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RESEARCH ARTICLE

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

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31 Abstract

- 32 1. Sex-biased mortality can lead to altered adult sex ratios (ASRs), which may in turn lead to
33 harassment and lower fitness of the rarer sex and changes in the mating system. Female
34 critically endangered swift parrots (*Lathamus discolor*) suffer high predation while nesting
35 due to an introduced mammalian predator, the sugar glider (*Petaurus breviceps*). High
36 predation on females is causing severe population decline alongside strongly biased adult
37 sex ratios ($\geq 73\%$ male).
- 38 2. Our six year study showed that 50.5% of critically endangered swift parrot nests had
39 shared paternity although the birds remained socially monogamous. Shared paternity
40 increased significantly with the local rate of predation on breeding females, suggesting
41 that rates of shared paternity increased when the ASR became more biased.
- 42 3. Nests that were not predated produced fewer fledglings as the local ASR became more
43 male biased possibly due to higher interference during nesting from unpaired males.
- 44 4. Population viability analyses showed that part of the predicted decline in the swift parrot
45 population is due to reduced reproductive success when paternity is shared. The models
46 predicted that the population would decline by 89.4% over three generations if the birds
47 maintained the lowest observed rate of shared paternity. This compares with predicted
48 population reductions of 92.1 – 94.9% under higher rates of shared paternity.
- 49 5. We conclude that biases in the ASR, in this case caused by sex-specific predation from an
50 introduced predator, can lead to changes in the mating system and negative impacts on
51 both individual fitness and long term population viability.

52

53

54 KEYWORDS

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

56 1 | INTRODUCTION

57

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

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

72
73 Greater competition by males for females due to biased ASRs may also lead to changes in the
74 mating system, primarily from monogamy to polyandry. Social polyandry is the rarest of
75 avian mating systems and falls into two distinct categories depending on whether the females
76 mate sequentially with single males who then care for the clutch alone (classical polyandry),
77 or with multiple males who care for the clutch together (cooperative polyandry, (Faaborg &
78 Patterson 1981; Oring 1986a). Whereas classical polyandry is a fixed mating system for a
79 small proportion of bird species, cooperative polyandry appears to be more flexible within
80 species, occurring when either females or the resources they need for nesting are scarce,
81 which may then lead to males sharing females (Hartley & Davies 1994). Even large, long-
82 lived taxa that are normally monogamous can change to cooperative polyandry when the
83 ASR becomes dramatically male-biased (Heinsohn *et al.* 2007; Janssen *et al.* 2008; Carrete *et*
84 *al.* 2013). In addition, many avian species exhibit genetic but not social polyandry as a result
85 of extra-pair copulations by females (Westneat & Stewart 2003).

86
87 Polyandry may increase both intra-sexual conflict for mating opportunities and inter-sexual
88 conflict such that males and females have differing optimal outcomes, for example in the
89 amount of male care of offspring (Kokko & Jennions 2012) and may lead to male adaptations
90 that are harmful to females (Arnqvist & Rowe 2005). In Seychelles magpie robins
91 (*Copsychus sechellarum*) intraspecific conflict was shown to slow down population recovery,
92 whereas the addition of an extra male to breeding pairs of bearded vultures, *Gypaetus*
93 *barbatus*, showed that males can behave in their own reproductive interests at the expense of
94 females who suffered lower breeding success in trios (Carrete *et al.* 2013). Although
95 theoretical models and some empirical research suggest that inter-sexual conflict may
96 become especially harmful as male bias in the ASR increases, there are still few examples
97 that consider the full life-history consequences and the impact on population growth and
98 viability (Holman & Kokko 2013).

