SD (i.e. full siblings) compared with 0.02 ± 0.08 SD (i.e. unrelated) for non-brood mates. Likewise, pairs that originated from the same nest cavity had mean kinship of 0.24 ± 0.23 SD, compared with 0.02 ± 0.07 SD for pairs from different cavities.

Based on the reconstructed pedigree (which we refined with the assignment of putative relatives and observations from the field), our sample of nestlings were the progeny of a total 34 breeding pairs. We found evidence of reproductive skew. Of the assigned breeding pairs, 21 bred only once over the five year study, producing 73 nestlings (40.3% of the assigned sample). Thirteen pairs bred two or more times over the study – eight pairs bred twice, four bred three times, and one pair bred four times. Repeat breeders produced 108 offspring (59.7% of the total), and those that bred three or more times produced 51 offspring (28.1% of the total). Over the whole study, one-time breeders produced an average of 3.5 ± 1.3 SD offspring per pair, compared to 7.1 ± 2.4 SD for two-time breeders, and 10.2 ± 1.9 SD for three- and four-time breeders.

We found one instance of a nestling that was unrelated to its brood-mates. Field observations suggest this may be attributable to egg dumping or attempted (but failed) usurpation

of the nest of a three-time breeding pair by another pair that did not rear any other nestlings in the sample.

We observed five instances of nest cavity switching by repeat breeders. There was no difference in the brood sizes of repeat-breeders that monopolized cavities (mean = 5.7 chicks/brood) and those that switched (mean = 4.9 chicks) ($t = 0.55$, d.f. = 19.46, $P = 0.59$). There was no difference in the morphology of cavities used by breeding pairs that stayed or those that switched (Pillai's Trace = 0.06, $F = 0.60$, d.f. = 3, $P = 0.6$).

Adjusted estimates of contemporary N_e fell into the range of 63 to 66 for all samples (28–29 at one site, and 42–44 for the other). AgeNe estimated the ratios for $N_e/N_{total} = 0.48$ and $N_e/N_{adult} = 0.85$. The pedigree-adjusted calculations resulted in $N_e/N_{total} = 0.52$ and $N_e/N_{adult} = 0.92$, which accounts for reproductive skew. We used these ratios for interpolating the census population sizes from the adjusted estimates (Table 1).

Pairwise F_{ST} between the two populations was 0.029. Although we found no evidence of direct kinships between the two subpopulations using the above approaches, there was no differentiation between them in the PCoA (Figure 1), and we found only weak clustering of individuals by subpopulations using DAPC. Discriminant analysis with all PCs initially retained supported the existence of only one cluster within the data (delta Bayesian Information Criterion, $\Delta BIC = 2.64$ between one and two clusters). The number that minimized root mean squared error via cross-validation was 130, and the number of retained PCs that maximized the α -score was 18.

The results of genetic diversity, inbreeding and mean kinship across both populations are reported in Table 2. Mean kinship was low between the subpopulations suggesting no recent interbreeding (which agreed with the pedigree), and we found small but significant evidence of inbreeding within each subpopulation because the standard errors did not overlap zero (Table 2). The F_{IS} confidence limits for site 1 were 0.027–0.039, and 0.039–0.050 for site 2.

Discussion

We evaluated evidence of reproductive skew in Vulnerable superb parrots. We revealed a strong reproductive skew toward 13 of 34 breeding pairs. Only five pairs bred three or more times over the study, producing nearly a third of all nestlings and nearly triple the productivity of one-time breeders. Repeat-breeders monopolized access to their nest

Table 1 Estimates of N_e derived from superb parrot SNPs using the linkage disequilibrium method, and adjusted estimates (for adjustment details see methods). We also present estimates of census population size both for the total population and adults only

Samples	N_e (95% CI)	Adjusted estimates			Census population sizes		Pedigree-adjusted population sizes	
		N_{e1}	N_{e2}	N_{e3}	N_{total}	N_{adults}	N_{total}	N_{adults}
All data	68 (62–75)	66	63	64	130–136	74–77	118–120	67–68
Site 1	45 (40–51)	44	42	42	86–91	49–51	78–80	44–45
Site 2	30 (26–34)	29	28	28	57–60	32–34	52–53	29–30

