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Reproductive Skew in an Endangered Parrot Population Driven by Multi-Year Monopolisation of Nest Site Clusters

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ABSTRACT

Reproductive skew is the unequal distribution of reproductive output between individuals. While expected to occur to some degree in most populations, extreme reproductive skew is often observed in species with strong social hierarchies or severely limited breeding resources. For small populations, highly skewed reproductive output can have a negative impact on genetic diversity and lead to increased inbreeding. We aimed to determine the extent of reproductive skew in the endangered Norfolk Island green parrot *Cyanoramphus cookii* population. This species has a small effective population size, a high rate of inbreeding, and is currently supported through the provision of a limited number of high-quality, predator-proofed nest sites. We examined the nest usage patterns and mating system of Norfolk Island green parrots by using nest monitoring data and 146 genetic samples (2013–2023) to reconstruct a pedigree. We found that 75% of the 32 monitored broods included in our pedigree were produced by just 40% (6/15) of the breeding females represented in our sample. These six females monopolised 2–3 nest sites each and bred up to four times in a 12-month period. Only two of these six females switched mates between nesting attempts. Males showed similar, but slightly different patterns due to mate switching by females. Norfolk Island green parrots appear to be largely monogamous, with 84% of broods showing no evidence of mixed parentage. However, two of 19 broods showed evidence of extra-pair paternity, and one showed evidence of extra-pair maternity. Our results reveal the tendency of pairs to monopolise a cluster of high-quality nest sites, creating a mechanism for increasing reproductive skew. These findings highlight the need to share conservation management resources equitably between individuals in small, threatened populations to support a larger proportion of breeding adults and maintain genetic diversity.

1 | Introduction

Reproductive skew, in which breeding-age individuals have unequal contributions to overall breeding output, is likely to be observed to some degree in most natural populations. Highly skewed reproduction is well documented and even expected in species with cooperative breeding or a strong social hierarchy (Nonacs and Hager 2011; Olivier and Higginson 2023). In these cases, it is most commonly driven by socially dominant individuals monopolising mating opportunities (Johnstone 2000). Reproductive skew is observed in various taxa, including birds (e.g., Southern pied babblers *Turdoides bicolor*; Nelson-Flower

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et al. 2018), mammals (e.g., Christmas Island flying-foxes *Pteropus natalis*; Lloyd-Jones et al. 2023), invertebrates (e.g., Tropical hover wasps *Liostenogaster flavolineata*; Sumner et al. 2002), fish (e.g., *Neolamprologus multifasciatus*; Bose et al. 2022) and reptiles (e.g., Tuatara *Sphenodon punctatus*; Miller et al. 2009). While often measured over a single breeding season, it can lead to significant differences in lifetime reproductive output between individuals, with potential genetic and evolutionary consequences (Snyder and Ellner 2024). Reproductive skew can also be increased by unequal access to key breeding resources. This is the case for some large-bodied cavity-nesting birds, for which suitable nesting hollows can be a limiting resource (e.g., Heinsohn and Legge 2003; Murphy et al. 2003; Stojanovic et al. 2023). If only some individuals gain exclusive access to scarce breeding sites, reproduction will become skewed.

Reproductive skew is not in and of itself a problem for conservation; indeed, it is present to some degree in many species (Ross et al. 2020). However, highly skewed reproduction can be detrimental to small populations, which often have lower levels of genetic diversity than large populations (Frankham 1996). When the number of breeders is limited, inbreeding in subsequent generations becomes more likely, increasing the risk of a reduction in fitness due to inbreeding depression (Hedrick and Kalinowski 2000; Reed and Frankham 2003). Reduced diversity can also limit a population's adaptive potential by restricting the genetic variation available for selection (Willi et al. 2006). Thus, reproductive skew can pose a real threat to the persistence of small, conservation-dependent populations (Miller et al. 2009; Stojanovic et al. 2023), and managers are encouraged to minimise skew when supporting small breeding populations (Wedekind 2002).

