

1 **Female need for paternal care shapes variation in extra-pair**
2 **paternity in a cooperative breeder**

3 **Laurence Cousseau¹, Dries Van de Loock¹²³, Mwangi Githiru³⁴, Carl Vangestel¹⁵ & Luc**
4 **Lens¹**

5

6 ¹ Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium

7 ² Evolutionary Ecology Group, University of Antwerp, Campus Drie Eiken, Universiteitsplein
8 1, 2610 Wilrijk, Belgium

9 ³ Ornithology section, Department of Zoology, National Museums of Kenya, P.O. Box
10 40658-00100, Nairobi, Kenya

11 ⁴ Wildlife Works, P.O. Box 310-80300, Voi, Kenya

12 ⁵ Royal Belgian Institute of Natural Sciences, Vautierstraat 26, 1000 Brussels, Belgium

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14 Corresponding author : laurence.cousseau@ugent.be

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21 **ABSTRACT**

22 Socially-monogamous females regularly mate with males outside the pair bond. The
23 prevailing explanation for this behavior is that females gain genetic benefits resulting from
24 increased fitness of extra-pair offspring. Furthermore, because of the risk of reduced paternal
25 care in response to cuckoldry, females are expected to seek extra-pair copulations when they
26 can rear offspring with little help from their social partner (“constrained female” hypothesis).
27 We tested these hypotheses and analyzed variation in paternal care in the Afrotropical,
28 facultative cooperative breeding placid greenbul (*Phyllastrephus placidus*). Overall, ca. 50%
29 of the offspring resulted from extra-pair (and extra-group) mating. Identified extra-pair males
30 were in most cases neighboring dominant males, yet never within-group subordinates. As
31 predicted by the constrained female hypothesis, the occurrence of extra-pair paternity (EPP)
32 increased with the number of cooperative helpers (and not with total group size). However,
33 dominant males did not adjust their food provisioning rates in response to EPP. Although
34 extra-pair males were more strongly related to the dominant female and less heterozygous
35 than the latter’s social mate, this did not result in more inbred extra-pair offspring, likely
36 because identified extra-pair males were not representative of the extra-pair male population.
37 While earlier studies on EPP mainly focused on male genetic quality, results from this study
38 provide evidence that female’s social context may affect extra-pair strategies too.

39

40 **Keywords:** constrained female hypothesis, cooperative breeding, extra-pair paternity, genetic
41 fitness benefits, paternal care, placid greenbul.

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43

44 INTRODUCTION

45 Extra-pair paternity (EPP), where offspring are sired by a male other than the female's social
46 partner, is very common in socially monogamous passerines. It is recorded in 86% of
47 songbirds where on average 11% of offspring are the results of extra-pair paternity (Griffith et
48 al. 2002). Females engaging in extra-pair matings may profit from fitness advantages such as
49 insurance against infertility of their mates (Wetton and Parkin 1991; Krokene 1998; Griffith et
50 al. 2002), access to additional resources (Gray 1997), securing a future partner (Heg et al.
51 1993) or receiving additional help at the nest by extra-pair males (Burke et al. 1989;
52 Kempenaers 1993). In addition, a large number of studies tested the hypothesis that females
53 gain genetic benefits resulting from increased fitness of extra-pair offspring (Kempenaers et
54 al. 1997; Foerster et al. 2003; Fossøy et al. 2008; but see Schmoll et al. 2009; Sardell et al.
55 2012). Increased genetic quality of offspring may result from female preference for males
56 with superior genes to those available from the within-pair mate ('good genes' hypothesis;
57 Neff and Pitcher 2005), or for males that maximize offspring heterozygosity (heterozygosity
58 hypothesis; Brown 1996; Kempenaers 2007). Females can maximize offspring heterozygosity
59 either by mating with a more heterozygous male (Mitton et al. 1993; Nietlisbach et al. 2016),
60 or with a genetically dissimilar, less related, male (genetic compatibility hypothesis; Zeh and
61 Zeh 1996; Tarvin et al. 2005; Kempenaers 2007). High heterozygosity has been associated
62 with several fitness benefits including increased survival (Coltman et al. 1998; Markert et al.
63 2004), reproductive success (Foerster et al. 2003; Charpentier et al. 2005) and resistance to
64 pathogens (Cassinello et al. 2001; Hawley et al. 2005). Besides this ongoing debate regarding
65 the relative importance of genetic fitness benefits in explaining the function of EPP, there is
66 growing evidence that extra-pair mating in females may also result from non-adaptive, or
67 even maladaptive, scenarios (Westneat and Stewart 2003; Forstmeier et al. 2014).

68

69 Besides benefits, however, females may suffer significant costs resulting from mating with
70 multiple males, such as aggression by social males as retaliation (Valera et al. 2003),
71 increased exposure to parasites and pathogens (Lombardo and Thorpe 2000) or reduced
72 parental care by the cuckolded male (Møller and Birkhead 1993; Arnqvist and Kirkpatrick
73 2005). Since parental care is costly, one may expect a positive relationship between the
74 certainty of paternity and the amount of care provided by the male (Sheldon 2002). Yet, while
75 observed in some species (Dixon et al. 1994; Sheldon 2002; Ball et al. 2017), reduced
76 paternal care when EPP occurs in the nest does not seem the rule (Dickinson 2003; Du et al.
77 2015; Barati et al. 2018), which raises the question why cuckolded males provide care to
78 unrelated offspring. First, males may have a low ability to assess paternity in their brood, and
79 natural selection may act against reduction of paternal care to avoid the potential costs of
80 harming own offspring (Dickinson 2003). Second, males may only reduce their investment if
81 both the cost of offspring care and the risk of cuckoldry are high (Griffin et al. 2013). Hence,
82 under some environmental or intrinsic conditions, natural selection may favor male tolerance
83 to unfaithful females if this does not compromise their fitness.

84

85 Because of the risk of reduced paternal care as a response to cuckoldry, it can be predicted
86 that females will solicit extra-pair copulations when offspring can be reared with little help
87 from their social partner ('constrained female hypothesis', Gowaty 1996). Gowaty (1996) thus
88 predicted that low quality females or who occupy low quality habitats are less likely to engage
89 in extra-pair copulations. In support of this, Hoi-Leitner et al. (1999) found more incidences
90 of EPP in serins (*Serinus serinus*) in areas where natural or experimental food abundance
91 around nests was higher during the female fertile phase.

92

93 In addition to female quality and environmental conditions, characteristics of the breeding
94 system may also reduce constraints on female's extra-pair behavior. By providing an
95 alternative source of paternal investment that can potentially compensate for reduced
96 investment or desertion by the social partner, the presence of helpers in cooperative breeding
97 species may reduce the level of female dependency on dominant male care. In such context,
98 the constrained female hypothesis predicts that females are more likely to engage in extra-pair
99 mating in the presence of helpers (Mulder et al. 1994; Webster et al. 2004; Brouwer et al.
100 2017). This hypothesis assumes that females can reliably predict the level of future care by
101 helpers prior to making a decision about whether or not to engage in extra-pair mating.

102

103 In this study, we analyze variation in EPP and paternal care in a facultative cooperative
104 breeding passerine from SE Kenya, and test whether females gain fitness benefits by extra-
105 pair mating. Placid greenbuls (*Phyllastrephus placidus*) offer an excellent model to test the
106 constrained female hypothesis within the context of cooperative breeding, for two reasons.
107 First, social groups are composed of a mix of helpers (i.e. subordinates who provide food to
108 the nestlings) and non-helping subordinates. This allows us to disentangle effects of
109 alloparental care provided by helpers from alternative group size effects that may also result
110 in higher EPP, such as extra-pair fertilization by within-group subordinates (Webster et al.
111 2004), reduced mate-guarding efficiency by the dominant male (Cohas et al. 2006) or territory
112 quality effects that may affect both group size (Komdeur 1992; Legge 2000) and EPP (Hoi-
113 Leitner et al. 1999). Second, as the placid greenbul is a facultative cooperative breeder, levels
114 of EPP of cooperative breeding females can be compared with those breeding without helpers.

