1   **Title page**

2   **Title:** Facultative adjustment of paternal care in the face of female infidelity in dunnocks.

3   **Authors' names:** Eduardo S. A. Santos[1, 2*] and Shinichi Nakagawa[1, 3]

4   **Affiliations:** [1] Department of Zoology, 340 Great King Street, University of Otago, Dunedin, New

5   Zealand. [2] BECO do Departamento de Zoologia, Universidade de São Paulo, São Paulo, Brazil. [3]

6   Evolution & Ecology Research Centre and School of Biological, Earth and Environmental Sciences,

7   University of New South Wales, Sydney, Australia.

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12   [*]**Correspondence:** Eduardo S. A. Santos

13   BECO do Departamento de Zoologia, Rua do Matão, Travessa 14, n° 101, Cidade Universitária, São

14   Paulo, 05508-090, Brazil. E-mail: eduardo.sa.santos@ib.usp.br; phone: + 55 (11) 3091-0989, fax: +55

15   (11) 3091-7802.

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17   **Running title:** Within-male adjustment of paternal care

18 **Abstract**

19 A much-debated issue is whether or not males should reduce parental care when they lose paternity

20 (i.e. the certainty of paternity hypothesis). While there is general support for this relationship across

21 species, within-population evidence is still contentious. Among the main reasons behind such problem

22 is the confusion discerning between- from within-individual patterns. Here, we tested this hypothesis

23 empirically by investigating the parental care of male dunnocks (*Prunella modularis*) in relation to

24 paternity. We used a thorough dataset of observations in a wild population, genetic parentage, and a

25 within-subject centring statistical approach to disentangle paternal care adjustment within-male and

26 between males. We found support for the certainty of paternity hypothesis, as there was evidence for

27 within-male adjustment in paternal care when socially monogamous males lost paternity to extra-pair

28 sires. There was little evidence of a between-male effect overall. Our findings show that monogamous

29 males adjust paternal care when paired to the same female partner. We also show that – in

30 monogamous broods – the proportion of provisioning visits made by males yields fitness benefits in

31 terms of fledging success. Our results suggest that socially monogamous females that engage in extra-

32 pair behaviour may suffer fitness costs, as their partners' reduction in paternal care can negatively

33 affect fledging success.

34

Introduction

36 Parental investment is stated as an investment by the parent in the young that increases the young's

37 chance of survival at a cost to the parent's future ability to invest in other offspring (Trivers 1972;

38 Smiseth et al. 2012). Thus, an individual should only invest into providing parental care when the

39 fitness benefits are greater than the costs. The amount of care that a parent should provide is

40 constrained by a series of factors, but mostly by factors that affect the reproductive value of current

41 young, and factors that affect the residual reproductive value of parents (Klug et al. 2012). From a

42 male parent perspective, the reproductive value of a brood should depend on the benefit that the

43 offspring will gain from his paternal care conditional on the relatedness between the offspring and

44 himself; a relationship known as Hamilton's rule (Hamilton 1964a; Hamilton 1964b). However, the

45 male's relatedness to offspring in a brood is frequently uncertain, as females often produce extra-pair

46 offspring. Extra-pair paternity is a common phenomenon across animals (e.g., reptiles: reviewed by

47 Uller and Olsson 2008; fish: reviewed by Coleman and Jones 2011, and it has been extensively

48 investigated in birds, reviewed by Griffith et al. 2002). Given the costs that parental care should exert

49 (Royle et al. 2012), the amount of paternal care should be related to a male's certainty of paternity

50 (Trivers 1972). This intuitive relationship has received large theoretical and empirical attention

51 (reviewed in Sheldon 2002; Griffin et al. 2013; Forstmeier et al. 2014; Schroeder et al. 2016), but the

52 results have been ambiguous.

53   Different types of theoretical models have three main predictions concerning the intra-specific

54 question of whether males should adjust paternal care when paternity is uncertain. First, an initial set

55 of models predicted that loss of paternity may seldom or rarely influence paternal care (Maynard

56 Smith 1978; Grafen 1980). These early models assumed that there is no paternity evaluation, and the

57 only cost of paternal care is time-out from the mating pool. A second group of models predicted that

58 males should decrease their total paternal care towards a brood when certainty of paternity is low (Xia

59 1992; Whittingham et al. 1992; Westneat and Sherman 1993). These models assumed that males have

60 the capacity of assessing their paternity. The third and final group of models predicted that loss of

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61   paternity may not only reduce paternal care, but it may also lead to discrimination against non-kin,

62   which would incur in changes in allocation towards individual offspring (Westneat and Sherman 1993;

63   Johnstone 1997).

64   Numerous empirical studies have tested whether a negative relationship between paternal care

65   and loss of paternity exists (hereafter, the certainty of paternity hypothesis) (reviewed in Griffin et al.

66   2013). While there is general meta-analytic support for the certainty of paternity hypothesis (Griffin et

67   al. 2013), there is also unexplained variation that may be caused by the sampling design of the study.