While conservation management actions can be used to address reproductive skew caused by limited breeding resources, they also have the potential to inadvertently increase reproductive skew. The Norfolk Island green parrot *Cyanoramphus cookii* (hereafter 'green parrot') is an endangered parrot species for which land clearance has drastically reduced the availability of breeding habitat and suitable nesting cavities (Hicks and Greenwood 1989; Gautschi et al. 2025). The species is primarily supported through predator control and the provision of secure, predator-proofed nest sites that are closely monitored and managed by national park staff (Ortiz-Catedral et al. 2018). However, many existing predator-proofed nest sites do not meet green parrot nest preferences, and interspecific competition for these nest sites is also high (Gautschi et al. 2022, 2025). Nests established outside of predator-proofed nest sites are susceptible to predation and have lower survival rates than predator-proofed nests (Gautschi et al. 2025). Thus, availability of preferred, predator-proofed nesting sites still appears to be a limitation for the breeding population, and birds that gain access to high-quality sites will receive significantly more breeding support than those that do not, potentially increasing reproductive skew.

Recent genetic analysis of the green parrot population indicated an estimated effective population size of just 44 individuals, and found that nearly 20% of sampled individuals were putatively inbred (Gautschi et al. 2024). Thus, ensuring as many green parrots as possible are breeding should be a priority to ensure existing genetic diversity is preserved (Gautschi et al. 2024). In this study we build upon the genetic analysis performed by Gautschi et al. (2024), using genetic samples collected between 2013 and 2023 to reconstruct a green parrot pedigree. We combine this pedigree with field data to examine patterns of nest use by individual birds, their mating system, and reproductive skew. We also examine samples obtained from natural, unmanaged nest sites to provide further insight into this unmonitored portion of the population. Our analysis provides valuable insights into the breeding behaviour of the Norfolk Island green parrot and how this behaviour interacts with management activities. We discuss how our findings can be used to refine future management and the broader lessons for the conservation of threatened species that are supported by intensive management actions.

2 | Methods

2.1 | Study Species and Location

Norfolk Island is a small island (~35 km^2) of volcanic origin, located in the South Pacific Ocean (29°02′S, 167°57′E). The island has a moderate subtropical climate and its native vegetation predominantly comprises subtropical rainforest, which is now mostly restricted to the slopes of Mount Pitt (318 m) and Mount Bates (319 m) within the Norfolk Island National Park (Commonwealth of Australia 2025). This is the primary breeding habitat of the Norfolk Island green parrot, a medium-sized parrot endemic to Norfolk Island that is closely related to the kākāriki (*Cyanoramphus* spp.) of New Zealand (Boon et al. 2001; Forshaw 2010). Green parrots breed year-round in tree hollows and root cavities, laying an average of five eggs and taking approximately 10 weeks to fledge young (Hicks and Greenwood 1989; Hicks and Preece 1991; Gautschi et al. 2025). While commonly seen in pairs and presumed to be socially monogamous, the exact nature of the green parrot breeding system is unknown.

2.2 | Genetic Sample Collection, DNA Extraction, Sequencing and Sexing

Since 2013, predator-proofed green parrot nests have been monitored on a monthly basis by Norfolk Island National Park staff as part of ongoing management activities, resulting in the documentation of more than 200 nesting attempts since 2013 (Gautschi et al. 2022, 2023, 2025). These nest sites are spread throughout the known breeding range of the species and comprise the vast majority of known nest sites. We analysed genetic samples collected by park staff at some of these nests between 2013 and 2023, alongside additional samples that we collected between 2021 and 2023. These comprised the same 188 samples (2015–2022) sequenced as part of the population genetic analysis performed by Gautschi et al. (2024), as well as an additional 48 samples sequenced in 2024. The additional samples were made up of 28 samples from birds caught in mistnets (May 2023), nine samples from nestlings (2013, 2014 and 2023), eight samples obtained opportunistically from feathers found on the ground (2021 and 2023) and three samples that

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were previously sequenced but did not return sufficient data for analysis (2021–2022). In total, nestlings from 47 breeding attempts in 27 different nest sites were genetically sampled. Further details of these samples are provided in Table S1. We stored, extracted and sequenced genetic samples as described in Gautschi et al. (2024). This involved the use of a Monarch Genomic DNA Purification Kit (New England Bio-Labs, Victoria, Australia) to extract DNA, and reduced representation sequencing of all samples by Diversity Arrays Technology (DArT, Canberra, Australia) (Kilian et al. 2012). We determined the sex of individuals using molecularly sexed individuals from Gautschi et al. (2024) to identify sex-linked loci. To do this we used the function *gl.report.sexlinked* in the package dartR v2.9.7 (Gruber et al. 2018) in R version 4.3.2 (R Core Team 2023) (Table S2).