115

116

117 MATERIAL AND METHODS

118 Study system and field procedures

119 The Taita Hills (3°25'S, 38°20'E, SE Kenya) (max. altitude 2200 m.a.s.l.) represent the
120 northernmost isolate of the Eastern-Arc Mountains, an ancient mountain chain boasting high
121 levels of endemism that suffered from an estimated 95% forest loss during the last 200 years,
122 mainly due to agricultural encroachment (Burgess et al. 2007; Pellikka et al. 2009).
123 Remaining indigenous cloud forest in the Taita Hills is fragmented into 13 habitat remnants of
124 different size and quality, embedded within a matrix of agricultural fields and exotic
125 plantations (Chege and Bytebier 2005; Aerts et al. 2011). Nine of these forest fragments host
126 populations of the socially-monogamous and facultative cooperative breeding placid greenbul
127 (*Phyllastrephus placidus*; formerly considered a subspecies of the Cabanis's greenbul *P.*
128 *cabanisi*), a common, medium-sized understory insectivore. Dispersal rates between the two
129 larger (> 80 ha) fragments (Ngangao and Chawia) are very low (Lens et al. 2002; Van de
130 Looock 2019) and both populations form distinct genetic clusters (Husemann et al. 2015). In
131 contrast, natal dispersal was recorded among four of the five small fragments (< 15 ha)
132 included in this study. Nests located in these fragments were lumped into a single small
133 population cluster in subsequent analyses. Overall, ca. 65% of placid greenbul pairs breed in
134 cooperative groups that contain one to five subordinate individuals of both sexes (among pairs
135 with subordinates, mean \pm s.d.: 1.5 ± 0.8). The vast majority of subordinates are offspring
136 from previous breeding season(s) that delayed their dispersal. In ca. 50% of these groups,
137 breeding pairs are assisted by up to three helpers to care the nestlings (among pairs with
138 helpers, mean \pm s.d.: 1.2 ± 0.5). Typically two eggs are laid and incubated by the dominant
139 female. Breeding pairs often renest after failure, and occasionally after success. Females often

140 renest with the same males on consecutive years. The maximum number of breeding attempts
141 observed by a pair was four times.

142

143 During six breeding seasons (2007-10 and 2012-15), nests were consistently mapped in seven
144 forest fragments (two large (> 80 ha) and five small (< 15 ha) ones) and were subsequently
145 monitored during the breeding season. A total of 512 nestlings were metal- and color-banded,
146 bled and measured (tarsus length (mm) and body mass (g)) when *c.* 10 days old. As a measure
147 of nestling body condition, we used Scaled Mass Index (SMI; Peig and Green 2009) which
148 scales the mass of all individuals to values that would be expected if they were all of identical
149 body size. Based on the 512 nestlings, we obtained a regression slope of 1.8 (as calculated
150 using the R package smart; Warton et al. 2012) and an average tarsus length of 23.64 mm.
151 Following Peig and Green 2009, we calculated SMI as: $\text{body mass} \times (23.64/\text{tarsus length})^{1.8}$.
152 At each nest, we estimated total group size based on focal observations and targeted mist-
153 netting. Upon capture, individuals were marked with unique color-ring combinations. In
154 addition, tarsus length (mm) and body mass (g) were measured, and blood or feather samples
155 were collected for genetic analysis. Some of the individuals were already color-ringed,
156 measured and sampled from previous ringing efforts (which started in 1996, the oldest placid
157 greenbul recorded was at least 19 years old). Dominant individuals were identified based on
158 cloacal swelling for males and on the presence of a brood patch or observed incubation for
159 females. A subordinate was considered helping if it was observed feeding nestlings through
160 video recordings. Food provisioning rates (feeds/h/nestling) and prey size were quantified
161 through standardized nest video recording (at least four hours of continuous recording when
162 nestlings were *ca.* 8 days old). More details are given in Supporting information S1. We only
163 extracted hourly provisioning rates for nests where video recordings revealed the identity of
164 visiting individuals in at least 70% of all cases. Tarsus length was used as a measure of

165 structural body size (Freeman and Jackson 1990; Senar and Pascual 1997). When individuals
166 were measured more than once, we used average values in our analyses. We did not estimate
167 body condition as proxy of male and female quality since body weight could not always be
168 measured during the fertile period of the female, when extra-pair copulation can occur.

169

170 **Parentage analysis, heterozygosity and pairwise relatedness**

171 Out of the 512 nestlings banded during 2007-15 (see higher), parentage could be assessed for
172 237 nestlings from 137 broods for which the dominant pair was genotyped. In total, 598
173 individuals (nestlings, subordinates and dominants) were genotyped with twelve
174 microsatellites, of which eight had been used in an earlier study (Ase18, Indigo41, Ls1,
175 Mcy μ 4, Pca3, Pfi04, Pfl54 and WBSW2; Husemann et al. 2015); while four additional ones
176 were developed for this study (CG1, CG31, CG34 and CG45; Supporting information S2).
177 We used the DNeasy Blood and Tissue kit to extract DNA from feathers and InstaGene
178 matrix kit for blood samples. PCR were performed in 6 μ L reactions containing 2 μ L DNA, 2
179 μ L of primer mix and 2 μ L of Qiagen multiplex PCR Master Mix (primer concentrations can
180 be found in Husemann et al. (2015) and Supporting information S2). The PCR products were
181 analyzed on an ABI 3130XL Genetic Analyzer (Applied Biosystems), and genotypes were
182 scored with GENEIOUS 7.0.5 (Kearse et al. 2012). Observed and expected heterozygosity
183 averaged over populations and loci were 0.64 and 0.63, respectively (n = 598; Supporting
184 information S2). Individuals were molecularly sexed using a set of sex-linked primers P2/P8
185 (Griffiths et al. 1998).

186

187 We used the exclusion method (Jones & Ardren, 2003) to assess whether dominant females
188 and males were the genetic parents of nestlings. Because genetic dissimilarities between

189 parents and offspring can arise due to genotyping errors, we defined the parentage exclusion
190 threshold by comparing mother-offspring genotypes. Among 237 nestlings, 19 (8%) showed a
191 genetic mismatch with the mother at one locus only. Thus, dominant males were excluded
192 genetic father if they showed mismatches at two or more loci with the offspring while taking
193 into account the mother's genotype We used the full-likelihood method with a weak prior in
194 the program COLONY 2.0.6.3 (Jones & Wang, 2010) to assign candidate fathers to extra-pair
195 offspring. We provided the genotypes of the dominant females as known mothers. Candidate
196 fathers comprised both genotyped males (594 ind) and unsexed individuals (150 ind) that
197 were more than one year old during the offspring's birth year. 414 of these individuals were
198 previously genotyped with the set of eight microsatellites (Husemann et al. 2015). We
199 excluded individuals trapped in a different population during the same year. All assigned
200 fathers showed a probability of the mother-father dyad of one and did not mismatch at more
201 than one locus with the offspring while taking into account the mother's genotype. Details on
202 COLONY performance and parameter settings can be found in Supporting information S2.
203 Using the same set of markers for parentage analysis as well as for heterozygosity and
204 relatedness estimates has earlier been shown to bias paternity assignment in favor of certain
205 genotypes (Wang, 2010; Wetzel & Westneat, 2009). In Supporting information S2, we
206 provide arguments indicating that our results are unlikely subject to such bias.

207

208 Individual genetic diversity was estimated using the standardized individual heterozygosity,
209 defined as the proportion of heterozygous loci divided by the mean heterozygosity of the
210 scored loci and was computed using the R package *inbreedR* (Stoffel et al. 2016). In order to
211 evaluate to what extent heterozygosity at the selected set of markers reflects genome-wide
212 heterozygosity, we estimated g_2 as a measure of identity disequilibrium (David et al. 2007)
213 with the R package *inbreedR* (Stoffel et al. 2016). G_2 statistics assess the level of covariance

214 of heterozygosity between markers standardized by their average heterozygosity (Miller and
215 Coltman 2014). Significance was tested using 1000 permutations and 95% confidence interval
216 was estimated using 1000 bootstraps. We found a non-significant, positive value (g_2 [95% CI]
217 = 0.0032 [-0.005 ; 0.008]; p-value = 0.27; n = 598).