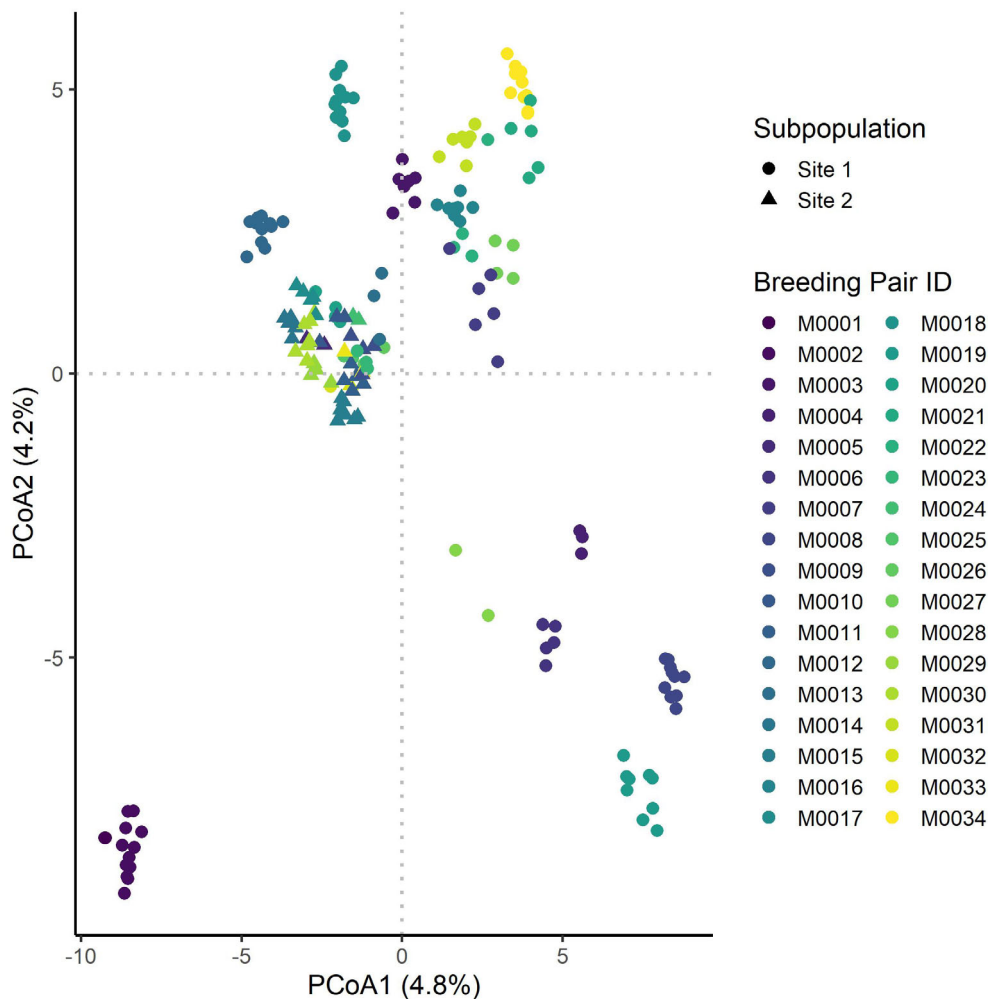


Figure 1 Principal coordinates analysis of superb parrots within Canberra, Australia. Individuals from both subpopulations overlapped and the axes show the proportion of variance explained. Clustering within subpopulations related to kinship, and the colors differentiate the progeny of individual breeding pairs based on a reconstructed pedigree.

Table 2 Population genetic diversity statistics for superb parrots over the two study sites

Study site	H_O	H_E	uH_E	F_{IS}	MK
All Data	0.25 ± 0.002	0.26 ± 0.001	0.26 ± 0.002	0.02 ± 0.002	0.02 ± 0.05
Site 1	0.26 ± 0.002	0.26 ± 0.002	0.27 ± 0.002	0.03 ± 0.003	0.02 ± 0.05
Site 2	0.24 ± 0.002	0.25 ± 0.002	0.26 ± 0.002	0.02 ± 0.004	0.03 ± 0.07

H_O = mean observed heterozygosity, H_E = mean expected heterozygosity, uH_E = unbiased expected heterozygosity, F_{IS} = inbreeding among individuals within populations, MK = mean kinship within each study site. All results are shown \pm standard error.

cavities – switching between nests was rare, but its occurrence was unrelated to tree cavity morphology. There was no difference in the brood sizes of breeders that switched compared to those that stayed in the same nest cavity. We show that reproductive skew, which is an important limitation on the number of breeders in small populations, exists in superb parrots. However, the relationship between reproductive skew and resource limitation we found differs to

that of other parrots. Eclectus parrot *Eclectus roratus* mothers in cavities prone to flooding have worse reproductive success and more extreme offspring sex ratio bias than those in better quality cavities (Heinsohn & Legge, 2003; Heinsohn, 2008). In contrast, superb parrot nest cavities rarely flood and are morphologically similar to one another, so the reasons for nest switching are not clear. Many nest cavities in our study were used only once, but remained

available throughout the study. Cavity occupancy by superb parrots was mostly governed by turnover among one-time breeders. Of the 181 nestlings successfully sequenced, we did not observe any convincing evidence of natal site breeding recruitment. Further study of the role of intra and interspecific nest competition as a potential driver of nest switching and juvenile survival rates may explain these observations.

