RESEARCH ARTICLE

Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot

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Abstract

1. Sex-biased mortality can lead to altered adult sex ratios (ASRs), which may in turn lead to harassment and lower fitness of the rarer sex and changes in the mating system. Female critically endangered swift parrots (*Lathamus discolor*) suffer high predation while nesting due to an introduced mammalian predator, the sugar glider (*Petaurus breviceps*). High predation on females is causing severe population decline alongside strongly biased adult sex ratios (≥73% male).

2. Our 6-year study showed that 50.5% of critically endangered swift parrot nests had shared paternity although the birds remained socially monogamous. Shared paternity increased significantly with the local rate of predation on breeding females, suggesting that rates of shared paternity increased when the ASR became more biased.

3. Nests that were not predated produced fewer fledglings as the local ASR became more male-biased possibly due to higher interference during nesting from unpaired males.

4. Population viability analyses showed that part of the predicted decline in the swift parrot population is due to reduced reproductive success when paternity is shared. The models predicted that the population would decline by 89.4% over three generations if the birds maintained the lowest observed rate of shared paternity. This compares with predicted population reductions of 92.1–94.9% under higher rates of shared paternity.

5. We conclude that biases in the ASR, in this case caused by sex-specific predation from an introduced predator, can lead to changes in the mating system and negative impacts on both individual fitness and long-term population viability.

KEYWORDS
adult sex ratio, fitness, *Lathamus discolor*, parrot, population viability, shared paternity

1 | INTRODUCTION

Anthropogenic threats to wild populations may impact differentially on individuals, biasing mortality in relation to age, size or sex (Boukal & Krivan, 2008; Garcia et al., 2012). When such mortality is sex-biased, the adult sex ratio (ASR) may become skewed with potentially severe consequences for population stability (Boukal & Krivan, 2008). Although theory suggests that the impacts on individuals and populations of fluctuations in the ASR of undisturbed wild populations are buffered by higher intra-sexual competition in the abundant sex (Clutton-Brock, Coulson, Milner-Gulland, Thomson, & Armstrong, 2002; Fisher, 1930; Greenwood, 1980), empirical studies

have shown that increased male bias can lead to suppressed survival and reproduction in females. Such negative effects on females were demonstrated experimentally in common lizards (*Lacerta vivipara*) which had more injuries, higher mortality and fewer offspring when ASRs were male-biased (Le Galliard, Fitze, Ferrière, & Clobert, 2005). However, other studies have failed to find such effects on female fitness or demography in spite of clear and sometimes dramatic evidence that harassment of females increases when the ASR is male-biased (Ewen, Thorogood, & Armstrong, 2011).

Greater competition by males for females due to biased ASRs may also lead to changes in the mating system, primarily from monogamy to polyandry. Social polyandry is the rarest of avian mating systems and falls into two distinct categories depending on whether the females mate sequentially with single males who then care for the clutch alone (classical polyandry), or with multiple males who care for the clutch together (cooperative polyandry, Faaborg & Patterson, 1981; Oring, 1986). Whereas classical polyandry is a fixed mating system for a small proportion of bird species, cooperative polyandry appears to be more flexible within species, occurring when either females or the resources they need for nesting are scarce, which may then lead to males sharing females (Hartley & Davies, 1994). Even large, long-lived taxa that are normally monogamous can change to cooperative polyandry when the ASR becomes dramatically male-biased (Carrete, Donazar, Margalida, & Bertran, 2013; Heinsohn, Ebert, Legge, & Peakall, 2007; Janssen, Arcese, Sloan, & Jewell, 2008). In addition, many avian species exhibit genetic but not social polyandry as a result of extra-pair copulations by females (Westneat & Stewart, 2003).

Polyandry may increase both intra-sexual conflict for mating opportunities and inter-sexual conflict such that males and females have differing optimal outcomes, for example, in the amount of male care of offspring (Kokko & Jennions, 2012) and may lead to male adaptations that are harmful to females (Arnqvist & Rowe, 2005). In Seychelles magpie robins (*Copsychus sechellarum*), intraspecific conflict was shown to slow down population recovery, whereas the addition of an extra male to breeding pairs of bearded vultures, *Gypaetus barbatus*, showed that males can behave in their own reproductive interests at the expense of females who suffered lower breeding success in trios (Carrete et al., 2013). Although theoretical models and some empirical research suggest that inter-sexual conflict may become especially harmful as male bias in the ASR increases, there are still few examples that consider the full life-history consequences and the impact on population growth and viability (Holman & Kokko, 2013).