218

219 We further estimated pairwise relatedness between dominant females and within-pair and
220 extra-pair males. To select the most optimal relatedness estimator we compared deviations
221 between true and estimated relatedness for a set of known parent-offspring ($r = 0.5$, $n = 237$)
222 and halfsib ($r = 0.25$, $n = 24$) dyads. We assessed the performance of seven relatedness
223 estimators (triadic likelihood estimator (Wang 2007), Wang moment estimator (Wang 2002),
224 Lynch & Li moment estimator (Lynch 1988; Li et al. 1993), Lynch & Ritland moment
225 estimator (Lynch and Ritland 1999), Ritland moment estimator (Ritland 1996), Queller &
226 Goodnight moment estimator (Queller and Goodnight 1989) and dyadic likelihood estimator
227 (Milligan 2003) using the program COANCESTRY (Wang 2011). Median deviations
228 between known and estimated relatedness values were small for nearly all estimators,
229 relatedness values were highly correlated across estimators, and the main results of the study
230 were not affected by the choice of the estimator (details in Supporting information S3). We
231 here present results for Queller and Goodnight estimator only as it showed high correlations
232 with all other estimators (min. Pearson's r correlation coefficients: 0.73 with Ritland , max. r :
233 0.91 with Lynch & Li, p-values <0.01)

234

235 **Statistical analyses**

236 *General procedure*

237 We fitted Generalized Estimating Equations (GEEs, geepack library; Halekoh et al. 2006)
238 with exchangeable working correlation structures to account for clustered data (Horton and
239 Lipsitz 1999). GEEs may be more suitable than linear mixed models when the primary
240 objective of an analysis is to make inferences on mean responses as a function of multilevel
241 covariates, rather than on the variance components (Heagerty and Zeger 2000; Fieberg et al.
242 2009). To prevent collinearity among predictor variables, we checked that pairwise Pearson's
243 r correlation coefficients were ≤ 0.30 . We used MuMIn package (Bartoń 2018) to produce all
244 subsets of models based on the global model for each response variable, and to rank them
245 based on the lowest corrected Quasi-likelihood under the Independence model Criterion value
246 (QICc) (Pan 2001) computed using the R package MESS (Ekstrøm 2018). We first retained
247 all models with $\Delta\text{QICc} \leq 2$ and then discarded the ones that were more complex versions of
248 simpler (nested) models with lower QICc values (Richards et al. 2011). When more than one
249 model was retained, we calculated model averaged parameter estimates and 95% confidence
250 intervals from these models using package MuMIn (Burnham and Anderson 2002; Bartoń
251 2018). All statistical analyses were performed using R 3.4.1 software (R Core Development
252 Team 2017).

253

254 *Factors shaping variation in EPP*

255 We fitted binomial GEEs to model variation in EPP using data from 177 nestlings of 104
256 nests. We either modeled (i) presence-absence of EPP in a brood (0 or 1) or (ii) the number of
257 extra-pair offspring in a brood (0 to 2). Fixed factors included year, population, number of
258 helpers (0, 1 or 2+), dominant female traits (standardized individual heterozygosity and tarsus
259 length) and dominant male traits (standardized individual heterozygosity, relatedness to the
260 dominant female and tarsus length). Nests located in the five small spatially clustered forest
261 fragments were lumped into a single small population cluster (thereby avoiding small sample

262 sizes). Population was hence modelled as a factor with three levels. Pair identity was
263 modelled as a clustering factor. In order to limit the number of models in the set of candidate
264 models, we limited the total number of explanatory variables in a single model to three, which
265 resulted in a set of 93 candidate models.

266

267 *Male food provisioning response to EPP*

268 We fitted Gaussian GEE models with pair identity as a clustering factor (i) to investigate
269 within-nest differences in food provisioning rates between dominant males and females (110
270 nests), and between dominant males and helpers (41 nests) and (ii) to test whether males
271 reduce their food provisioning rates in response to EPP (81 nests). Individual food
272 provisioning rates were regressed on mean prey sizes and their residuals were included as
273 response variables in the models. In both analyses, the number of helpers (0 to 2+), population
274 and year were included as categorical fixed effects, while in the latter, EPP (either added as a
275 binary or as the proportion of extra-pair nestlings in the brood) and nestling age were included
276 as additional covariates (nestling age was included in all competing models).

277

278 *Quality of extra-pair mates and extra-pair nestlings*

279 To test whether females mated with males of higher quality than their social mate, we
280 performed randomized paired t-tests to compare three trait values (standardized individual
281 heterozygosity, relatedness with dominant female and tarsus length) between cuckolded males
282 and extra-pair sires. We removed duplicated “dominant female – dominant male – extra-pair
283 male” triads from the 17 broods for which we were able to assign the extra-pair sire, resulting
284 in a sample size of 13. We used randomized tests in order to take into account that within- and
285 extra-pair males were not from separate statistical populations (i.e. in at least two cases a

286 cuckolded mate also gained extra-pair paternity) (Wetzel and Westneat 2009; Harrison et al.
287 2013). We performed 10 000 permutations of pairwise values between both groups of males.
288 We then compared the observed t value derived from a paired t -test on the empirical data to
289 the distribution of t values generated by the randomization. We used a paired t -test to compare
290 SMI (25 nests, 52 nestlings), tarsus length and standardized individual heterozygosity (26
291 nests, 54 nestlings) of within- and extra-pair nestlings from a same brood. Finally, we used
292 Pearson's correlation coefficient (r) to assess whether more related parents produced less
293 heterozygous offspring.

294

295

296 **RESULTS**

297 A total of 110 out of 237 (46%) genotyped offspring (137 broods) were sired by extra-pair
298 males, while 74 broods (54%) contained at least one extra-pair young. In 48 broods with
299 extra-pair offspring, the dominant male did not sire any offspring. In all seven broods with
300 multiple extra-pair offspring for which the extra-pair male was identified, a single male sired
301 all extra-pair offspring. Genetic fathers could be assigned to 24 extra-pair offspring. These
302 extra-pair sires comprised seven unique individuals, of which four bred in surrounding
303 territories during the same year (max. distance between territories: 218 m). Three of these
304 males sired extra-pair young with the same respective dominant female during multiple
305 breeding seasons. Another extra-pair male, mating with four different females, was not
306 observed breeding during the years when EPP occurred but was breeding in years before and
307 after. The two remaining identified extra-pair males were never observed breeding, rendering
308 it impossible to assess whether they were active breeders or floating failed breeders. We
309 observed one case of reciprocal cuckoldry. Known male subordinates ($n = 56$) were never
310 assigned as extra-pair fathers. More details are given in Supporting information S2.

311

312 **Factors shaping variation in EPP**

313 Variation in the occurrence of EPP was best explained by the number of helpers which was
314 included in all top models ($\Delta\text{QICc} \leq 2$) (model-average estimate and 95% confidence interval:
315 0.73 [0.15; 1.32], Table 1a, Fig. 1). Pairs breeding with 2 or more helpers had 67% chance
316 more to have extra-pair young in a brood than pairs breeding without helpers. While female
317 tarsus length was also included in the best-supported model, it was absent from the second
318 best model and its confidence interval included 0 (model-average estimate and 95%
319 confidence interval: 0.37 [-0.49; 1.23]), suggesting weak evidence that tarsus length was an

320 important predictor of the data. Effects of male characteristics on the occurrence of EPP was
321 weakly supported by the data (Table 1a). In order to disentangle effects of food provisioning
322 behavior from other group size effects on the occurrence of EPP, we ran a complementary
323 analysis on a subset of data (breeding seasons 2012-2015 for which total group sizes were
324 known with the highest level of accuracy) where we compared both the effect of the number
325 of helpers and of the total number of subordinates (i.e. sum of helping and non-helping ones)
326 (details in Supporting Information S4). Results from this analysis showed that the total
327 number of subordinates (effect size and 95% confidence interval: 0.04 [-0.61; 0.70]) did not
328 better predict the occurrence of EPP than the number of subordinates that helped with
329 providing food to the nestlings (Table S4, Fig. 1). When modelling variation in the proportion
330 of extra-pair young in a brood, the best-supported model was the null model suggesting that
331 none of the tested variables were important predictors of the data.