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

118

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

127

128 **2 | MATERIALS AND METHODS**

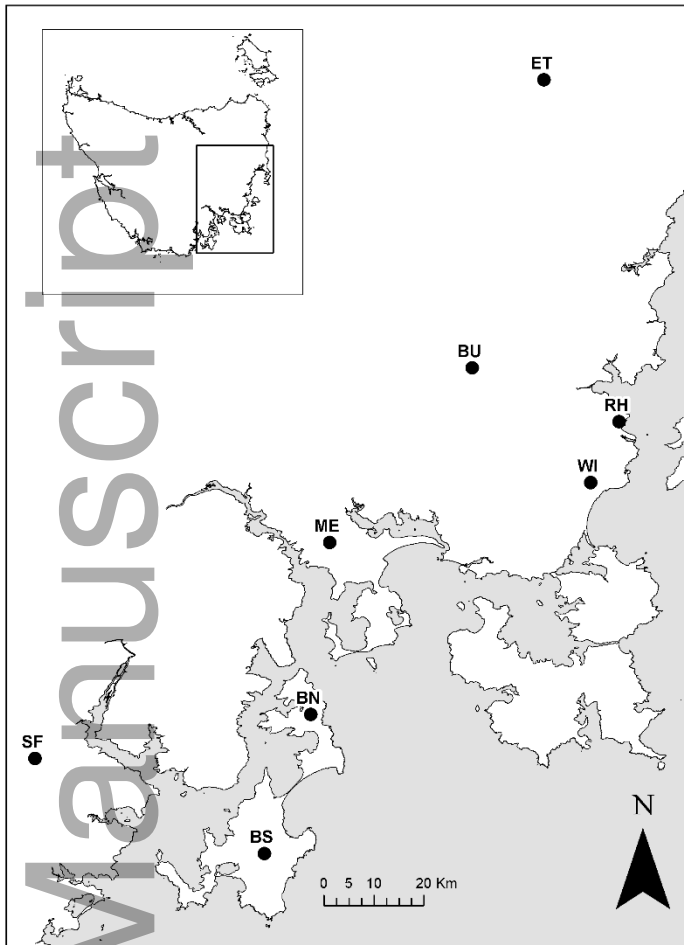
129 **2.1 | Study system**

130 Swift parrots are a socially monogamous, migratory species that breeds along the eastern
131 seaboard of the large island of Tasmania off southern Australia, and two smaller islands
132 (Bruny and Maria) close to the east coast of Tasmania (Forshaw 2002). They require overlap

133 of ephemeral nectar food resources (flowering *Eucalyptus globulus* and *E. ovata*) and nesting
134 habitat (tree cavities in old growth forest) for successful breeding (Webb *et al.* 2017). Swift
135 parrots are nomadic within their breeding range to the extent that breeding may occur
136 anywhere in eastern Tasmania where an appropriate combination of habitats occurs each year
137 (Fig. 1). However, in any given breeding season only a fraction of the broader breeding range
138 is occupied depending on where food is available (Webb *et al.* 2017). A recent study
139 confirmed a lack of population genetic structure in swift parrots with the whole population
140 likely to move between breeding locations each year (Stojanovic *et al.* 2018). The present
141 study was conducted across a range of forest types over most of the breeding range between
142 2010 and 2016 (Fig. 1).

143
144 Swift parrots lay a clutch of three to (rarely) six eggs. Females perform all incubation and
145 care of nestlings up to 10 days after hatching; however males make large contributions to
146 feeding nestlings after this time. Extra-pair males have been observed courtship feeding the
147 breeding female but these are often chased aggressively from the nest area by the pair male
148 (unpublished data).

149
150 Nesting swift parrots suffer intense predation by sugar gliders (Stojanovic *et al.* 2014). Sugar
151 gliders are native to continental Australia, but were introduced to Tasmania as early as the
152 19th century (Gunn 1851; Heinsohn 2004; Campbell *et al.* 2018). Importantly, sugar gliders
153 are now present at all swift parrot breeding sites thus far monitored on the main island of
154 Tasmania, although rates of predation on breeding females vary considerably. They are
155 absent from Bruny and Maria Islands where the swift parrots sometimes breed (Stojanovic *et*
156 *al.* 2014) (Fig. 1).