Male-biased adult sex ratios are the norm in birds (Donald, 2007), yet most bird species remain socially monogamous, and polyandry when it occurs is usually genetic rather than social (Gowaty, 1996; Lack, 1968). Parrots as a taxon are considered to be mostly socially and genetically monogamous (Toft & Wright, 2015) but have been shown in a few circumstances to adopt cooperative polyandry when females have limited breeding opportunities placing further constraints on males (Ekstrom, Burke, Randrianaina, & Birkhead, 2007; Heinsohn et al., 2007). In this paper, we outline a revealing case of a parrot species that appears to have adopted high rates of genetic polyandry under recent circumstances where anthropogenic influences have dramatically altered the ASR in favour of males. Introduced sugar gliders (*Petaurus breviceps*) kill breeding female swift parrots (*Lathamus discolor*) in their nest hollows, usually while they are incubating eggs, across breeding sites in Tasmania (Stojanovic, Webb, Alderman, Porfirio, & Heinsohn, 2014). Breeding males have not been observed to suffer additional mortality from sugar gliders. The birds are nomadic and gain a limited reprieve from sugar glider predation in occasional years when ephemeral food resources allow them to nest on predator free islands (Webb et al., 2014) but the mean annual mortality of adult females is none the less extremely high at over 50% per year. We have demonstrated via population viability analysis (PVA) that the swift parrot population is in dramatic decline from the impact of predation alone with a projected decrease of over 90% in 16 years (Heinsohn et al., 2015).

Here, we use data from a 6-year study to test the prediction that biases in the swift parrot ASR created by sex-specific predation push the mating system from monogamy towards genetic polyandry, and that genetic polyandry in turn entails negative consequences for reproductive success and population viability (Holman & Kokko, 2013). Our analysis provides an important demonstration that, together with the direct impacts of increased mortality on adult females and nestlings, biases induced in the ASR can have further negative impacts on long-term population viability via costs associated with increased rates of polyandrous mating.

2 | MATERIALS AND METHODS

2.1 | Study system

Swift parrots are a socially monogamous, migratory species that breeds along the eastern seaboard of the large island of Tasmania off southern Australia, and two smaller islands (Bruny and Maria) close to the east coast of Tasmania (Forshaw, 2002). They require overlap of ephemeral nectar food resources (flowering *Eucalyptus globulus* and *E. ovata*) and nesting habitat (tree cavities in old growth forest) for successful breeding (Webb et al., 2017). Swift parrots are nomadic within their breeding range to the extent that breeding may occur anywhere in eastern Tasmania where an appropriate combination of habitats occurs each year (Figure 1). However, in any given breeding season, only a fraction of the broader breeding range is occupied depending on where food is available (Webb et al., 2017). A recent study confirmed a lack of population genetic structure in swift parrots with the whole population likely to move between breeding locations each year (Stojanovic, Cook, et al., 2018; Stojanovic, Olah, Webb, Peakall, & Heinsohn, 2018). The present study was conducted across a range of forest types over most of the breeding range between 2010 and 2016 (Figure 1).

Swift parrots lay a clutch of three to (rarely) six eggs. Females perform all incubation and care of nestlings up to 10 days after hatching; however, males make large contributions to feeding nestlings after this time. Extra-pair males have been observed courtship feeding the breeding female but these are often chased aggressively from the nest area by the pair male (unpublished data).