332

333 **Food provisioning response to EPP**

334 Dominant males contributed to food provisioning on average less than dominant females
335 (42%). However, between-nest variation in parental care division was high, as in 41% of the
336 nests, dominant males provided food more frequently to nestlings than dominant females.
337 Variation in parental care between mates was best explained by the number of helpers (Table
338 2a). All other models showed a $\Delta\text{QICc} > 2$. Average food provisioning rates by both parents
339 were most similar in pairs breeding alone or with one helper. In cooperative groups with two
340 or more helpers, however, dominant males contributed more than dominant females (Fig. 2).
341 In ten out of 67 nests without helpers, we did not record any food provisioning activity by
342 dominant males, while absence of nestling feeding by dominant females was only recorded in
343 one of the two nests with three helpers.

344

345 Variation in food provisioning rates between dominant males and helpers was also best
346 explained by the number of helpers (model-averaged estimate and 95% confidence interval:
347 0.22 [-0.27; 0.71]) (Table 2b). However, the second best model was the null model (QICc
348 weight of the two best models: 37% vs. 34%) suggesting only moderate support for the
349 number of helpers. Food provisioning rates by dominant males were on average 63% higher
350 than those by helpers and increased when two or more subordinates helped.

351

352 When modelling variation in male food provisioning, the best-supported model was the null
353 model (Table 3) suggesting that extra-pair paternity in a brood and number of helpers were
354 not important predictors of the data.

355

356 **Are extra-pair mates and extra-pair offspring of higher quality?**

357 Extra-pair mates were significantly less heterozygous (on average 0.88 *versus* 1.14; $t = 2.32$,
358 $p\text{-value} = 0.04$), and also more related to the dominant female (Queller & Goodnight moment
359 estimator; on average 0.12 *versus* -0.04; $t = -2.37$, $p\text{-value} = 0.04$), than the social mates that
360 were cuckolded (randomized paired t -test, $df = 12$) (Fig. 3). Tarsus length ($t = 0.94$, $p\text{-value} =$
361 0.37) did not differ significantly between extra-pair and social mates (randomized paired t -
362 test, $df = 12$) (Fig. 3). Extra-pair offspring were not more heterozygous (paired t -test, $t = -$
363 0.68 , $df = 27$, $p\text{-value} = 0.50$) or in better condition (paired t -test, SMI: $t = -0.22$, $n = 26$, p -
364 $value = 0.82$; tarsus length: $t = 0.33$, $df = 27$, $p\text{-value} = 0.74$) than within-pair offspring (Fig.
365 4). Relatedness between mates and heterozygosity of their offspring was negatively correlated
366 (social pairs: Pearson's $r = -0.47$, $df = 125$, $p\text{-value} < 0.01$; identified extra-pair couples:
367 Pearson's $r: -0.46$, $df = 22$, $p\text{-value} = 0.02$).

369

370 **DISCUSSION**

371

372 As predicted by the constrained female hypothesis, we found that the occurrence of EPP
373 increased with the number of helpers and female body size, while EPP did not vary with total
374 group size. Contrary to our prediction, dominant males did not adjust their food provisioning
375 rates in response to EPP. The few identified extra-pair males were in most cases males
376 breeding in surrounding nests and never within-group subordinates. Extra-pair sires were less
377 heterozygous and more related to the dominant female than their within-pair males. While this
378 may result in more inbred extra-pair offspring, within- and extra-pair offspring did not differ
379 in level of heterozygosity nor in body condition.

380

381 **Empirical support for the constrained female hypothesis**

382 A relationship between EPP and cooperative groups was first shown in the superb fairy-wren
383 (*Malurus cyaneus*) (Mulder et al. 1994) where up to 70% of the nests of cooperative-breeding
384 pairs contained at least one extra-pair offspring, compared to only 15% in non-cooperative
385 nests. This pattern was subsequently supported by studies of three other cooperative-breeding
386 wren species (Webster et al. 2004; Brouwer et al. 2017), while a reverse relationship was
387 observed in the variegated fairy-wren (*Malurus lamberti*) (Johnson and Pruett-Jones 2018).
388 Possible mechanisms underlying such strategy need further investigation since females should
389 be able to assess expected levels of future care by helpers during the mating phase already.
390 Yet, which intrinsic or external factors determine the propensity of helping in subordinate
391 greenbuls currently remains unknown. To our knowledge, only one other study (in Seychelles
392 warblers *Acrocephalus sechellensis*; Raj Pant et al. 2019) disentangled the effect of helpers

393 from total group size and they found an opposite result (i.e. a positive effect of group size and
394 no effect of the number of helpers). This highlights the need for a better understanding on
395 how social context and mating systems shape EPP.

396

397 Apart from the number of helpers, female body size also predicted the occurrence of EPP in
398 her brood. This may provide additional support for the constrained female hypothesis which
399 predicts higher incidence of EPP in higher quality females. In placid greenbuls, larger females
400 lay larger eggs (Van de Loock 2019) which is assumed to increase nestling survival and
401 growth rate (Krist 2011) and to reduce female dependency on male care. Yet, while body size
402 is indeed often used as a proxy for individual quality in the EPP literature (e.g. Akçay and
403 Roughgarden 2007; Lampila et al. 2011; Harrison et al. 2013), avian studies showing positive
404 effects of body size on fitness are still scant. Given this lack of general support for positive
405 relationships between female body size and individual quality, and based on the fact that the
406 95% confidence interval for the effect of tarsus length on the occurrence of EPP overlapped
407 with 0 (Table 1), we cannot conclude that this result is fully consistent with the constrained
408 female hypothesis.

409

410 **Male response to EPP**

411 Our results further support the view that reduced paternal care is not a systematic response to
412 increased EPP. Rather, it may depend on the costs of care and the risk of EPP (Griffin et al.
413 2013). While genetic analysis enable us to evaluate the latter, our data do not allow us to
414 estimate potential fitness costs of paternal food provisioning directly. Yet, the fact that male
415 breeders, in contrast to females (Van de Loock 2019), did not adopt a load-lightening strategy
416 and thus that their relative contribution to care increased with the number of helpers, suggests

417 that costs of paternal care are relatively low in our study species. The risk of EPP, on the other
418 hand, appears substantial, given that extra-pair males sired 46% of the offspring and dominant
419 males were fully cuckolded in 35% of their brood. Yet, in long-lived species with low adult
420 annual mortality and long-lasting pair bonds (as reported for the placid greenbul; Husemann
421 et al. 2015; Van de Loock et al., unpubl. data), within-pair life-time reproductive success
422 likely remains substantial, especially so if males are successful in acquiring paternity both
423 within and outside pairs.

424

425 **Female benefits arising from EPP**

426 EPP may provide genetic benefits to females through increased fitness of extra-pair offspring.
427 Identified extra-pair males appeared to be dominant individuals, which would support the
428 ‘good genes’ hypothesis (Neff and Pitcher 2005), as such individuals are generally of high
429 quality. However, only one male gained paternity in several neighboring nests, while all other
430 extra-pair males consistently mated with the same females over consecutive years. Such
431 pattern suggests that extra-pair males were not necessarily superior males that were able to
432 monopolize reproduction. Moreover, extra-pair males were not larger or more heterozygous
433 than within-pair males, and EPP did not result in fitter extra-pair offspring, which would be
434 expected from the ‘good genes’ and heterozygosity hypotheses. On the contrary, identified
435 extra-pair males were both less heterozygous and more related to the dominant females than
436 cuckolded males.