157

158 **FIGURE 1** Map of the study area in Tasmania, Australia. Populations where swift parrot
159 genetic samples were collected were: North (BN) and South Bruny Island (BS), Buckland
160 (BU), Eastern Tiers (ET), Meehan Range (ME), Rheban (RH), Southern Forests (SF), and
161 Wielangta (WI).

162

163 **2.2 | Genetic sample collection**

164 DNA was analysed for 371 nestlings from 85 nests that had more than one nestling over six
165 breeding seasons. Genetic samples were not available for Maria Island or Devonport, but all
166 other sites considered by Heinsohn *et al.* (2015) were included in this study. Swift parrot
167 nests were identified across the study area during standardised monitoring (Webb *et al.*,
168 2014). Nests were identified using behavioural cues of swift parrots and accessed using
169 single rope climbing techniques (Stojanovic *et al.* 2015). Nestling swift parrots were

170 temporarily removed from their nest cavities (Stojanovic *et al.* 2015) and blood was collected
171 using brachial venepuncture. Blood was stored on FTA paper (Whatman™).

172

173 **2.3 | DNA extraction and microsatellite genotyping**

174 DNA extraction from blood stored on FTA paper was performed following the standard
175 procedure for nucleated erythrocytes (Smith & Burgoyne 2004). We used seven
176 microsatellite loci previously used for swift parrots: Cfor1415, Cfor2627 (Chan 2005), pC13
177 (Carneiro *et al.* 2013), and SCMA 01, SCMA 04, SCMA 07, SCMA 29 (Olah *et al.* 2016;
178 Stojanovic *et al.* 2018). Laboratory analysis followed Olah *et al.* (2016). Briefly, M13 PCR
179 tags were attached to all forward primers (Schuelke 2000) and all loci were amplified
180 individually. PCR products were multiplexed in the same lane using different fluorescent tags
181 and genotyped on an ABI 3130XL sequencer (Applied Biosystem). We used a negative
182 control for contamination checking and a positive control to ensure consistent size scoring
183 across all genotyping runs. Results were scored using Geneious version R6 (Kearse *et al.*
184 2012) with 112 full genotypes constructed across seven loci. Approximately, 25 % of the
185 samples were repeated to estimate genotyping errors. Loci were screened for the presence of
186 null alleles across all samples with MicroChecker 2.2.3 (Van Oosterhout *et al.* 2004).

187

188 **2.4 | Genetic relatedness classification and detection of multiple paternity**

189 For classification of relatedness we used a subset of the total samples (N = 291) that
190 contained only nestlings with a maximum of one missing locus and with at least two siblings
191 per nest. We followed the two-program congruency approach described in Turjeman *et al.*
192 (2016a) to determine relationships among nestlings. First we used the software program ML-
193 RELATE (Kalinowski, Wagner & Taper 2006) to determine the most likely pairwise
194 relationships. Then we used the program COLONY 2 (Jones & Wang 2010) to confirm or
195 discard relationship classifications. We used the following relationship categories for
196 pairwise relatedness between siblings in each software: full siblings (FS), half siblings (HS),
197 unrelated (U), not full siblings (NFS; where 'full siblings' relationship could be rejected but
198 differentiation between the categories of 'half siblings' and 'unrelated' could not be made),
199 and non-conclusive (NC) cases where conclusions could not be reached. For both software
200 programs we used the settings described in (Turjeman *et al.* 2016b). When ML-RELATE and
201 COLONY 2 did not give the same results we used the following rules: (1) when ML-
202 RELATE showed an NFS relationship and COLONY 2 showed a HS, we accepted HS; (2)
203 when ML-RELATE showed NC, we accepted the COLONY 2 result. We classified nests as

204 FS (if all sibling pairs had FS relationships) or HS (if at least one sibling pair had a HS or
205 NFS relationship). Nests with more than 50% NC relationships were not classified.