Nesting swift parrots suffer intense predation by sugar gliders (Stojanovic et al., 2014). Sugar gliders are native to continental
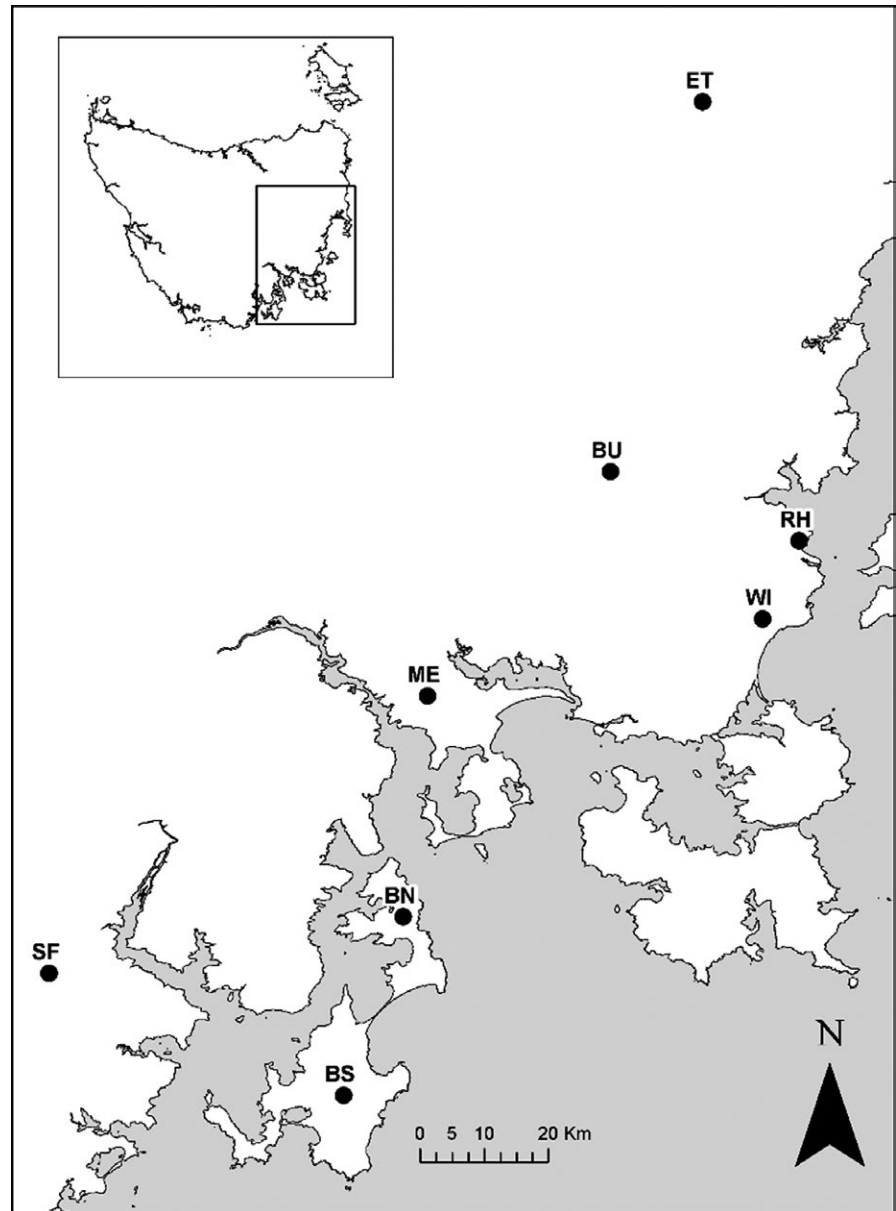
FIGURE 1 Map of the study area in Tasmania, Australia. Populations where swift parrot genetic samples were collected were as follows: North (BN) and South Bruny Island (BS), Buckland (BU), Eastern Tiers (ET), Meehan Range (ME), Rheban (RH), Southern Forests (SF) and Wielangta (WI)

Australia, but were introduced to Tasmania as early as the 19th century (Campbell et al., 2018; Gunn, 1851; Heinsohn, 2004). Importantly, sugar gliders are now present at all swift parrot breeding sites thus far monitored on the main island of Tasmania, although rates of predation on breeding females vary considerably. They are absent from Bruny and Maria Islands where the swift parrots sometimes breed (Stojanovic et al., 2014; Figure 1).

2.2 | Genetic sample collection

DNA was analysed for 371 nestlings from 85 nests that had more than one nestling over six breeding seasons. Genetic samples were not available for Maria Island or Devonport, but all other sites considered by Heinsohn et al. (2015) were included in this study. Swift parrot nests were identified across the study area during standardised monitoring (Webb et al., 2014). Nests were identified using behavioural cues of swift parrots and accessed using single rope climbing techniques (Stojanovic et al., 2015). Nestling swift parrots were temporarily removed from their nest cavities (Stojanovic et al., 2015), and blood was collected using brachial venepuncture. Blood was stored on FTA paper (Whatman™).

2.3 | DNA extraction and microsatellite genotyping

DNA extraction from blood stored on FTA paper was performed following the standard procedure for nucleated erythrocytes (Smith & Burgoyne, 2004). We used seven microsatellite loci previously used for swift parrots: Cfor1415, Cfor2627 (Chan, 2005), pCl3 (Carneiro, Jimenez, Vergara, & White, 2013), and SCMA 01, SCMA 04, SCMA 07, SCMA 29 (Olah, Heinsohn, Brightsmith, Espinoza, & Peakall, 2016; Stojanovic, Cook, et al., 2018; Stojanovic, Olah, et al., 2018). Laboratory analysis followed Olah et al. (2016). Briefly, M13 PCR tags

were attached to all forward primers (Schuelke, 2000) and all loci were amplified individually. PCR products were multiplexed in the same lane using different fluorescent tags and genotyped on an ABI 3130XL sequencer (Applied Biosystem). We used a negative control for contamination checking and a positive control to ensure consistent size scoring across all genotyping runs. Results were scored using GENEIOUS version R6 (Kearse et al., 2012) with 112 full genotypes constructed across seven loci. Approximately, 25% of the samples were repeated to estimate genotyping errors. Loci were screened for the presence of null alleles across all samples with MICROCHECKER 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004).