437

438 Why females would prefer less heterozygous males as extra-pair mate remains puzzling. The
439 fact that they were more strongly related to extra-pair males than to their social partners,
440 however, conforms with a growing number of studies showing that females do not avoid

441 relatives as extra-pair mates (Kleven et al. 2005; Wang and Lu 2011; Harrison et al. 2013).
442 Yet results from our study should be interpreted with caution for several reasons. First, our
443 data showed no evidence for identity disequilibrium (as judged from the g_2 statistic). This
444 indicates that heterozygosity quantified through our set of markers may be a poor proxy of
445 individual quality as it does not represent genome-wide effects of heterozygosity (Miller and
446 Coltman 2014). Second, extra-pair males identified in our study may not constitute a
447 representative sample from the extra-pair male population, as we were unable to identify 80%
448 of extra-pair males, resulting in a small sample size, while a small number of males was
449 responsible for the majority of extra-pair matings. While relatedness between mates and
450 heterozygosity of their offspring was negatively correlated, within- and extra-pair offspring
451 showed similar levels of heterozygosity, making it unlikely that females systematically
452 choose more similar males. Such discrepancy may be due to incomplete sampling and
453 genotyping of the breeding population or because most of EPP is caused by unsampled
454 floaters. However, a performance assessment of COLONY (Supporting information S2)
455 showed that about half of within-pair males were not assigned as genetic fathers although they
456 were in the set of candidate fathers. This is likely because we assumed a probability of 45%
457 that the true father was in the set of candidate fathers, in order to reduce the probability of
458 misassignment (Supporting information S2).

459

460 Notwithstanding the limitations described above, none of our results point towards genetic
461 gain by females from extra-pair matings. While this certainly merits further investigation,
462 females may still benefit in other, non-genetic ways. First, EPP may offer a way to recruit
463 extra-paternal care, either as food provision or nest defense. While within-group extra-pair
464 paternity has been observed in several bird species (Mulder et al. 1994; Whittingham et al.
465 1997; Webster et al. 2004; Rubenstein 2007; Wang and Lu 2011), we did not find evidence of

466 subordinates siring offspring in our study, likely because the large majority of subordinates
467 consisted of retained offspring (Cousseau et al. unpubl. data). Second, extra-pair males may
468 provide indirect help by providing access to territorial resources to unfaithful females (Gray;
469 1997). Although speculative at this stage, this may explain why home ranges of female
470 greenbuls occasionally overlap during the breeding season (Apfelbeck, unpubl. data) and
471 social groups frequently mix during the non-breeding season (Van de Loock, pers. obs.).
472 Extra-pair copulations may hence facilitate cooperation between neighboring groups through
473 increased inclusive fitness of extra-pair males. Hence, notwithstanding the ubiquity of extra-
474 pair copulations in avian species, many questions about the underlying drivers currently
475 remain unanswered.

476 **SUPPLEMENTARY MATERIAL**

477 Supplementary data are available at Behavioral Ecology online.

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487 **DATA ACCESSIBILITY**

488 Analyses reported in this article can be reproduced using the data provided by Cousseau et al.
489 (2019).

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493 **REFERENCES**

- 494 Aerts R, Thijs KW, Lehouck V, Beentje H, Bytebier B, Matthysen E, Gulinck H, Lens L,
495 Muys B. 2011. Woody plant communities of isolated Afromontane cloud forests in Taita
496 Hills, Kenya. *Plant Ecol.* 212(4):639–649. doi:10.1007/s11258-010-9853-3.
- 497 Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits.
498 *Evol Ecol Res.* 9(5):855–868.
- 499 Arnqvist G, Kirkpatrick M. 2005. The Evolution of Infidelity in Socially Monogamous
500 Passerines: The Strength of Direct and Indirect Selection on Extrapair Copulation Behavior in
501 Females. *Am Nat.* 165(S5):S26–S37. doi:10.1086/429350.
- 502 Ball AD, van Dijk RE, Lloyd P, Pogány Á, Dawson DA, Dorus S, Bowie RCK, Burke T,
503 Székely T. 2017. Levels of extra-pair paternity are associated with parental care in penduline
504 tits (Remizidae). *Ibis (Lond 1859).* 159(2):449–455. doi:10.1111/ibi.12446.
- 505 Barati A, Andrew RL, Gorrell JC, McDonald PG. 2018. Extra-pair paternity is not driven by
506 inbreeding avoidance and does not affect provisioning rates in a cooperatively breeding bird,
507 the noisy miner (*Manorina melanocephala*). Griffin A, editor. *Behav Ecol.* 29(1):244–252.
508 doi:10.1093/beheco/axx158.
- 509 Bartoń K. 2018. Multi-model inference. R package version 1.42.1. [http://cran.r-project](http://cran.r-project.org/web/packages/MuMIn/index)
510 [org/web/packages/MuMIn/index](http://cran.r-project.org/web/packages/MuMIn/index).
- 511 Brouwer L, van de Pol M, Aranzamendi NH, Bain G, Baldassarre DT, Brooker LC, Brooker
512 MG, Colombelli-Négrel D, Enbody E, Gielow K, et al. 2017. Multiple hypotheses explain
513 variation in extra-pair paternity at different levels in a single bird family. *Mol Ecol.*
514 26(23):6717–6729. doi:10.1111/mec.14385.

515 Brown JL. 1997. A theory of mate choice based on heterozygosity. *Behav Ecol.* 8(1):60–65.
516 doi:10.1093/beheco/8.1.60.

517 Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM, Kilahama FB,
518 Loader SP, Lovett JC, Mbilinyi B, et al. 2007. The biological importance of the Eastern Arc
519 Mountains of Tanzania and Kenya. *Biol Conserv.* 134(2):209–231.
520 doi:10.1016/j.biocon.2006.08.015.

521 Burke T, Davies NB, Bruford MW, Hatchwell BJ. 1989. Parental care and mating behaviour
522 of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting.
523 *Nature.* 338(6212):249–251. doi:10.1038/338249a0.

524 Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical
525 information-theoretic approach. 2nd ed. New York, Springer-Verlag.

526 Cassinello J, Gomendio M, Roldan ERS. 2001. Relationship between Coefficient of
527 Inbreeding and Parasite Burden in Endangered Gazelles. *Conserv Biol.* 15(4):1171–1174.
528 doi:10.1046/j.1523-1739.2001.0150041171.x.

529 Charpentier M, Setchell JM, Prugnolle F, Knapp LA, Wickings EJ, Peignot P, Hossaert-
530 McKey M. 2005. Genetic diversity and reproductive success in mandrills (*Mandrillus sphinx*).
531 *Proc Natl Acad Sci U S A.* 102(46):16723–16728. doi:10.1073/pnas.0507205102.

532 Chege J, Bytebier B. 2005. Vegetation Structure of Four Small Forest Fragments in Taita
533 Hills, Kenya. *J East African Nat Hist.* 94(1):231–234. doi:10.2982/0012-
534 8317(2005)94[231:vsosfsf]2.0.co;2.

535 Cohas A, Yoccoz NG, Da Silva A, Goossens B, Allainé D. 2006. Extra-pair paternity in the
536 monogamous alpine marmot (*Marmota marmota*): The roles of social setting and female mate
537 choice. *Behav Ecol Sociobiol.* 59(5):597–605. doi:10.1007/s00265-005-0086-8.

538 Coltman DW, Bowen WD, Wright JM. 1998. Birth weight and neonatal survival of harbour
539 seal pups are positively correlated with genetic variation measured by microsatellites. *Proc R*
540 *Soc London Ser B Biol Sci.* 265(1398):803–809. doi:10.1098/rspb.1998.0363.

541 Cousseau L, Van de Loock D, Githiru M, Vangestel C, Lens L. 2019. Data from: Female need
542 for paternal care shapes variation in extra-pair paternity in a cooperative breeder. *Dryad*
543 *Digital Repository.* <https://doi.org/10.5061/dryad.bcc2fqz7s>.

544 David P, Pujol B, Viard F, Castella V, Goudet J. 2007. Reliable selfing rate estimates from
545 imperfect population genetic data. *Mol Biol Evol.* 16:2474–2487. doi:10.1111/j.1365-
546 294X.2007.03330.x.

547 Dickinson JL. 2003. Male share of provisioning is not influenced by actual or apparent loss of
548 paternity in western bluebirds. *Behav Ecol.* 14(3):360–366. doi:10.1093/beheco/14.3.360.

549 Dixon A, Ross D, O'Malley SLC, Burke T. 1994. Paternal investment inversely related to
550 degree of extra-pair paternity in the reed bunting. *Nature.* 371(6499):698–700.
551 doi:10.1038/371698a0.