206

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

215

216

217

218 **2.5 | Adult sex ratios, reproductive success, and population viability analyses**

219 Following the methods of Stojanovic et al. (2014) using the program MARK (White &
220 Burnham 1999), we compiled mortality rates of nesting females due to predation by sugar
221 gliders for seven regions shown in Figure 1 (north and south Bruny Island were combined
222 into one region for this purpose). We measured fledging success for all monitored nests as the
223 number of nestlings expected to fledge as of the last nest inspection.

224

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

232

233 To estimate the population wide ASR for each year of the study we used Model 2 in
234 Heinsohn et al. (2015) to estimate the number of adult (2 years old and over) males and
235 females remaining at the end of each breeding season (i.e. after predation on nesting
236 females). We used these values to estimate the population wide proportion of adult males at
237 the start of the next breeding season from 2010 until 2015. The published PVAs (Heinsohn et

238 al. 2015) used mean predation rates on adult females of 56.4% over a number of years in a
239 largely deterministic model. However in this paper we used the mortality rates specific to
240 each year, calculated from the proportion of the parrot population that nested in predator
241 infested habitat, to determine changes to male and female numbers, and hence annual
242 variations in the ASR, more precisely. Annual adult female mortality rates, including
243 background mortality and that caused by sugar gliders, calculated for use in the models were:
244 2010, 56.4%; 2011, 58.5%; 2012, 61.7%; 2013, 52.4%; 2014, 53.0%; 2015, 61.7%.

245

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

256

257 We constructed three new PVA models to isolate the impact on the population projection of
258 increased levels of shared paternity associated with higher mortality of females. We kept the
259 high predation rate on adult females and other settings, including a starting population of
260 2158 individuals, and other values used in Model 2 of Heinsohn *et al.* (2015) but adjusted
261 population wide reproductive success to three levels. Model A explored population size after
262 16 years (3 generations) if shared paternity occurred at the lowest rate observed in this study
263 (33%) and consequently the population enjoyed higher breeding success (see Results). Model
264 B examined the final population size if shared paternity occurred at the mean levels observed
265 in this study (50.5%). Model C predicted final population size if shared paternity occurred at
266 the highest rate recorded in our study (95%).

267

268 **3 | RESULTS**

269 **3.1 | Population genetics, relatedness and mating system**

270 The total number of alleles per locus ranged between 3-20, mean observed heterozygosity
271 was 0.68, while the expected heterozygosity value was 0.683 (Table 1). The variability of all

272 seven microsatellite loci was predicted to recover all unique genotypes even among siblings,
 273 over our large sample of individuals ($PI_{sibs(7)} = 0.002$, $N = 94-111$, Table 1).

274

275 **Table 1.** Summary of microsatellite diversity showing the number of alleles (N_a), effective
 276 number of different alleles (N_e), observed heterozygosity (H_O), expected heterozygosity
 277 (H_E), fixation index (F), probability of identity (PI), and probability of identity for siblings
 278 (PI_{sibs}). All calculations were performed in GenAlEx (Peakall & Smouse 2006; Peakall &
 279 Smouse 2012) based on a subsample ($N = 111$) of the 350 genotyped individuals containing a
 280 single randomly selected representative from each nest. The number of successfully
 281 genotyped samples at each locus are shown for the total ($NTot$) and the subsample ($NSub$).