2.4 | Genetic relatedness classification and detection of multiple paternity

For classification of relatedness, we used a subset of the total samples (N = 291) that contained only nestlings with a maximum of one missing locus and with at least two siblings per nest. We followed the two-program congruency approach described in Turjeman et al. (2016) to determine relationships among nestlings. First, we used the software program ML-RELATE (Kalinowski, Wagner, & Taper, 2006) to determine the most likely pairwise relationships. Then, we used the program COLONY 2 (Jones & Wang, 2010) to confirm or discard relationship classifications. We used the following relationship categories for pairwise relatedness between siblings in each software: full-siblings (FS), half-siblings (HS), unrelated (U), not full-siblings (NFS; where "full-siblings" relationship could be rejected but differentiation between the categories of "half-siblings" and "unrelated" could not be made) and non-conclusive (NC) cases where conclusions could not be reached. For both software programs, we used the settings described in (Turjeman et al., 2016). When ML-RELATE and COLONY 2 did not give the same results, we used the following rules: (a) when ML-RELATE showed an NFS relationship and COLONY 2 showed a HS, we accepted HS; (b) when ML-RELATE showed NC, we accepted the COLONY 2 result. We classified nests as FS (if all sibling pairs had FS relationships) or HS (if at least one sibling pair had a HS or NFS relationship). Nests with more than 50% NC relationships were not classified.

We also looked for extra cases of multiple paternity that were not detected by the relatedness analysis above. We used the number of different alleles within families, and looked for cases where the number of alleles exceeded the maximum possible under a scenario of single paternity. These included instances where all individuals were heterozygous and the number of different alleles exceeds four, or one nestling was homozygous and the number of different alleles exceeds three. We used Fisher's exact test comparing FS nests to any other categories to see whether swift parrots deviate significantly from genetic monogamy (allowing a 1% of EPC of all copulations).

2.5 | Adult sex ratios, reproductive success and population viability analyses

Following the methods of Stojanovic et al. (2014) using the program MARK (White & Burnham, 1999), we compiled mortality rates of

nesting females due to predation by sugar gliders for seven regions shown in Figure 1 (north and south Bruny Island were combined into one region for this purpose). We measured fledging success for all monitored nests as the number of nestlings expected to fledge as of the last nest inspection.

We modified previously published population viability analyses (Heinsohn et al., 2015) using VORTEX 10 (Lacy & Pollak, 2012) to estimate (a) the population-wide ASR at the beginning of each breeding season, and (b) the long-term impact on population size of monogamous versus polyandrous breeding. We used the settings of the preferred model from our previous analysis, see Model 2 and Table 1 in Heinsohn et al. (2015), as these comprise a realistic portrayal of the population including the mean proportion of the birds that nested at high predation sites (on mainland Tasmania) versus low predation sites on offshore islands.

To estimate the population-wide ASR for each year of the study, we used Model 2 in Heinsohn et al. (2015) to estimate the number of adult (2 years old and over) males and females remaining at the end of each breeding season (i.e., after predation on nesting females). We used these values to estimate the population-wide proportion of adult males at the start of the next breeding season from 2010 until 2015. The published PVAs (Heinsohn et al., 2015) used mean predation rates on adult females of 56.4% over a number of years in a largely deterministic model. However in this paper, we used the mortality rates specific to each year, calculated from the proportion of the parrot population that nested in predator infested habitat, to determine changes to male and female numbers, and hence annual variations in the ASR, more precisely. Annual adult female mortality rates, including background mortality and that caused by sugar gliders, calculated for use in the models were as follows: 2010, 56.4%; 2011, 58.5%; 2012, 61.7%; 2013, 52.4%; 2014, 53.0%; and 2015, 61.7%.

We used Generalised Linear Models in the statistical package Genstat (12th Edition) (Payne, Murray, Harding, Baird, & Soutar, 2009) to analyse spatial and temporal factors affecting the frequency of shared paternity, and the impact of skewed adult sex ratios and shared paternity on reproductive success. Nests were assigned a binary response (multiple paternity = yes, single paternity = no) and analysed in a GLM with binomial link function. The number of fledglings produced at each nest was analysed with a GLM using a Poisson link function. The number of eggs/nestlings was included as a variate in all models. Time of season was tested and controlled for in all analyses by including as a variate the number of days since the first breeding attempt by any bird within the same season. Nest hollows were not known to be re-used within or between seasons so were only used once in each analysis.