2.3 | Data Filtering

Genetic sequencing returned a dataset containing 230 genotypes and 10,027 SNPs (single nucleotide polymorphisms). We used the R package sequoia v2.8.3 (Huisman 2017) to construct a pedigree using these SNPs. High-quality data are required (Huisman 2021), so we applied a stringent filtering protocol, using the dartR package. Unfortunately, this resulted in some broodmates and even entire broods being excluded from our analysis. We adjusted the data filters until we had high-quality SNPs in which all known duplicate samples within our dataset could be identified at a low genotyping error rate (1.5%) using the duplicate check module in sequoia. Most notably, we applied a reproducibility threshold of 100%, an individual call rate threshold of 80%, a locus call rate threshold of 90% and a minor allele threshold of 30% (all filtering steps are shown in the R script, Supplement 1). The resulting dataset contained 153 genotypes and 342 SNPs. In total, we identified seven duplicate samples in sequoia and removed the older and/or poorer quality samples, leaving 146 genotypes and 342 SNPs in our dataset (Table S3).

2.4 | Pedigree Reconstruction

To inform pedigree reconstruction, sex and hatch year (or minimum/maximum hatch years) were included in our dataset. We determined sex for all individuals (see above) and added hatch year when known from nest monitoring records. For birds captured in mist-nets, we set maximum hatch year to a year prior to sample collection. For individuals without a known hatch year, we could not reliably estimate minimum hatch year without information generated in the pedigree itself, so we left minimum hatch year blank for these individuals. We performed full pedigree reconstruction using the pedigree module within the function *sequoia*, with genotyping error rate set to 1.5% and complexity of the mating system set to 'simple' to improve low assignment rates (Huisman 2021). We calculated the $\log_{10}$-likelihood ratio of parental assignments (using the function *CalcOHLLR*) to determine the confidence level of parent–parent-offspring configurations. Alongside this, we repeatedly looked for additional pairwise relationships that were not assigned in *sequoia* (by running functions *GetMaybeRel* and *CalcPairLL*). We used this to refine data filtering and *sequoia* parameters to ensure the pedigree reconstruction was optimised and to provide a second source of evidence alongside the final reconstructed pedigree.

2.5 | Nest Site Usage and Mating System

While sequoia considers the likelihood of alternative relationships before assignment during pedigree reconstruction, some relationships may be difficult for the model to interpret, particularly in complex breeding systems and when age data is not available for all individuals (Huisman 2021). In light of this, we elected to assess nest site usage and mating system using only broods for which we had associated field data (hatching location and date). This allowed assignments to be cross-referenced, increasing confidence in our results. To analyse patterns of nest site usage, we used all known broods for which at least one nestling was successfully genotyped and passed our filtering protocol ($n = 32$). To analyse the species' mating system, we examined the genetic relationships between broodmates (full-sibling, half-sibling or neither) in broods for which at least two nestlings had been successfully genotyped and passed our filtering protocol ($n = 19$). The average number of nestlings successfully genotyped for these 19 nests was 2.5 ± 1.84 SD, and they had an average brood size of 3.8 ± 1.13 SD. Therefore 67% of each brood was successfully genotyped on average. Only two of these nests had less than 50% of the brood genotyped. The average brood size for the species is 3.1 ± 1.26 SD (Gautschi et al. 2025). We used instances of repeated nesting (appearance of individuals as the dam/sire of multiple known broods) to examine the mating system employed across a longer time scale.

Due to novel findings regarding the importance of natural nests for the green parrot population (Gautschi et al. 2023, 2025), we examined the samples collected at natural nests in greater depth. We inspected the pedigree to determine whether birds using these sites were also associated with managed nest sites (either as nestlings or breeding adults), patterns of nest use at these nests, and whether the pedigree contained further evidence of unmonitored nesting.

3 | Results

3.1 | Pedigree Reconstruction

Of 146 genotyped individuals, 11 were assigned a genotyped dam, 34 were assigned a genotyped sire, and none were assigned both a genotyped dam and sire (Table S4). The difference in the number of genotyped dams and sires probably reflects the large male sex-bias of adult birds captured during mist-netting (Gautschi et al. 2024). A further 41 genotyped individuals were assigned dummy parents (a non-genotyped individual indicating some connection between genotyped individuals) and 60 were not assigned dummy or genotyped parents. Of these 60 birds, the majority (85%) were adult birds captured in mist-nets between 2021 and 2023.