282

Locus	$NTot$	$NSub$	N_a	N_e	H_O	H_E	F	PI	PI_{sibs}
CI3	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		

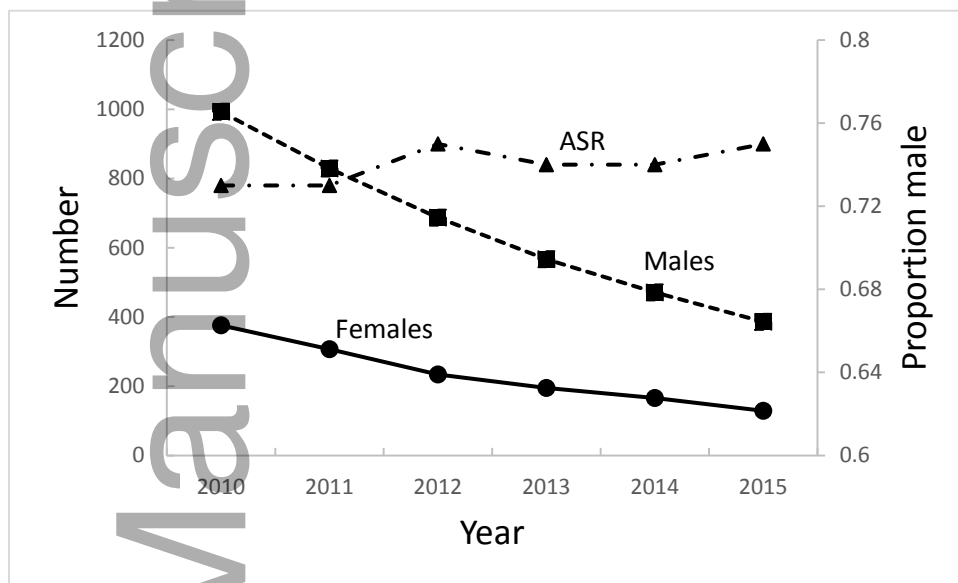
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284 We analyzed a total of 374 pairwise relationships between siblings and found 264 (70.6%) FS
 285 and 74 (19.8%) HS relationships, while in 36 (9.6%) cases conclusions could not be reached.
 286 Out of the total 85 nests used for this analysis, in 82 cases (96.5%) we successfully classified
 287 at least 50% of the siblings per nest. Among these resolved nests 60% ($N = 49$) contained
 288 only full-siblings, while 40% ($N = 33$) contained at least one half-sibling relationship. We
 289 reconfirmed seven cases, and found ten extra cases, of multiple paternity using the number of
 290 different alleles within families, bringing the number of nests with multiple paternity to 43/85
 291 (50.5%). The proportion of nests with at least one half-sibling was significantly higher than
 292 expected under a monogamous breeding strategy (Fisher's exact test, $P < 0.001$).

293

294 **3.2 | Adult sex ratios, frequency of multiple paternity and impact on reproductive**
295 **success**

296 The modeled trajectories over the study for adult males and females, and the resulting ASR
297 expressed as proportion of males, are shown in Figure 2. The estimated proportion of males
298 in the adult population at the start of each breeding season varied little, ranging from 0.73 to
299 0.75.



302
303 **FIGURE 2** The modeled number of adult (2+) males (squares) and females (circles) (left
304 axis) in each of the six years in our study and the resulting proportion of adult males (ASR,
305 triangles) (right axis).

306
307 Rates of multiple paternity varied significantly across years ($\chi^2_5 = 2.81$, $P = 0.015$) but were
308 not significantly affected by the number of nestlings in the brood (range = 2-5, $\chi^2_1 = 0.54$) or
309 timing of breeding within the season ($\chi^2_1 = 2.08$). There was no significant effect of the
310 limited range of population-wide ASRs reported above on the likelihood of multiple paternity
311 ($\chi^2_1 = 0.94$). However, swift parrots settled to breed in different areas within and between
312 seasons over the study (Webb *et al.* 2017), and multiple paternity increased significantly at
313 sites where there was higher predation on nesting females ($\chi^2_1 = 4.26$, $P = 0.039$, Fig. 3a).
314 This suggests that local changes to the ASR, caused by loss of adult females to predators
315 while nesting, were a determinant of whether polyandrous mating occurred at the remaining
316 nests. The predation rates on breeding females at seven breeding sites used in this analysis,
317 calculated using the program MARK (Stojanovic *et al.* 2014), are given in the caption to Fig.