We constructed three new PVA models to isolate the impact on the population projection of increased levels of shared paternity associated with higher mortality of females. We kept the high predation rate on adult females and other settings, including a starting population of 2158 individuals, and other values used in Model 2 of Heinsohn et al. (2015) but adjusted population-wide reproductive success to three levels. Model A explored population size after 16 years (3 generations) if shared paternity occurred at the lowest rate observed in this

TABLE 1 Summary of microsatellite diversity showing the number of alleles (N_a), effective number of different alleles (N_e), observed heterozygosity (H_O), expected heterozygosity (H_E), fixation index (F), probability of identity (PI) and probability of identity for siblings (PI_{sibs})

Locus	N_{Tot}	N_{Sub}	N_a	N_e	H_O	H_E	F	PI	PI_{sibs}
Cl3	349	111	5	1.6	0.369	0.395	0.065	0.431	0.660
C1415	346	110	6	3.1	0.636	0.681	0.065	0.154	0.448
SCMA04	310	98	17	6.5	0.867	0.847	−0.024	0.036	0.336
C2627	350	111	17	7.0	0.892	0.857	−0.041	0.035	0.330
SCMA01	346	108	20	10.2	0.870	0.902	0.035	0.017	0.303
SCMA07	331	104	8	2.8	0.644	0.651	0.011	0.149	0.462
SCMA29	304	94	3	1.8	0.404	0.448	0.098	0.392	0.624
Over all loci								8.4E-08	2.9E-03
Mean			10.9	4.8	0.669	0.683	0.030		
SE			2.6	1.2	0.083	0.076	0.019		

All calculations were performed in GenAlEx (Peakall & Smouse, 2006, 2012) based on a subsample ($N = 111$) of the 350 genotyped individuals containing a single randomly selected representative from each nest. The number of successfully genotyped samples at each locus is shown for the total (N_{Tot}) and the subsample (N_{Sub}).

study (33%) and consequently the population enjoyed higher breeding success (see Results). Model B examined the final population size if shared paternity occurred at the mean levels observed in this study (50.5%). Model C predicted final population size if shared paternity occurred at the highest rate recorded in our study (95%).

3 | RESULTS

3.1 | Population genetics, relatedness and mating system

The total number of alleles per locus ranged between 3 and 20, mean observed heterozygosity was 0.68, while the expected heterozygosity value was 0.683 (Table 1). The variability of all seven microsatellite loci was predicted to recover all unique genotypes even among siblings, over our large sample of individuals ($PI_{sibs(7)} = 0.002$, $N = 94$–111, Table 1).

We analysed a total of 374 pairwise relationships between siblings and found 264 (70.6%) FS and 74 (19.8%) HS relationships, while in 36 (9.6%) cases conclusions could not be reached. Out of the total 85 nests used for this analysis, in 82 cases (96.5%), we successfully classified at least 50% of the siblings per nest. Among these resolved nests, 60% ($N = 49$) contained only full-siblings, while 40% ($N = 33$) contained at least one half-sibling relationship. We reconfirmed seven cases, and found ten extra cases, of multiple paternity using the number of different alleles within families, bringing the number of nests with multiple paternity to 43/85 (50.5%). The proportion of nests with at least one half-sibling was significantly higher than expected under a monogamous breeding strategy (Fisher's exact test, $P < 0.001$).

3.2 | Adult sex ratios, frequency of multiple paternity and impact on reproductive success

The modelled trajectories over the study for adult males and females, and the resulting ASR expressed as proportion of males, are shown in Figure 2. The estimated proportion of males in the adult

population at the start of each breeding season varied little, ranging from 0.73 to 0.75.

Rates of multiple paternity varied significantly across years ($\chi^2_5 = 2.81$, $p = 0.015$) but were not significantly affected by the number of nestlings in the brood (range = 2–5, $\chi^2_1 = 0.54$) or timing of breeding within the season ($\chi^2_1 = 2.08$). There was no significant effect of the limited range of population-wide ASRs reported above on the likelihood of multiple paternity ($\chi^2_1 = 0.94$). However, swift parrots settled to breed in different areas within and between seasons over the study (Webb et al., 2017), and multiple paternity increased significantly at sites where there was higher predation on nesting females ($\chi^2_1 = 4.26$, $p = 0.039$, Figure 3a). This suggests that local changes to the ASR, caused by loss of adult females to predators while nesting, were a determinant of whether polyandrous mating occurred at the remaining nests. The predation rates on breeding females at seven breeding sites used in this analysis, calculated using the program MARK (Stojanovic et al., 2014), are given in the caption to Figure 3. There were no significant interactions between any of the variables presented above ($0.150 < p < 0.980$).