3.2 | Mating System

In total, 19 broods known from nest monitoring had at least two broodmates represented in the reconstructed pedigree

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(48 genotyped individuals in total). In the pedigree 42/48 (88%) were assigned as a full-sibling of their broodmates. The remaining six individuals from three broods were identified as half-siblings of their broodmate (two pairs related through the dam, and one pair related through the sire). Thus, 2/19 broods showed evidence of extra-pair paternity and 1/19 showed evidence of extra-pair maternity. Overall, the parental $\log_{10}$-likelihood ratio was 4.9 ($n = 48$), representing a moderate level of confidence that the parent–parent-offspring configuration was correct for these parentage assignments (Table S4). No alternative close relationships between broods were identified by running *GetMaybeRel* and *CalcPairLL* conditional on the reconstructed pedigree (Table S5).

3.3 | Reproductive Skew

Thirty-two known broods from 20 nest sites were included in the pedigree (at least one offspring genotyped per nest). In total, 66/146 genotyped samples were connected to these broods: 61 as offspring and five as parents. These 32 broods were produced by 15 females (two genotyped and 13 dummy). However, reproductive output was highly skewed, with six females producing 2–7 broods each, accounting for 24 broods (75% of all broods) and 47 genotyped offspring (77% of all offspring included in the pedigree; Table 1). These broods resulted in an average of 2.92 fledged offspring (Table 1); considerably higher than the average reported by Gautschi et al. (2025) of 1.97. Just two of these females produced 12 of these broods (38%) and 29 of the genotyped offspring (48%). According to nesting records, they produced at least 34 successfully fledged offspring between them (Table 1).

Eighteen males (three genotyped and 15 dummy) were identified as the sires of these same 32 broods. Multiple broods were recorded for 7 males, producing 2–7 broods each, accounting for 23 broods (72% of all broods) and 45 genotyped offspring (74% of all offspring included in the pedigree; Table 2), indicating only slightly lower reproductive skew in males due to mate switching and extra-pair paternity. We do not present the total recorded offspring or successfully fledged offspring for these males, as we are less certain of the paternity than the maternity of non-genotyped individuals. The eight broods produced by a dam and sire that did not appear as parents of another clutch accounted for the remaining 14 genotyped offspring. These had an average brood size of 3.4, of which all survived to fledging.

TABLE 1 | Females identified as the dam of more than one monitored brood.

ID	Genotyped	Broods	Genotyped offspring	Recorded offspring	Fledged offspring	Years	Max. broods/yr	Mates	Nest sites
F1	No	7	15	22	19	2.7	4	1	2
F2	No	5	14	16	15	1.9	4	2	3
2022_48	Yes	4	7	11	10	1.9	3	3	2
F3	No	3	3	9	9	0.4	3	1	2
F12	No	3	5	12	8	1.2	2	1	3
F8	No	2	3	9	9	0.2	2	1	2

Note: Genotyped offspring represents the number of offspring from these broods included in the filtered dataset used for pedigree reconstruction; Recorded offspring represents the combined total brood sizes of the broods linked to the female; Fledged offspring represents the combined total number of fledged offspring from these broods; Years represents the total time period between first and last broods; Max. broods/yr represents the maximum number of broods recorded within a 12-month period; Mates represents the number of sires recorded across all broods; Nest sites represents the number of nest sites used.

TABLE 2 | Males identified as the sire of more than one monitored brood.

ID	Genotyped	Broods	Genotyped offspring	Years	Max. broods/yr	Mates	Nest sites
2023_04	Yes	7	15	2.7	4	1	2
NIGP_129	Yes	3	8	0.4	3	1	3
M5	No	3	5	0.8	3	1	2
M1	No	3	3	0.4	3	1	2
M8	No	3	5	1.2	2	1	3
M6	No	2	3	0.2	2	1	2
M3	No	2	6	0.9	2	1	2

Note: Genotyped offspring represents the number of offspring from these broods included in the filtered dataset used for pedigree reconstruction; Years represents the total time period between first and last broods; Max. broods/yr represents the maximum number of broods recorded within a 12-month period; Mates represents the number of dams recorded across all broods; Nest sites represents the number of nest sites used.