318 3. There were no significant interactions between any of the variables presented above (0.150
319 < P < 0.980).

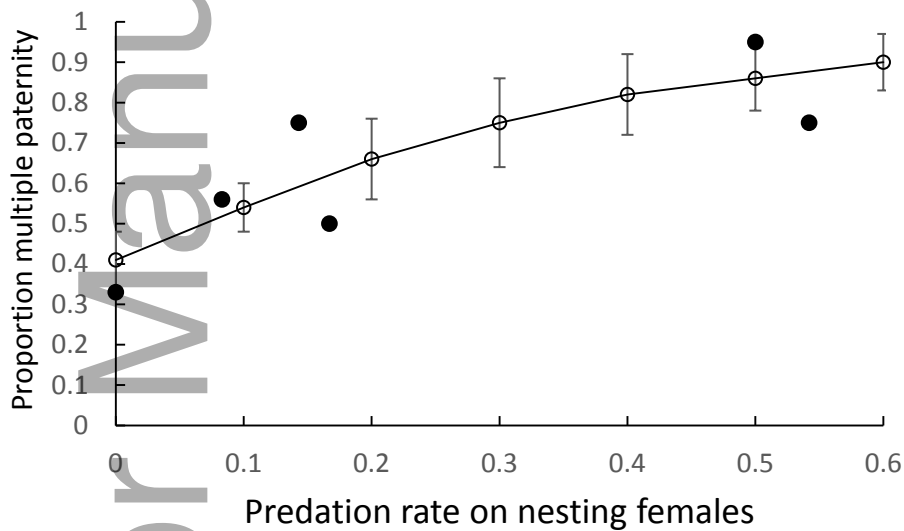
320

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

327

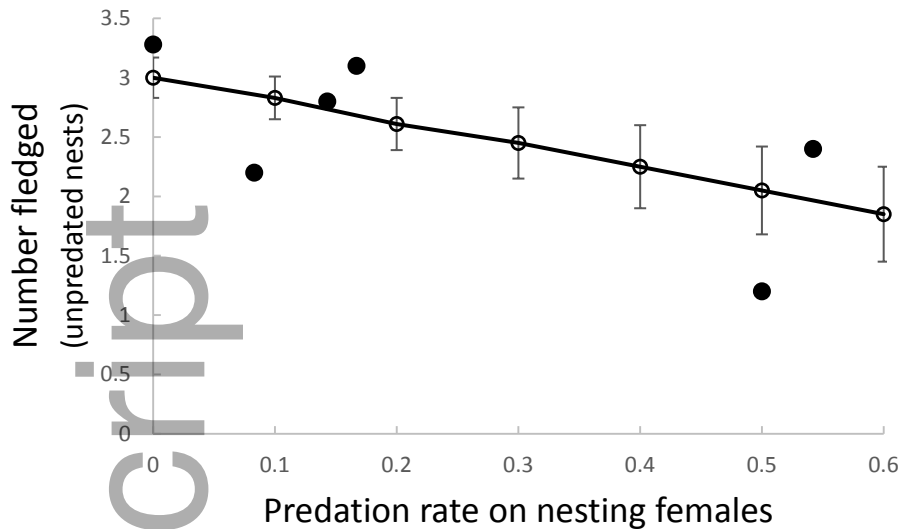
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329 (a)



330

331 (b)