Clutch size did not differ significantly across sites ($\chi^2_1 = 1.67$). However, fewer fledglings were produced at unpredated nests as the site-specific predation rate on adult females increased ($\chi^2_1 = 4.63$, $p = 0.031$, Figure 3b), suggesting that local differences in the ASR caused by loss of adult females to predators while nesting, were a determinant of nest success. There was no significant difference in number of fledglings at single and multiple paternity nests ($\chi^2_1 = 1.90$), or between years ($\chi^2_1 = 2.01$).

3.3 | Impact of shared paternity on population viability

Predicted final population sizes differed significantly between the three modelled PVA scenarios ($p < 0.001$) demonstrating the impact on population size of lower reproductive success associated with shared paternity. Model A, using the reproductive success when
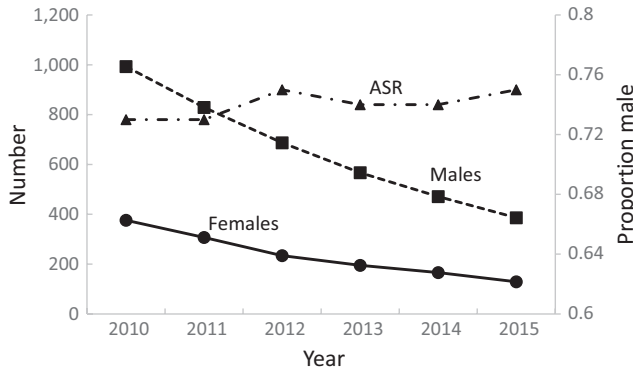
FIGURE 2 The modelled number of adult (2+) males (squares) and females (circles) (left axis) in each of the 6 years in our study and the resulting proportion of adult males (ASR, triangles) (right axis)

rates of shared paternity were lowest, predicted that the swift parrot population would decline by 89.4% over three generations. This compares with a population reduction of 92.1% under mean rates of shared paternity (Model B) and 94.9% if shared paternity is at its highest level observed in this study (Model C).

4 | DISCUSSION

Critically endangered swift parrots are in steep population decline due to the impact of an introduced predator, the sugar glider, that preys on nesting females and their offspring (Heinsohn et al., 2015; Stojanovic et al., 2014). In addition to the direct impact on the remaining population, this study suggests that the strong male bias in the adult sex ratio due to sex-specific predation has further ramifications for individual fitness and population viability. Our results show that swift parrots have an unusually high (50.5% of nests) yet variable rate of shared paternity (genetic polyandry) compared to most parrot species (Toft & Wright, 2015). Although we do not know the extent of shared paternity prior to the introduction of the predator, it is likely that the consistently male-biased ASR (≥73% male) further promotes this form of mating in this species (Emlen & Oring, 1977; Oring, 1986b). Results over our 6-year study support this contention by showing that rates of shared paternity are higher for highly mobile swift parrots when they breed in regions with higher predation on nesting females, and hence with more (within season) male-biased ASRs. Here, we discuss likely causes of the high rate of shared paternity compared to other parrot species, and how the anthropogenically induced sex ratio bias in swift parrots affords an unusual opportunity to isolate the costs of genetic polyandry on individual fitness and population viability (Holman & Kokko, 2013).