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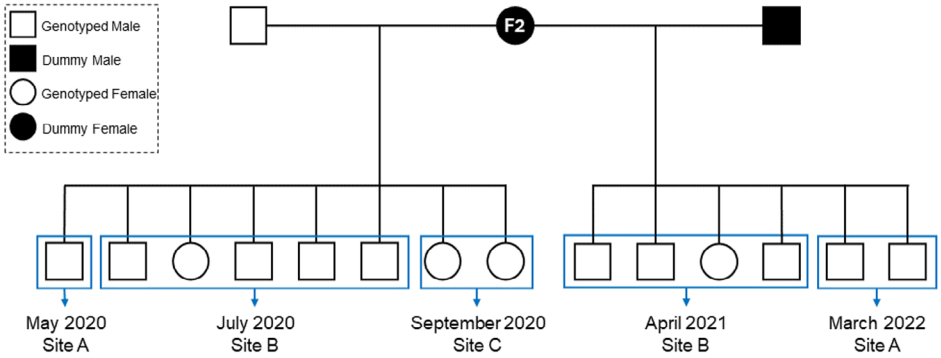


FIGURE 1 | Family tree showing the mates and offspring of dummy (non-genotyped) female F2 from five broods assigned to her in the reconstructed pedigree. Dates represent the month in which samples were collected from nestlings for each brood. This figure only includes sampled offspring that were included in the reconstructed pedigree.

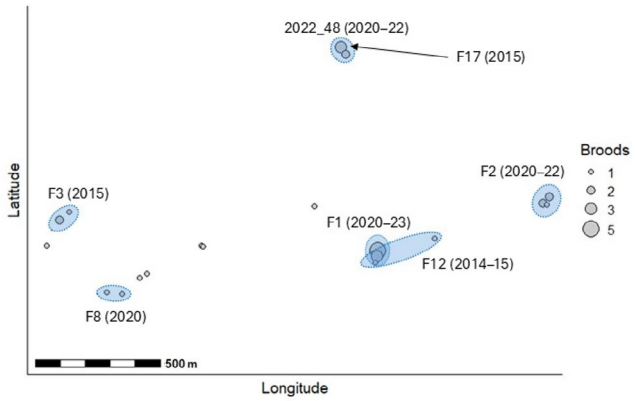


FIGURE 2 | Map showing all monitored broods ($n = 32$) represented in the reconstructed pedigree. The size of the grey circles is proportional to the number of broods produced at each nest site. Blue ellipses represent a cluster of nests used by a female, and the year(s) in which nesting occurred is represented in parentheses. The label for F17 (2015) represents a single nesting attempt from this female within a cluster occupied by female 2022_48. This map does not include nest sites and broods that were not represented in the reconstructed pedigree. Latitude and longitude are not disclosed due to the sensitive nature of nest site locations.

3.4 | Patterns of Nest Usage

The six females for which multiple broods were recorded used 2–3 nest sites each, with four of six females found to use the same nest site more than once. Nest sites used by the same female were in close proximity, with the maximum distance between sites ranging from approximately 20 to 250 m (Figure 2). Breeding was recorded for these females over an average of 1.4 years (range 0.2–2.7 years; Table 1) and they were recorded producing up to four successful broods within a 12-month period (Table 1). Only two nest sites were found to be used by completely different pairs over time; however, both instances were at least five years apart. Almost identical patterns of nest usage were observed for male birds; however, they were recorded breeding over a shorter period of time on average (0.9 years) due to mate switching by females (Table 2). An example family tree from our analysis, showing a dummy (non-genotyped) female producing four broods across three nest sites over a 12-month period and exhibiting mate switching behaviour, is presented in Figure 1. The spatial distribution of all nest sites represented in the reconstructed pedigree, showing the number of broods at each site and nest clusters used by each female, is presented in Figure 2.