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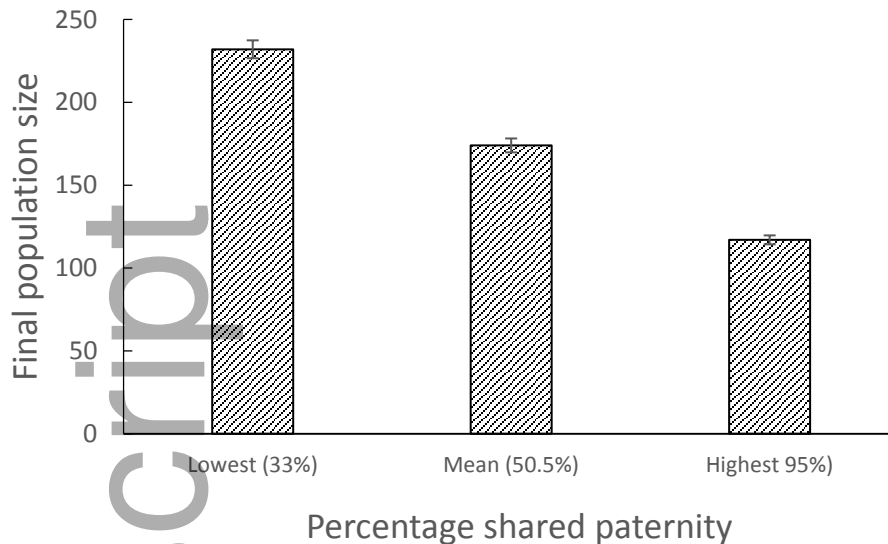
333 **FIGURE 3** (a) observed (closed circles) and predicted proportion (open circles) \pm s.e. of
 334 nests with multiple paternity against rates of predation on nesting adult females. (b) Mean
 335 number of fledglings (closed circles) and number predicted (open circles) \pm s.e. for
 336 unpredated nests against the site specific rate of predation on nesting females (NB two sites
 337 with predation rate of 0.5, Rheban and Southern Forests, are presented as one value in both
 338 Fig. 3a and 3b). The predation rates on breeding females at seven breeding sites used in this
 339 analysis, calculated using the program MARK (Stojanovic *et al.* 2014), were as follows:
 340 Bruny Island (0, n= 56), Buckland (0.08, n= 19), Meehan Range (0.14, n= 9), Wielangta
 341 (0.17, n= 7), Rheban (0.50, n=6), Southern Forests (0.50, n=16), Eastern Tiers (0.54, n=29).

342

343 **3.3 | Impact of shared paternity on population viability**

344 Predicted final population sizes differed significantly between the three modelled PVA
 345 scenarios ($P < 0.001$) demonstrating the impact on population size of lower reproductive
 346 success associated with shared paternity. Model A, using the reproductive success when rates
 347 of shared paternity were lowest, predicted that the swift parrot population would decline by
 348 89.4% over three generations. This compares with a population reduction of 92.1% under
 349 mean rates of shared paternity (Model B) and 94.9% if shared paternity is at its highest level
 350 observed in this study (Model C).

351



352

353 **FIGURE 4** Simulated population size (\pm s/e) after 16 years (3 generations) if swift parrots
 354 exhibit the lowest observed rate (33%) of shared paternity (Model A: population decrease =
 355 89.4%), the mean rate (50.5%) of shared paternity reported here, (Model B: population
 356 decrease = 92.1%), and the highest rate observed in this study (95%), (Model C: population
 357 decrease = 94.9%).

358

359 4 | DISCUSSION

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

375 opportunity to isolate the costs of genetic polyandry on individual fitness and population
376 viability (Holman & Kokko 2013).