Our finding that paternity was shared at 50.5% of swift parrot nests adds to a small number of studies that challenge the traditional view that parrots are largely monogamous (Toft & Wright, 2015). Studies of parrot mating systems using molecular techniques are still few but now include one species with 100% genetic monogamy (burrowing parrots, *Cyanoliseus patagonus*; Masello, Sramko, Quillfeldt, Joerg, & Lubjuhn, 2002), and other socially monogamous
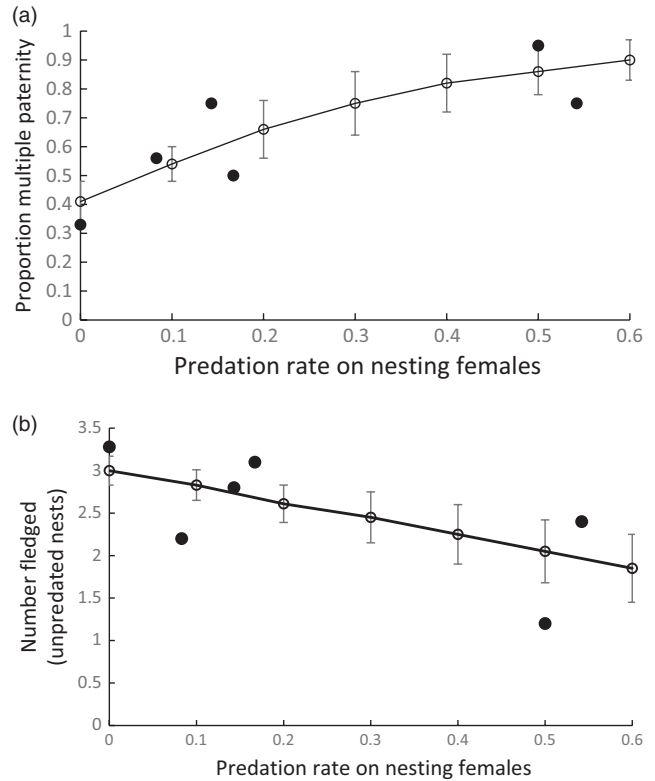

FIGURE 3 (a) observed (closed circles) and predicted proportion (open circles) ± *SE* of nests with multiple paternity against rates of predation on nesting adult females. (b) Mean number of fledglings (closed circles) and number predicted (open circles) ± *SE* for unpredated nests against the site-specific rate of predation on nesting females (NB two sites with predation rate of 0.5, Rheban and Southern Forests, are presented as one value in both Figure 3a,b). The predation rates on breeding females at seven breeding sites used in this analysis, calculated using the program MARK (Stojanovic et al., 2014), were as follows: Bruny Island (0, *n* = 56), Buckland (0.08, *n* = 19), Meehan Range (0.14, *n* = 9), Wielangta (0.17, *n* = 7), Rheban (0.50, *n* = 6), Southern Forests (0.50, *n* = 16), and Eastern Tiers (0.54, *n* = 29)

species with both modest (green-rumped parrotlets, *Forpus passerinus* 14% nests, Beissinger, 2008) and higher rates of shared paternity (40% nests, monk parakeets, *Myiopsitta monachus*, (Martínez, de Aranzamendi, Masello, & Bucher, 2013). A small number of parrot species are also known to have more extreme social and genetic mating systems including lek promiscuity (kakapos, *Strigops habroptilus*, (Merton, Morris, & Atkinson, 1984) and cooperative polyandry and polygynandry (Ekstrom et al., 2007; Heinsohn et al., 2007). The growing body of evidence suggests that parrots as a taxon may display a similar range and frequency of social and genetic mating systems to that seen in Passerines, the bird order now known to be most closely related to parrots (Jarvis et al., 2014). However, the parrot species thus far targeted for molecular analysis of parentage may be skewed towards the more unusual species, and further studies of socially monogamous parrots are required.

The more extreme mating systems found amongst parrots may help in interpreting the causes of high rates of shared paternity in
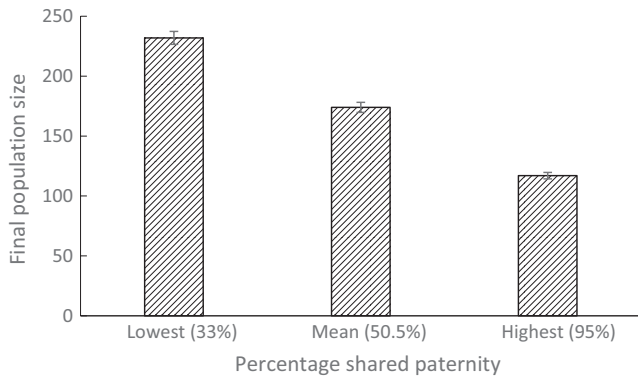
FIGURE 4 Simulated population size (± s/e) after 16 years (3 generations) if swift parrots exhibit the lowest observed rate (33%) of shared paternity (Model A: population decrease = 89.4%), the mean rate (50.5%) of shared paternity reported here, (Model B: population decrease = 92.1%), and the highest rate observed in this study (95%), (Model C: population decrease = 94.9%)

swift parrots. *Eclectus* parrots (*Eclectus roratus*) for example breed polyandrously because limited availability of nest hollows places severe restrictions on the availability of breeding females, and encourages males to share mates, albeit with some conflict (Heinsohn, 2008; Heinsohn et al., 2007). In swift parrots, genetic polyandry increases at breeding sites where female mortality is higher, suggesting that unpaired males target already paired females more when the local ASR becomes more male-biased. It should be noted that swift parrots have not been observed either to live in stable groups as happens in *Eclectus* parrots, or for the males to form coalitions to maximise their chances at achieving mating success (Hartley & Davies, 1994). Instead, social monogamy prevails with the socially paired male aggressively chasing other males away from the nest, even though the females have been observed to accept food surreptitiously from the interlopers and to mate with them (unpublished data). Thus, unlike *Eclectus* parrots and other species (e.g., dunnocks, *Prunella modularis*; Davies, 1992) biases in the ASR appear to promote genetic but not necessarily social polyandry in swift parrots.