552 Du B, Guan M, Ren Q, Chen G. 2015. Cuckolded male ground tits increase parental care for
553 the brood. *Anim Behav.* 110:61–67. doi:10.1016/j.anbehav.2015.09.023.

554 Ekstrøm C. 2018. Package 'MESS'. <https://cran.r-project.org/web/packages/MESS/index>.

555 Fieberg J, Rieger RH, Zicus MC, Schildcrout JS. 2009. Regression modelling of correlated
556 data in ecology: Subject-specific and population averaged response patterns. *J Appl Ecol.*
557 46(5):1018–1025. doi:10.1111/j.1365-2664.2009.01692.x.

558 Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B. 2003. Females increase
559 offspring heterozygosity and fitness through extra-pair matings. *Nature.* 425(6959):714–717.
560 doi:10.1038/nature01969.

561 Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014. Female extra-pair mating:
562 Adaptation or genetic constraint? *Trends Ecol Evol.* 29(8):456–464.
563 doi:10.1016/j.tree.2014.05.005.

564 Fossøy F, Johnsen A, Lifjeld JT. 2008. Multiple genetic benefits of female promiscuity in a
565 socially monogamous passerine. *Evolution (N Y).* 62(1):145–156. doi:10.1111/j.1558-
566 5646.2007.00284.x.

567 Freeman S, Jackson W. 1990. Univariate metrics are not adequate to measure avian body size.
568 *Auk.* 107(1):69–74. doi:10.2307/4087803.

569 Gowaty P. 1996. Battle of sexes and origins of monogamy. In: *Partnerships in Birds: the*
570 *Study of Monogamy.* Oxford University Press. p. 21–52.

571 Gray EM. 1997. Female red-winged blackbirds accrue material benefits from copulating with
572 extra-pair males. *Anim Behav.* 53(3):625–639. doi:10.1006/anbe.1996.0336.

573 Griffin AS, Alonzo SH, Cornwallis CK. 2013. Why Do Cuckolded Males Provide Paternal
574 Care? *PLoS Biol.* 11(3):1–9. doi:10.1371/journal.pbio.1001520.

575 Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds : a review of
576 interspecific. *Mol Ecol.* 11:2195–2212.

577 Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. *Mol Ecol.*
578 7(8):1071–1075. doi:10.1046/j.1365-294x.1998.00389.x.

579 Halekoh U, Højsgaard S, Yan J. 2006. The R Package geepack for Generalized Estimating
580 Equations. *J Stat Softw.* 15(2):1–11. doi:10.18637/jss.v015.i02.

581 Harrison XA, York JE, Cram DL, Young AJ. 2013. Extra-group mating increases inbreeding
582 risk in a cooperatively breeding bird. *Mol Ecol.* 22(22):5700–5715. doi:10.1111/mec.12505.

583 Hawley DM, Sydenstricker K V., Kollias G V., Dhondt AA. 2005. Genetic diversity predicts
584 pathogen resistance and cell-mediated immunocompetence in house finches. *Biol Lett.*
585 1(3):326–329. doi:10.1098/rsbl.2005.0303.

586 Heagerty PJ, Zeger SL. 2000. Marginalized multilevel models and likelihood inference. *Stat*
587 *Sci.* 15(1):1–19. doi:10.1214/ss/1009212671.

588 Heg D, Ens BJ, Burke T, Jenkins L, Kruijt JP. 1993. Why does the typically monogamous
589 oystercatcher (*Haematopus ostralegus*) engage in extra-pair copulations? *Behaviour.* 126(3–
590 4):247–290.

591 Hoi-Leitner M, Hoi H, Romero-Pujante M, Valera F. 1999. Female extra-pair behaviour and
592 environmental quality in the serin (*Serinus serinus*): A test of the “constrained female
593 hypothesis.” *Proc R Soc B Biol Sci.* 266(1423):1021–1026. doi:10.1098/rspb.1999.0738.

594 Horton NJ, Lipsitz SR. 1999. Review of software to fit generalized estimating equation
595 regression models. *Am Stat.* 53(2):160–169. doi:10.1080/00031305.1999.10474451.

596 Husemann M, Cousseau L, Callens T, Matthysen E, Vangestel C, Hallmann C, Lens L. 2015.
597 Post-fragmentation population structure in a cooperative breeding Afrotropical cloud forest
598 bird: Emergence of a source-sink population network. *Mol Ecol.* 24(6):1172–1187.
599 doi:10.1111/mec.13105.

600 Johnson AE, Pruett-Jones S. 2018. Reproductive promiscuity in the variegated fairy-wren: an
601 alternative reproductive strategy in the absence of helpers? *Anim Behav.* 139:171–180.
602 doi:10.1016/j.anbehav.2018.03.015.

603 Jones AG, Ardren WR. 2003. Methods of parentage analysis in natural populations. *Mol Ecol.*
604 12(10):2511–2523. doi:10.1046/j.1365-294X.2003.01928.x.

605 Jones OR, Wang J. 2010. COLONY: A program for parentage and sibship inference from

606 multilocus genotype data. *Mol Ecol Resour.* 10(3):551–555. doi:10.1111/j.1755-
607 0998.2009.02787.x.

608 Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A,
609 Markowitz S, Duran C, et al. 2012. Geneious Basic: An integrated and extendable desktop
610 software platform for the organization and analysis of sequence data. *Bioinformatics.*
611 28(12):1647–1649. doi:10.1093/bioinformatics/bts199.

612 Kempnaers B. 1993. A Case of Polyandry in the Blue Tit: Female Extra-Pair Behaviour
613 Results in Extra Male Help. *Ornis Scand.* 24(3):246. doi:10.2307/3676741.

614 Kempnaers B. 2007. Mate Choice and Genetic Quality: A Review of the Heterozygosity
615 Theory. *Adv Study Behav.* 37(07):189–278. doi:10.1016/S0065-3454(07)37005-8.

616 Kempnaers B, Verheyen GR, Dhondt AA. 1997. Extrapair paternity in the blue tit (*Parus*
617 *caeruleus*): Female choice, male characteristics, and offspring quality. *Behav Ecol.* 8(5):481–
618 492. doi:10.1093/beheco/8.5.481.

619 Kleven O, Jacobsen F, Robertson RJ, Lifjeld JT. 2005. Extrapair mating between relatives in
620 the barn swallow: A role for kin selection? *Biol Lett.* 1(4):389–392.
621 doi:10.1098/rsbl.2005.0376.

622 Komdeur J. 1992. Importance of habitat saturation and territory quality for evolution of
623 cooperative breeding in the Seychelles warbler. *Nature.* 358(6386):493–495.
624 doi:10.1038/358493a0.

625 Krokene C. 1998. The function of extrapair paternity in blue tits and great tits: good genes or
626 fertility insurance? *Behav Ecol.* 9(6):649–656. doi:10.1093/beheco/9.6.649.

627 Lampila S, Orell M, Kvist L. 2011. Willow tit *Parus montanus* extrapair offspring are more
628 heterozygous than their maternal half-siblings. *J Avian Biol.* 42(4):355–362.

629 doi:10.1111/j.1600-048X.2011.05349.x.

630 Legge S. 2000. The effect of helpers on reproductive success the laughing kookaburra. *J*
631 *Anim Ecol.* 69(4):714–724. doi:10.1046/j.1365-2656.2000.00429.x.

632 Lens L, Van Dongen S, Norris K, Githiru M, Matthysen E. 2002. Avian persistence in
633 fragmented rainforest. *Science.* 298(May 1999):1236–1238. doi:10.1126/science.1075664.

634 Li CC, Weeks BE, Chakravarti A. 1993. Similarity of DNA fingerprints due to chance and
635 relatedness. *Hum Hered.* 43(1):45–52. doi:10.1159/000154113.

636 Lombardo MP, Thorpe PA. 2000. Microbes in tree swallow semen. *J Wildl Dis.* 36(3):460–
637 468. doi:10.7589/0090-3558-36.3.460.

638 Van de Loock D. 2019. Life-history strategies of a facultative cooperative breeder in a
639 fragmented Afrotropical cloud forest. PhD thesis. Ghent University.