68   The discussions on what approaches are most appropriate to examine the certainty of paternity

69   hypothesis were published almost 20 years ago (Kempenaers and Sheldon 1997; Kempenaers and

70   Sheldon 1998; Lifjeld et al. 1998; Wagner et al. 1998; Sheldon 2002), but are still pertinent given the

71   large variation reported recently (Griffin et al. 2013). Kempenaers and Sheldon (1997), and Sheldon

72   (2002) suggested that in order to reduce the effect of confounding factors, and to appropriately test the

73   certainty of paternity hypothesis, two approaches should be used: 1) the analysis of sequential

74   breeding attempts by the same male-female pair, or 2) experimental studies that remove/detain mated

75   males or females during the fertile period of the female. Almost certainly due to logistic difficulties of

76   the first approach, most studies to date have examined the certainty of paternity hypothesis either

77   using simple correlational or experimental evidence across broods from different pairs (see Griffin et

78   al. 2013 for a recent meta-analysis that includes both types of studies; and see Schroeder et al. 2016

79   for an example of the first approach).

80   The aim of this study was to test whether males reduce their paternal care (i.e. certainty of

81   paternity hypothesis) or not when their share of paternity decreases in a brood. To achieve this aim, we

82   conducted a field study that replicated the seminal investigation by Burke et al. (1989) of paternity and

83   paternal care in the dunnock, *Prunella modularis*, using a population introduced into New Zealand.

84   Dunnocks breed in 'cooperatively' polyandrous groups, and females copulate with several males; both

85   their social partners and extra-group males (Burke et al. 1989; Santos et al. 2015a). It has been shown

86   (Davies 1992) that male dunnocks provide paternal care in relation to their share of mating access with

87   a female. More specifically, this only occurred in polyandrous and polygynandrous groups when a

88   second male also fed the young (Davies 1992). Thus, male dunnocks are likely to have been selected

89   to perceive their certainty of paternity. We investigated whether variation in paternal care (within-

90   male and between-males, and within-pair and between-pairs) is associated with levels of paternity

91   using a simple statistical approach, within-subject centring (see van de Pol and Wright 2009). We also

92   estimated the repeatability of paternal care as a further test of whether males alter their levels of care

93   between different breeding attempts in which paternity often differed. Moreover, we investigated

94   whether levels of paternal care yielded benefits to current offspring or costs to the males that provided

95   care.

96   **Materials and methods**

97   **General procedures**

98   Dunnocks have a complex and variable social mating system, with birds from the same population

99   breeding in socially monogamous, polyandrous, polygynous or polygynandrous groups (Davies 1992;

100   Santos and Nakagawa 2013). We studied a population of dunnocks in a 7-hectare area of the Dunedin

101   Botanic Garden, Dunedin, New Zealand, during three breeding seasons (September to January, 2009-

102   2012). Dunnocks were introduced into New Zealand in the 19th century, and approximately 185

103   individuals were released around Dunedin (see Santos 2012; Moulton et al. 2014, but see Pipek et al.

104   2015). Effective population size at our study site has been estimated at 54 breeding individuals (Santos

105   et al. 2013). All adults and nestlings were individually colour ringed (nestlings: day 9), and blood

106   sampled under the Animal Ethics Committee of the University of Otago, permit no. 08/09 and the

107   New Zealand National Bird Banding Scheme Institutional Permit to Band Birds no. 2008/075.

108   **Genotyping and assignment of paternity**

109   To determine paternity, we screened the genotypes of individuals using a set of 16 polymorphic

110   microsatellite loci (for further details of molecular methods see Santos et al. 2015a, and Santos et al.

111   2015b. We assigned paternity using *MasterBayes* version 2.47 (Hadfield et al. 2006) (see Santos et al.

112   2015a for details). Overall, irrespective of social group composition, *MasterBayes* assigned 17.0%

113   (49/288) of chicks as extra-group young (EGY), and 26.5% of broods (26/98) contained ≥ 1 EGY. Of

114   the chicks of socially monogamous pairs, 23.3% (32/137) were assigned as EGY, whereas only 9.9%

115   (14/143) of the chicks of socially polyandrous groups were assigned as EGY. Within polyandrous

116   groups, subordinate males sired 44.0% (63/143) of chicks (Santos et al. 2015a).

117   **Measuring paternal care**

118   We identified members and characterized the social group composition by conducting thorough

119   behavioural observations within each territory (further details of behavioural work in Santos and

120   Nakagawa 2013). The dominance status of co-breeding males was inferred from behavioural

121   observations of displacement at feeding sites, singing perches and from the vicinity of the group's

122   female. We recorded nestling provisioning behaviour using GoPro Hero HD cameras with 16 GB

123   memory cards. Video cameras were set at 10 to 15 cm from the nest rim focusing into the nest cup.