377

378 Our finding that paternity was shared at 50.5% of swift parrot nests adds to a small number of
379 studies that challenge the traditional view that parrots are largely monogamous (Toft &
380 Wright 2015). Studies of parrot mating systems using molecular techniques are still few but
381 now include one species with 100% genetic monogamy (burrowing parrots, *Cyanoliseus*
382 *patagonus* (Masello *et al.* 2002)), and other socially monogamous species with both modest
383 (green-rumped parrotlets, *Forpus passerinus* 14% nests, (Beissinger 2008)) and higher rates
384 of shared paternity (40% nests, monk parakeets, *Myiopsitta monachus*, (Martínez *et al.*
385 2013). A small number of parrot species are also known to have more extreme social and
386 genetic mating systems including lek promiscuity (kakapos, *Strigops habroptilus*, (Merton,
387 Morris & Atkinson 1984) and cooperative polyandry and polygynandry (Ekstrom *et al.* 2007;
388 Heinsohn *et al.* 2007). The growing body of evidence suggests that parrots as a taxon may
389 display a similar range and frequency of social and genetic mating systems to that seen in
390 Passerines, the bird order now known to be most closely related to parrots (Jarvis *et al.* 2014).
391 However the parrot species thus far targeted for molecular analysis of parentage may be
392 skewed towards the more unusual species, and further studies of socially monogamous
393 parrots are required.

394

395 The more extreme mating systems found amongst parrots may help in interpreting the causes
396 of high rates of shared paternity in swift parrots. *Electus* parrots (*Electus roratus*) for
397 example breed polyandrously because limited availability of nest hollows places severe
398 restrictions on the availability of breeding females, and encourages males to share mates,
399 albeit with some conflict (Heinsohn *et al.* 2007; Heinsohn 2008). In swift parrots, genetic
400 polyandry increases at breeding sites where female mortality is higher, suggesting that
401 unpaired males target already paired females more when the local ASR becomes more male-
402 biased. It should be noted that swift parrots have not been observed either to live in stable
403 groups as happens in *Electus* parrots, or for the males to form coalitions to maximise their
404 chances at achieving mating success (Hartley & Davies 1994). Instead social monogamy
405 prevails with the socially paired male aggressively chasing other males away from the nest,
406 even though the females have been observed to accept food surreptitiously from the
407 interlopers and to mate with them (unpublished data). Thus, unlike *Electus* parrots and other

408 species (e.g. dunnocks, *Prunella modularis*) (Davies 1992) biases in the ASR appear to
409 promote genetic but not necessarily social polyandry in swift parrots.

410

411 The diminished reproductive success of swift parrots when the ASR is male biased may be
412 driven by heightened inter-locus sexual conflict, or differences between the sexes in optimal
413 breeding behaviour (Holman & Kokko 2013). The increase in shared paternity seen in these
414 conditions does not increase reproductive success for females, as occurs for example in
415 dunnocks (Davies 1992), and instead appears to incur a cost to both females and pair males.
416 The remaining females who have avoided predation lose some reproductive success as the
417 ASR becomes more biased (Figure 3b), but pair males suffer greater losses if they also share
418 paternity. Our anecdotal observations suggest that lower reproductive success may be due to
419 greater harassment by additional unpaired males that attempt to courtship feed, and mate
420 with, nesting females. These interlopers are met with frequent aggression by the resident
421 males who chase them from the nest area and may cause important losses of time and energy
422 for the resident pair. Under this scenario it is possible that females could accept extra mates
423 without (or with less) cost to their reproduction but resident males, who have more to lose,
424 behave in ways that protect their own optimum outcome at the expense of females. Bearded
425 vulture trios also suffer lower breeding success than pairs but a major difference is that the
426 males seem to co-exist more peacefully (Carrete *et al.* 2013).

427

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

441 simple lack of females as mates (Steifetten & Dale 2006; Grayson *et al.* 2014) (Gilroy &
442 Lockwood 2012; Morrison *et al.* 2016).

443

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

465

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472

473 **AUTHOR'S CONTRIBUTIONS**

474 RH, MW, and DS conceived the ideas and designed field methodology; DS and MW
475 collected the field data; GO and RP analysed the molecular data; RH led the writing of the
476 manuscript with major contributions from GO, RP, and DS. All authors contributed critically
477 to the drafts and gave final approval for publication.

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481 **DATA ACCESSIBILITY**

482 Data from this study have been archived in *figshare*:

483 <https://doi.org/10.6084/m9.figshare.7238081.v1> (Heinsohn et al. 2018)

484

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