3.5 | Samples From Natural Nests

Three samples obtained from natural nest sites were included in the pedigree. Two of these samples came from a natural nest site on private property. The first was collected in February 2022 when a recently fledged bird (2022_56) was killed by a cat near the site. The second sample came from a female bird (2022_79) that was attacked on the same nest by a black rat *Rattus rattus* two months later (see Gautschi et al. (2025) for further details). These two birds were identified as parent-offspring in the reconstructed pedigree, confirming that both nesting attempts involved the same female. The third sample (2022_63) was collected from a natural nest within the national park in May 2022, in which an attempted predation event was assumed to have occurred due to the presence of many feathers within the nest hollow (see Gautschi et al. (2025) for further details). The reconstructed pedigree identified this female as the dam of three individuals captured in mist-nets in 2022 and 2023 (2022_27, 2023_06B and 2023_10). These birds are not known from nest monitoring in the national park, adding to recent evidence that green parrots are reproducing in natural unmonitored nest sites in addition to the nests monitored by park staff (Gautschi et al. 2023).

4 | Discussion

In this study we present a case of reproductive skew in a largely monogamous species driven by the monopolisation of high-quality nest sites by breeding pairs. In the context of our study system, this reproductive skew may have been exacerbated by management actions, which while effective at promoting nesting success, have led to a disproportionate number of breeding attempts by some individuals. We found that among our sample of 32 broods from known nests, 75% were produced by just six females, while nine females were responsible for the remaining 25%. Males showed similar patterns to females. Thus,

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reproductive output appears to be skewed for both sexes. Our results indicate that females repeatedly use clusters of two to three predator-proofed nest sites and are capable of successfully breeding up to four times over a 12-month period, effectively monopolising these sites. While most broods exhibited monogamy, evidence of extra-pair maternity, extra-pair paternity, and mate switching was also present. We also found further evidence indicating that green parrots have been breeding successfully in natural, unprotected nest sites (Gautschi et al. 2023, 2025). Here we discuss novel insights gained from our pedigree reconstruction, their implications for the future conservation management of the Norfolk Island green parrot and lessons for the management of other small, threatened populations that could be subject to similar mechanisms.

4.1 | Nest Usage Patterns and Reproductive Skew

Our results indicate that breeding female green parrots often return to previously successful breeding locations, both within and between years, and can successfully produce up to four broods in a 12-month period. Nest site fidelity is commonly observed in parrots and has been linked to previous success at a nest site (Berkunsky and Reboreda 2009; Salinas-Melgoza et al. 2009; Saunders et al. 2018; Dawson Pell et al. 2021). Green parrot females were most commonly recorded using a cluster of two to three nest sites, rather than a single nest site. However, our sample also shows repeated nesting attempts at the same nest site within just a few months, suggesting a willingness to re-use nest sites within a short period of time. This supports previous observational data on green parrot nest site use (Hicks and Preece 1991; Hill 2002). In all cases females monopolised high-quality nest sites, with no other female using the same nest site within close temporal proximity (except for the single instance of extra-pair maternity). While we found two instances of the same nest being used by completely different pairs, these nesting attempts were more than five years apart. Our sample was skewed towards a small number of females, with six of 15 females being responsible for 75% of broods and 77% of genotyped offspring (and a further subset of just two females being responsible for 38% of broods and 48% of genotyped offspring). Males showed similar patterns to females regarding nest clustering, repeated nesting attempts and reproductive skew; however, these aspects were slightly less pronounced due to mate switching by female birds. It is important to consider that there were large temporal gaps in the collection of genetic samples (e.g., 2015 to 2019) and collecting data from each known nest and each nestling was not always possible. Thus, while our sample does not provide an in-depth analysis of all nesting activity, it does provide an informative overview of nest usage patterns in the suite of nests subject to intensive management and monitoring, which are of great importance to the species' conservation.

Lifetime reproductive output often varies considerably between individuals within a population due to reproductive fitness or stochasticity (van Daalen and Caswell 2017). This can present issues for small populations by reducing the effective population size and thus negatively impacting population viability (Anthony and Blumstein 2000; Miller et al. 2009). Reduced genetic diversity can also limit adaptive potential (Willi et al. 2006), compromising the ability of species to persist in the face of complex and ever-changing threats. The green parrot already has a small estimated effective population size of just 44, well below the minimum effective population size considered necessary to minimise inbreeding depression and retain evolutionary potential (Frankham et al. 2014). Thus, it is critical to avoid further erosion of genetic diversity, and all efforts should be made to manage the breeding of the species in a way that minimises reproductive skew.