The diminished reproductive success of swift parrots when the ASR is male-biased may be driven by heightened inter-locus sexual conflict, or differences between the sexes in optimal breeding behaviour (Holman & Kokko, 2013). The increase in shared paternity seen in these conditions does not increase reproductive success for females, as occurs for example in dunnocks (Davies, 1992), and instead appears to incur a cost to both females and pair males. The remaining females who have avoided predation lose some reproductive success as the ASR becomes more biased (Figure 3b), but pair males suffer greater losses if they also share paternity. Our anecdotal observations suggest that lower reproductive success may be due to greater harassment by additional unpaired males that attempt to courtship feed, and mate with, nesting females. These interlopers are met with frequent aggression by the resident males who chase them from the nest area and may cause important losses of time and energy for the resident pair. Under this scenario, it is possible that females could

accept extra mates without (or with less) cost to their reproduction but resident males, who have more to lose, behave in ways that protect their own optimum outcome at the expense of females. Bearded vulture trios also suffer lower breeding success than pairs but a major difference is that the males seem to co-exist more peacefully (Carrete et al., 2013).

Our study also offers rare insight into how increasing rates of shared paternity, in this case probably driven by biased ASRs, affect population viability. We partitioned the components of predicted population decline in swift parrots due to direct predation from those due to lowered breeding success when the ASR becomes more biased. This analysis predicts that the population of swift parrots will decrease by an additional 2.7% over 16 years due to the impact of lower reproductive success when shared paternity is at 50.5%, and that the decrease could be as much as 5.5% if shared paternity occurs at the highest rates recorded. It is important to note that we do not know the natural rate of shared paternity which may have been much lower before the advent of high sex–specific predation by sugar gliders. Reproductive success may have been even higher in the past if the ASR was more balanced and shared paternity was lower. Population growth rates in other threatened species have also been compromised by biased adult sex ratios but these studies have not evaluated the impact on long-term population trends due to a biased ASR (e.g., lower breeding success) beyond the simple lack of females as mates (Gilroy & Lockwood 2012; Grayson et al. 2014; Steifetten & Dale 2006).

Studies have rarely tested for a link between the degree of polyandry and how this may affect population trajectories (Holman & Kokko, 2013). Within-sex conflict has been implicated in slower population growth rates in Seychelles magpie robins (Lo'pez-Sepulcre, Norris, & Kokko, 2009), and as discussed above, individual fitness and population growth may both decrease in bearded vultures when unmated males join established pairs to breed cooperatively (Carrete et al., 2013). However in hihi, *Notiomystis cincta*, extreme harassment by males of females under highly skewed ASRs appears not to reduce female survival or breeding success (Ewen et al., 2011). In their major review of the consequences of polyandry for population viability, Holman and Kokko (2013) stress that there may be no visible demographic consequences of polyandrous mating if females go on producing more progeny than can survive. Both positive and negative effects of polyandry on demographic parameters may only become apparent once birth and death rates are modified by environmental change. The plummet towards extinction of swift parrots due to an introduced sex-specific predator may offer the necessary circumstances for elucidating the impact of sexual conflict and increased genetic polyandry on individual fitness and population viability. Our study adds to a growing body of studies showing that anthropogenic threats to wild populations may impact differentially on individuals and have further, less obvious, consequences for threatened species (Boukal & Krivan, 2008; Garcia et al., 2012). In the case of swift parrots, measures to limit the impact of sugar gliders (Stojanovic, Cook, et al., 2018; Stojanovic, Olah, et al., 2018) should improve population growth both by limiting female mortality and increasing reproductive rates via higher rates of monogamy.

AUTHORS' CONTRIBUTIONS

R.H., M.W., and D.S. conceived the ideas and designed field methodology; D.S. and M.W. collected the field data; G.O. and R.P. analysed the molecular data; R.H. led the writing of the manuscript with major contributions from G.O., R.P., and D.S. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data from this study have been archived in figshare: https://doi.org/10.6084/m9.figshare.7238081.v1 (Heinsohn, Olah, Webb, Peakall, & Stojanovic, 2018).

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