Our pedigree showed that the nestlings in our sample were the progeny of only 68 individual parrots. This agreed well with our estimates of the number of individual breeding adults in the population estimated using N_{adults} (74–77). The relatively high N_e/N ratio in these populations (0.48) is comparable to that measured in the Critically Endangered swift parrot *Lathamus discolor* (0.52) using the same estimators (Olah *et al.*, 2021b), and to other birds with low fecundity (e.g., 0.41 in *Accipiter gentilis*, 0.45 in *Grus japonensis*, 0.48 in *Aphelocoma coerulescens*) but estimated using demographic estimates (Frankham, 2009). Given the similarity of our estimates of population size using different methods, the number of breeding superb parrots across the study area is likely small, and turnover occurred primarily among one-time breeders. Reproductive skew depresses N_e in small populations (Miller *et al.*, 2009), and – if no immigration occurs – superb parrots in Canberra may be at risk of temporal decline in N_e . Indeed, the inbreeding we observed may suggest this process is already occurring. However, inbreeding in this population was significant but very small, meaning that realized biological impacts may currently be minimal. Superb parrots are relatively long-lived, with a maximum life span of 20 years and a generation length of 4.6 years (Bird *et al.*, 2020), so our five-year study is too brief to demonstrate long-term trends. However, we provide baseline data about population N_e , genetic diversity, inbreeding and spatial structure of superb parrots against which future comparisons may be made. Our results also raise new questions about the demographic implications for superb parrots of reproductive skew and limited nesting resources:

- 1 if reproductive success is skewed toward only a handful of repeat-breeding pairs of superb parrots, is juvenile survival and recruitment to the breeding population similarly skewed?
- 2 why did one-time breeders fail to monopolize their nests and breed again, and what happens to them (i.e. do they breed once because they die)?
- 3 F_{ST} , PCoA, and DAPC suggest the two subpopulations are not strongly differentiated, meaning their reproductive isolation may only be recent. Given the intervening habitat seems permeable, is there some other barrier (e.g. behavioral or social) to contemporary breeding dispersal between nesting aggregations?

Our results are interesting, but further research into the spatial distribution of nesting resources, behavior and breeding recruitment are needed to explain the population dynamics of superb parrots in the study area.

Reproductive skew is well understood in context of species reintroductions (Miller *et al.*, 2009; McLennan

et al., 2018) and in behaviorally complex, social species (Allainé, 2000; Anthony & Blumstein, 2000; Heinsohn & Legge, 2003), especially those with intense sexual competition (Say, Naulty, & Hayden, 2003; Tatarenkov *et al.*, 2008). However, superb parrots are monogamous, and despite flocking and nesting in aggregations (Higgins, 1999), they lack more complex social behaviors that lead to reproductive skew in other species. This, in the context of the limited availability of tree cavities suitable for nesting in the study area (Stojanovic *et al.*, 2020c), makes our study system an interesting example of how local resource availability can influence species that might reasonably be expected to have low variance in individual reproductive success. Pedigrees are one of the most foundational population genetic tools (Anderson & Garza, 2006; Olah *et al.*, 2021a), and they offer powerful insights into the demographic processes even of open populations. Using pedigrees can enable managers to identify reproductive skew early and ideally, prevent missed opportunities to avoid irreversible loss of genetic diversity (Miller *et al.*, 2009).

Linking variance in individual reproductive success to the availability of critical resources can help to identify options for conservation interventions. Widespread and ongoing loss of breeding habitat across the range of superb parrots (Manning, Lindenmayer, & Barry, 2004; Manning, Fischer, & Lindenmayer, 2006; Manning & Lindenmayer, 2009; Manning *et al.*, 2013) is likely to exacerbate the effects of nest cavity scarcity we observed. Habitat restoration using generic artificial nest boxes for superb parrots have failed (Lindenmayer *et al.*, 2017) and targeted solutions for other species increased interspecific competition (Stojanovic, Young, & Troy, 2019; Stojanovic *et al.*, 2020a). Given uncertainty about the availability of nesting sites for superb parrots (Stojanovic *et al.*, 2020c) and the challenges associated with artificial nests, protecting known suitable cavities is a logical first step toward relieving competition for superb parrots. Even so, the availability of suitable tree cavities did not guarantee equal reproductive success among breeding superb parrot pairs. This, especially in the context of landscape scale habitat deterioration, hints that complex but undescribed behaviors are important determinants of fitness and nest cavity monopolization in this species. We hope that our study encourages others to reappraise superficially healthy populations for reproductive skew, and to identify potential aspects of underlying resource availability that may contribute to variance in reproductive success.

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Conflict of interest

The authors have no conflicts of interest to declare.

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Author contributions

DS and LR conceived the ideas and designed methodology; DS, LR, FA and MC collected the data; DS, EM, GO, FA and CH analyzed the data; DS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Ethics statement

This research was conducted with a scientific permit from the ACT Government (#LT201795) and permission from the ANU Animal Ethics and Experimentation Committee (#A2018-54).

Data availability statement

Data are archived with the Canberra Government.

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