4.2 | Mating System

Our results indicated that green parrots are predominantly genetically monogamous. However, some deviations from monogamy were recorded, which could slightly reduce reproductive skew by providing breeding opportunities for a larger number of individuals. Of 19 broods with more than one offspring genotyped, two broods (10.5%) showed evidence of extra-pair paternity. As we were often unable to sample and/or genotype all members of a brood, this is a conservative estimate of extra-pair paternity. Extra-pair paternity is relatively common in birds, even among socially monogamous species; recorded in approximately three quarters of socially monogamous species, and on average occurring in 33% of broods and accounting for 19% of offspring (Brouwer and Griffith 2019). Among socially monogamous parrots, rates of extra-pair paternity are highly variable, with some species exhibiting no extra-pair maternity (e.g., burrowing parrots *Cyanoliseus patagonus* (Masello et al. 2002); crimson rosellas *Platycercus elegans* (Eastwood et al. 2018)), and others displaying extra-pair paternity in up to 50% of nests (e.g., swift parrots *Lathamus discolor* (Heinsohn et al. 2019)).

One of the broods in our sample showed evidence of extra-pair maternity. This was supported by field data, which indicated that the half-siblings differed in age by at least one week; an abnormal egg-laying interval for a nesting female. This could represent a case of quasi-parasitism or conspecific brood parasitism (egg-dumping) (Griffith et al. 2004; Lyon and Eadie 2008). Quasi-parasitism, in which a male facilitates the laying of an egg in the nest by an extra-pair female with whom he has mated, is rare, but has been found to occur in some socially monogamous bird species (Griffith et al. 2004; Li et al. 2009; Petrželková et al. 2015). Conspecific brood parasitism, in which a female lays an egg among the clutch of an unrelated pair of the same species, is much more frequently observed (Lyon and Eadie 2008) and is more common than quasi-parasitism among parrots (e.g., Masello et al. 2002; Martínez et al. 2013; Eastwood et al. 2018; Stojanovic et al. 2023). However, without high-quality associated behavioural data, the actual cause of this instance of extra-pair maternity cannot be determined and alternative explanations such as rapid mate switching cannot be ruled out (Griffith et al. 2004; Osorio-Beristain et al. 2006).

Two of six females identified as the dam of more than one brood switched mates between nesting attempts. For one of these females (Female F2), we captured and sampled her first mate after a brood had already been produced with her new mate, indicating that this was a case of divorce rather than widowing. Divorce is relatively common among birds (Culina et al. 2015). In fact, Jeschke and Kokko (2008) found an annual divorce rate of nearly 24% among 158 avian species. A high rate of mate

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switching has also been found in socially monogamous parrots such as the crimson rosella *Platycercus elegans* (32%; Eastwood et al. 2018). However, in other parrots, pair bond fidelity is reportedly much higher (Beissinger 2008). Due to our small sample of repeat nesting of females, we cannot provide an accurate estimate of mate switching prevalence for the green parrot; however, the two instances found in our sample of six females suggest it does occur at some level.

4.3 | Implications for Management

Our finding that breeding females (and their usually monogamous mate) repeatedly use a cluster of two to three nest sites and can breed up to four times in a 12-month period has important implications for the use of predator-proofed nest sites to support breeding birds. For over three decades, the single green parrot population on Norfolk Island has been supported through the provision of predator-proofed nest sites (Hicks and Greenwood 1989; Gautschi et al. 2022, 2025). Predator-proofed nest sites often occur in clusters, limiting the number of breeding pairs that have access to these nests. As suitable predator-proofed nest sites result in higher rates of nest survival than unmanaged nests (Gautschi et al. 2025), breeders in areas with such sites are receiving a disproportionate amount of management support compared with birds nesting in natural sites elsewhere. This likely contributes to the reproductive skew observed in this study. While in theory this could improve offspring fitness if fitter individuals gain access to better breeding resources, any benefits are likely to be far outweighed by the loss of genetic diversity in such a small population. Thus, steps should be taken to minimise reproductive skew by supporting more breeding adults within the Norfolk Island National Park. This may be achieved by distributing predator-proofed nest sites more evenly throughout the national park. Our results indicate that green parrots are capable of reusing a single nest site within a short period of time. Thus, reducing nest site clustering is unlikely to limit their breeding potential but could greatly improve the quality of breeding sites available to other breeding adults, without necessarily increasing the number of nests needing to be maintained and monitored. More breeding adults could also be supported through effective predator control, which may allow greater green parrot breeding success in natural nests across the island (Gautschi et al. 2023). Indeed, the discovery of a parent-offspring relationship between a female bird associated with a natural nest site and three adult males captured in mist-nets supports the idea that green parrots are capable of successful breeding in unprotected sites under the current predator control regime (Gautschi et al. 2023, 2025).