640 Lynch M. 1988. Estimation of relatedness by DNA fingerprinting. *Mol Biol Evol.* *Mol.*
641 *Biol.*(5):584–599. doi:10.1093/oxfordjournals.molbev.a040518.

642 Lynch M, Ritland K. 1999. Estimation of pairwise relatedness with molecular markers.
643 *Genetics.* 152(4):1753–1766.

644 Markert JA, Grant PR, Grant BR, Keller LF, Coombs JL, Petren K. 2004. Neutral locus
645 heterozygosity, inbreeding, and survival in Darwin’s ground finches (*Geospiza fortis* and *G.*
646 *scandens*). *Heredity (Edinb).* 92(4):306–315. doi:10.1038/sj.hdy.6800409.

647 Miller JM, Coltman DW. 2014. Assessment of identity disequilibrium and its relation to
648 empirical heterozygosity fitness correlations: A meta-analysis. *Mol Ecol.* 23(8):1899–1909.
649 doi:10.1111/mec.12707.

650 Milligan BG. 2003. Maximum-likelihood estimation of relatedness. *Genetics.* 163:1153–

651 1167.

652 Mitton JB, Schuster WSF, Cothran EG, De Fries JC. 1993. Correlation between the individual
653 heterozygosity of parents and their offspring. *Heredity (Edinb)*. 71(1):59–63.
654 doi:10.1038/hdy.1993.107.

655 Møller AP, Birkhead T. 1993. Certainty of Paternity Covaries with Paternal Care in Birds.
656 *Behav Ecol Sociobiol*. 33(4):261–268.

657 Moreno J, Martínez JG, González-Braojos S, Cantarero A, Ruiz-de-Castañeda R, Precioso M,
658 López-Arrabé J. 2015. Extra-pair paternity declines with female age and wing length in the
659 pied flycatcher. *Ethology*. 121(5):501–512. doi:10.1111/eth.12364.

660 Mulder RA, Dunn PO, Cockburn A, Lazenby-Cohen KA, Howell MJ. 1994. Helpers liberate
661 female fairy-wrens from constraints on extra-pair mate choice. *Proc R Soc B Biol Sci*.
662 255(1344):223–229. doi:10.1098/rspb.1994.0032.

663 Neff BD, Pitcher TE. 2005. Genetic quality and sexual selection: An integrated framework for
664 good genes and compatible genes. *Mol Ecol*. 14(1):19–38. doi:10.1111/j.1365-
665 294X.2004.02395.x.

666 Nietlisbach P, Keller LF, Postma E. 2016. Genetic variance components and heritability of
667 multiallelic heterozygosity under inbreeding. *Heredity (Edinb)*. 116(1):1–11.
668 doi:10.1038/hdy.2015.59.

669 Pan W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics*.
670 57(1):120–125. doi:10.1111/j.0006-341X.2001.00120.x.

671 Peig J, Green AJ. 2009. New perspectives for estimating body condition from mass/length
672 data: The scaled mass index as an alternative method. *Oikos*. 118(12):1883–1891.
673 doi:10.1111/j.1600-0706.2009.17643.x.

674 Pellikka PKE, Lötjönen M, Siljander M, Lens L. 2009. Airborne remote sensing of
675 spatiotemporal change (1955-2004) in indigenous and exotic forest cover in the Taita Hills,
676 Kenya. *Int J Appl Earth Obs Geoinf.* 11(4):221–232. doi:10.1016/j.jag.2009.02.002.

677 Queller DC, Goodnight KF. 1989. Estimating Relatedness Using Genetic Markers. *Evolution*
678 (N Y). 43(2):258. doi:10.2307/2409206.

679 R Core Development Team. 2017. A language and environment for statistical computing.

680 Raj Pant S, Komdeur J, Burke TA, Dugdale HL, Richardson DS. 2019. Socio-ecological
681 conditions and female infidelity in the Seychelles warbler. *Behav Ecol.*:1–11.
682 doi:10.1093/beheco/arz072.

683 Richards SA, Whittingham MJ, Stephens PA. 2011. Model selection and model averaging in
684 behavioural ecology: The utility of the IT-AIC framework. *Behav Ecol Sociobiol.* 65(1):77–
685 89. doi:10.1007/s00265-010-1035-8.

686 Ritland K. 1996. Estimators for pairwise relatedness and individual inbreeding coefficients.
687 *Genet Res.* 67(2):175–185. doi:10.1017/s0016672300033620.

688 Rubenstein DR. 2007. Female extrapair mate choice in a cooperative breeder: Trading sex for
689 help and increasing offspring heterozygosity. *Proc R Soc B Biol Sci.* 274(1620):1895–1903.
690 doi:10.1098/rspb.2007.0424.

691 Sardell RJ, Arcese P, Keller LF, Reid JM. 2012. Are there indirect fitness benefits of female
692 extra-pair reproduction? Lifetime reproductive success of within-pair and extra-pair offspring.
693 *Am Nat.* 179(6):779–793. doi:10.1086/665665.

694 Schmoll T, Schurr FM, Winkel W, Epplen JT, Lubjuhn T. 2009. Lifespan, lifetime
695 reproductive performance and paternity loss of within-pair and extra-pair offspring in the coal
696 tit *Parus ater*. *Proc R Soc B Biol Sci.* 276(1655):337–345. doi:10.1098/rspb.2008.1116.

697 Senar JC, Pascual J. 1997. Keel and tarsus length may provide a good predictor of avian body
698 size. *ardea*. 85:269–274.

699 Sheldon BC. 2002. Relating paternity to paternal care. *Philos Trans R Soc B Biol Sci*.
700 357(1419):341–350. doi:10.1098/rstb.2001.0931.

701 Smith SB, McKay JE, Murphy MT, Duffield DA. 2016. Spatial patterns of extra-pair
702 paternity for spotted towhees *Pipilo maculatus* in urban parks. *J Avian Biol*. 47(6):815–823.
703 doi:10.1111/jav.00931.

704 Stoffel MA, Esser M, Kardos M, Humble E, Nichols H, David P, Hoffman JI. 2016.
705 *inbreedR*: an R package for the analysis of inbreeding based on genetic markers. *Methods*
706 *Ecol Evol*. 7(11):1331–1339. doi:10.1111/2041-210X.12588.

707 Tarvin KA, Webster MS, Tuttle EM, Pruett-Jones S. 2005. Genetic similarity of social mates
708 predicts the level of extrapair paternity in splendid fairy-wrens. *Anim Behav*. 70(4):945–955.
709 doi:10.1016/j.anbehav.2005.01.012.

710 Valera F, Hoi H, Kristín A. 2003. Male shrikes punish unfaithful females. *Behav Ecol*.
711 14(3):403–408. doi:10.1093/beheco/14.3.403.

712 Wang C, Lu X. 2011. Female ground tits prefer relatives as extra-pair partners: Driven by kin-
713 selection? *Mol Ecol*. 20(13):2851–2863. doi:10.1111/j.1365-294X.2011.05070.x.

714 Wang J. 2002. An Estimator for Pairwise Relatedness Using Molecular Markers.
715 1215(March):1203–1215.

716 Wang J. 2007. Triadic IBD coefficients and applications to estimating pairwise relatedness.
717 *Genet Res*. 89(3):135–153. doi:10.1017/S0016672307008798.

718 Wang J. 2010. Do marker-based paternity assignments favour heterozygous and unrelated
719 males? *Mol Ecol*. 19(9):1898–1913. doi:10.1111/j.1365-294X.2010.04601.x.

720 Wang J. 2011. Coancestry: A program for simulating, estimating and analysing relatedness
721 and inbreeding coefficients. *Mol Ecol Resour.* 11:141–145. doi:10.1111/j.1755-
722 0998.2010.02885.x.

723 Warton DI, Duursma RA, Falster DS, Taskinen S. 2012. smatr 3- an R package for estimation
724 and inference about allometric lines. *Methods Ecol Evol.* 3(2):257–259. doi:10.1111/j.2041-
725 210X.2011.00153.x.

726 Webster MS, Tarvin KA, Tuttle EM, Pruett-Jones S. 2004. Reproductive promiscuity in the
727 splendid fairy-wren: Effects of group size and auxiliary reproduction. *Behav Ecol.* 15(6):907–
728 915. doi:10.1093/beheco/arh093.