5 | Conclusion

We present a case of reproductive skew driven by unequal access to breeding resources. While primarily resulting from a limited number of suitable breeding sites following extensive habitat loss and the introduction of mammalian predators, this reproductive skew is likely to be exacerbated by management actions that offer high-quality breeding resources, in the form of multiple predator-proofed nests, to a small number of breeding adults. While these actions have been crucial for the green parrot's recent demographic recovery (Ortiz-Catedral et al. 2018), our study shows that these intensive management actions could have unintended genetic consequences for the population.

The resource-driven reproductive skew observed in this study is unlikely to be specific to the Norfolk Island green parrot and is probably an understudied phenomenon in threatened species. Furthermore, conservation efforts worldwide are limited by resource restraints (Bottrill et al. 2008), leading not only to inequitable support between species (Guénard et al. 2025), but also inevitably between individuals. Our study highlights the need to consider the genetic consequences of intensive conservation management actions on an ongoing basis to ensure they are benefiting both short-term and long-term population viability. To build on our findings, we encourage further analysis of the interaction between management actions and reproductive skew in other small, threatened populations.

Author Contributions

D.G., R.H., D.S. and L.E.N. conceived and designed the research. M.W., D.G., R.H., L.O.-C., N.A.M., D.S., E.D.D. and R.C. undertook field data collection. D.G. performed DNA extractions. D.G., D.S. and L.E.N. performed data analysis. D.G., R.H., D.S., L.E.N., N.A.M., L.O.-C., R.C., E.D.D., P.O. and M.W. wrote and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Ethics Statement

Fieldwork was performed under Australian National University Animal Ethics Committee approval (A2020_13) and a permit to conduct scientific research in a Commonwealth reserve, or was conducted as part of ongoing management and monitoring by Norfolk Island National Park under the *Norfolk Island National Park and Norfolk Island Botanic Garden Management Plan 2008–2018* (Director of National Parks 2008) and the *Norfolk Island National Park and Norfolk Island Botanic Garden Management Plan 2020* (Director of National Parks 2020). This research

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supports the objectives of the *Norfolk Island Region Threatened Species Recovery Plan* (Director of National Parks 2010; Commonwealth of Australia 2025).

Data Availability Statement

The datasets generated during and/or analysed during the current study contain sensitive information on an endangered species. Enquiries regarding access to data should be directed to the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Details of the 48 newly sequenced genetic samples included in this study, in addition to samples previously sequenced as part of Gautschi et al. (2024). **Table S2:** The six single nucleotide polymorphisms (SNPs) identified as sex-linked loci in the dartR package, for which all molecularly sexed individuals (110 males and 51 females) returned data, and female heterozygosity and male heterozygosity were 100% and 0% respectively. **Table S3:** The 146 genotyped individuals included in the reconstructed pedigree by year of sample collection and sex. **Table S4:** Reconstructed pedigree showing brood ID (Brood), brood year (Year), nest site ID (Site), parentage assignments (Dam and Sire), associated $\log_{10}$-likelihood ratios (LLRdam, LLRsire and LLRpair), opposite homozygote pairs (OHdam and OHsire) and Mendelian errors (MEpair) produced using the functions *sequoia* and *CalcOHLLR* in the sequoia package. **Table S5:** Results from *GetMaybeRel* and *CalcPairLL* in the sequoia package, showing possible missed relationships and $\log_{10}$-likelihoods conditional on the reconstructed pedigree. Columns 3 to 9 represent Parent-offspring (PO), Full sibling (FO), Half sibling (HS), Grandparent (GP), Full avuncular (FA), Half avuncular (HA) and Unrelated (U). TopRel indicates the most likely relationship between ID1 and ID2 and LLR represents the $\log_{10}$-likelihood ratio between this relationship and the next most likely relationship.

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