729 Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and
730 conflict. *Annu Rev Ecol Evol Syst.* 34:365–396. doi:10.1146/132439.

731 Wetton JH, Parkin DT. 1991. An association between fertility and cuckoldry in the house
732 sparrow, *Passer domesticus*. *Proc R Soc B Biol Sci.* 245(1314):227–233.
733 doi:10.1098/rspb.1991.0114.

734 Wetzel DP, Westneat DF. 2009. Heterozygosity and extra-pair paternity: Biased tests result
735 from the use of shared markers. *Mol Ecol.* 18(9):2010–2021. doi:10.1111/j.1365-
736 294X.2009.04114.x.

737 Whittingham LA, Dunn PO, Magrath RD. 1997. Relatedness, polyandry and extra-group
738 paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behav*
739 *Ecol Sociobiol.* 40(4):261–270. doi:10.1007/s002650050341.

740 Zeh JA, Zeh DW. 1996. The evolution of polyandry I: Intragenomic conflict and genetic
741 incompatibility. *Proc R Soc B Biol Sci.* 263(1377):1711–1717. doi:10.1098/rspb.1996.0250.

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743 **TABLES**

744 **Table 1.** Model selection of factors explaining variation in (a) the proportion of broods with at least one extra-pair young and in (b) the
 745 proportion of extra-pair young in a brood (n = 104 nests). Effect sizes and 95% confidence intervals are reported for each explanatory variable.

Model	Intercept	# Helpers	Female characteristics		Male characteristics		Popu- lation	Year	K	QL	QICc	ΔQICc	Weight
			Tarsus	Het.	Het.	Tarsus	Rel.						
(a)	-17.07 [-38.28; 4.14]	0.77 [0.17; 1.37]	0.64 [-0.16; 1.43]						3	-68.45	142.55	0.00	0.13
	-0.08 [-0.59; 0.42]	0.69 [0.14; 1.24]							2	-69.77	143.18	0.63	0.10
	-15.59 [-36.76; 5.58]	0.79 [0.19; 1.39]	0.62 [-0.17; 1.41]		-1.14 [-3.09; 0.82]				4	-68.00	143.55	0.99	0.08
	-26.58 [-55.08; 1.92]	0.76 [0.16; 1.36]	0.60 [-0.21; 1.41]			0.38 [-0.47; 1.24]			4	-68.34	144.17	1.61	0.06
	1.14 [0.94; 3.23]	0.72 [0.17; 1.27]			-1.23 [-3.23; 0.77]				3	-69.41	144.44	1.89	0.05
	-12.92 [-36.79; 10.95]	0.69 [0.13; 1.25]				0.47 [-0.40; 1.33]			3	-69.38	144.44	1.89	0.05
	-17.03 [-38.32; 4.26]	0.77 [0.16; 1.37]	0.64 [-0.16; 1.43]				-0.10 [-2.08; 1.89]		4	-68.44	144.60	2.04	0.05
	-17.55 [-39.69; 4.60]	0.76 [0.16; 1.36]	0.65 [-0.16; 1.46]	0.13 [-1.91; 2.16]					4	-68.42	144.77	2.22	0.04
	-0.08 [-0.60; 0.45]	0.69 [0.14; 1.24]					-0.14 [-2.01; 1.80]		3	-69.75	145.15	2.60	0.04
	0.20 [-0.23; 0.64]								1	-71.81	145.77	3.22	0.03
(b)	-0.11 [-0.50; 0.27]								1	-71.61	147.10	0.00	0.21
	-0.33 [-0.80; 0.14]	0.43 [-0.07; 0.93]							2	-70.36	147.66	0.56	0.16

1.63	0.48	-1.96		3	-69.74	149.47	2.37	0.06
[-0.13; 3.40]	[-0.01; 0.98]	[-3.66; -0.27]						
1.80		-1.89		2	-71.22	149.55	2.45	0.06
[0.00; 3.59]		[-3.61; -0.17]						
-15.69			0.56	2	-71.03	149.65	2.55	0.06
[-37.75; 6.36]			[-0.24; 1.36]					

746

747 Model rank is based on Quasi-likelihood under the Independence model Criterion value corrected for small sample size (QICc). Het. and Rel. corresponds to, respectively heterozygosity and
748 relatedness to the dominant female (Queller & Goodnight moment estimator). K is the number of parameters estimated for fixed effects (including the intercept), QL is the quasi-likelihood of the
749 model, Δ QICc denotes the change in QICc relative to the best model and weight is the QICc weight of the model. Only top ranked models (Δ QICc < 3) and the null model are presented. Only
750 variables that appeared in these top ranked models are presented. Retained models are in bold.

751

752

753 **Table 2.** Model selection of factors explaining variation in within-nest differences in food provisioning rates (a) between dominant males and
 754 females (n = 110 nests) and (b) between dominant males and helpers (n = 41 nests). Difference between residuals, obtained from regressing food
 755 provisioning rates (feeds/h/nestling) to mean prey size, was used as a response variable. Effect sizes and 95% confidence intervals are reported
 756 for each explanatory variable.

757

Model	Intercept	# Helpers ¹	Population ²	Year	K	QL	QICc	ΔQICc	Weight
(a)	-0.41 [-0.68; -0.14]	1 helper: -0.01 [-0.37; 0.35] >1 helpers: 0.96 [0.51; 1.42]			2	-53.13	111.00	0.00	0.66
	-0.23 [-0.61; 0.16]	1 helper: -0.01 [-0.37; 0.35] >1 helpers: 0.91 [0.41; 1.42]	Ngangao: -0.28 [-0.69; 0.13] Small fragments: -0.38 [-0.93; 0.18]		5	-51.94	113.03	2.03	0.24
	-0.34				1	-57.00	116.12	5.12	0.05
(b)	-0.17 [-0.84; 0.46]	>1 helpers: 0.42 [0.06; 0.80]			2	-13.04	29.50	0.00	0.37
	0.35 [0.09; 0.59]				1	-13.70	29.71	0.18	0.34
	0.64 [0.32; 0.95]		Ngangao: -0.53		3	-12.50	31.22	1.65	0.16

765

766 **Table 3.** Model selection of factors explaining variation in male food provisioning rates (n = 81 nests). Residuals, obtained from regressing food
 767 provisioning rates (feeds/h/nestling) to mean prey size, were used as a response variable. Effect sizes and 95% confidence intervals are reported
 768 for each explanatory variable.

Intercept	Nestling age	# Helpers ¹	Occurrence EPP	Proportion EP young	Population ²	Year	K	QL	QICc	ΔQICc	Weight
-0.50 [-1.27; 0.28]	0.05 [-0.05; 0.15]						2	-20.47	45.08	0.00	0.35
-0.48 [-1.26; 0.31]	0.05 [-0.05; 0.15]			-0.06 [-0.39; 0.28]			5	-20.44	46.84	1.76	0.15
-0.51 [-1.28; 0.27]	0.05 [-0.05; 0.15]		0.03 [-0.28; 0.34]				3	-20.46	47.30	2.22	0.12
-0.42 [-1.19; 0.36]	0.04 [-0.06; 0.14]	1 helper: -0.15 [-0.47; 0.18] >1 helpers: 0.08 [-0.22; 0.37]					4	-20.24	47.44	2.36	0.11
-0.31 [-1.08; 0.46]	0.05 [-0.06; 0.16]				Ngangao: -0.38 [-0.74; -0.02] Small fragments: -0.14 [-0.70; 0.43]		4	-19.24	47.62	2.54	0.10

769

770 Model rank is based on Quasi-likelihood under the Independence model Criterion value corrected for small sample size (QICc). K is the number of parameters estimated for fixed effects
 771 (including the intercept), QL is the quasi-likelihood of the model, ΔQICc denotes the change in QICc relative to the best model and weight is the QICc weight of the model. Only top ranked
 772 models (ΔQICc < 3) and the null model (i.e. nestling age only) are presented. Retained models are in bold. ¹ The reference number of helpers was 0 for model (a) and 1 for model (b). ² The
 773 reference population was Chawia.