124   We filmed nests on two consecutive days (nestlings age: 8 and 9 days). Chick age had very little, and

125   non-significant, effect on paternal care, thus it was not included in the final analyses ($\beta_{(slope\ of\ chick\ age)}$ =

126   0.016, 95% CI: -0.089 to 0.129). We chose to film the nests at this stage because this is the peak

127   provisioning period of dunnocks (Hatchwell and Davies 1990). These recordings were also used to

128   ascertain social group composition. We quantified male parental care as the number of visits and the

129   number of feeds during the segment of the recordings encompassed between the first provisioning

130   visit of any adult and finishing at the end of the recorded file (defined as effective observational time,

131   Nakagawa et al. 2007; mean effective observational time = 2.10 hours (SD: 0.573), *n* = 158 focal

132   observations from 77 different nests).

133   **Statistics**

134   We analysed our paternal care data using Bayesian mixed-effects models (BMM), with Poisson error

135   distribution within the package *MCMCglmm* (Hadfield 2010) for *R* version 3.3.0 (R Core Team 2016).

136   Because we have reasons to expect the number of visits and the number of feeds to be proportional to

137   the length of the observation period, we included the natural logarithm of the effective observation

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138 time as an offset in the exposure Poisson BMMs, and fixed its coefficient to 1 (Snijders and Bosker

139 2011; see Supporting Information for more details). By using the offset term, we avoided having to

140 convert the raw count data into a ratio, thus making interpretation of the results more convenient. We

141 included the type of social group composition (categorical with 2 levels: monogamous and

142 polyandrous), and brood size (continuous; centred and scaled) as predictors.

Correlation between number of visits and number of feeds

144 First, we estimated the correlation between the number of visits and the number of feeds because these

145 two variables are likely to be highly correlated (see Supporting Information S1 for details of bivariate-

146 response model to estimate the correlation). We found a strong positive correlation between the

147 number of visits and the number of feeds (posterior mean correlation: $r_{between-individual}$ = 0.940; 95% CI:

148 0.753 to 0.985; $r_{within-individual}$ = 0.786; 95% CI: 0.681 to 0.859). Here, we present results of models

149 using the number of visits as a measure of paternal care.

Adjustment of paternal care

151 As we were mainly interested in the effect of the proportion of EGY on within male paternal care, we

152 used individual centring to separate within- versus between-individual effects in our BMMs (van de

153 Pol and Wright 2009). This approach allowed us to quantify the effect of the proportion of EGY on

154 paternal care among sequential broods of a particular male (within-male effect; n = 17 pairs with 2 or

155 more breeding attempts together), and to quantify the effect between males (between-male difference;

156 n = 66 pairs).

157   We found evidence of within-male adjustment of care (see Result section below);

158 monogamous males adjust their visitation rate according to the extra-pair offspring produced by their

159 partners. Thus, we wanted to know whether this within-individual adjustment was caused by: (i)

160 different female partners producing different numbers of extra-pair offspring; or (ii) same female

161 partners producing different number of extra-pair offspring in successive broods with the same male.

162 We built another model with number of visits of socially monogamous males as the response variable.

163   In this model, we used three fixed effects: within-male within pair deviation, within-male but between

164   pair deviation, and between males. In addition to male identity and nest identity, we included pair

165   identity as another random effect.

166   Finally, to account for the multilevel nature of our data, we included male identity and nest

167   identity as random effects in all the models. We estimated the repeatability of paternal care in order to

168   assess individual male consistency among different breeding attempts (see Supporting Information S1

169   for details). We present back-transformed (original count scale) model estimates as posterior means

170   and their 95% credible intervals (95% CI). We considered parameters with 95% CIs not spanning zero

171   to be statistically significant.

172   To test whether males reduce paternal care or not when paternity decreases, we fit the

173   proportion of extra-group young (EGY) in a brood as a predictor in our exposure Poisson BMM. We

174   considered the effect of within-group paternity by subordinate co-breeding males on the paternal care

175   of dominant and subordinate co-breeding males in separate models. These analyses were a more

176   appropriate way to compare our findings with those of Burke et al. (1989), as in their study there was

177   no evidence of extra-group paternity, but the authors found that dominant co-breeding males in

178   socially polyandrous groups were more likely to feed young in broods in which they gained paternity.

179   In order to provide a similar analysis to that conducted by Burke et al. (1989) on whether subordinate

180   males were less likely to provide care when they gained no paternity, we also investigated whether

181   there was a difference in the number of visits by subordinate males that gained paternity in a brood,

182   versus those that did not gain any paternity. This analysis was achieved using an exposure Poisson

183   BMM, fitting whether subordinate males gained paternity or not as a categorical predictor.

184   We investigated whether paternal care was beneficial to broods by estimating the effect of the

185   relative participation by males to the total nest visitation on the proportion of young that fledged from

186   each nest. We fit a binomial Bayesian model, in *MCMCglmm*, with the proportion of young that

187   fledged as the response variable (we used the *cbind* function to combine the number of fledglings and

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188   number of young that failed to fledge as the response variable), and the proportion of nest visits by

189   males (centred, scaled) (Schielzeth 2010) as a continuous predictor. We also included the type of

190   social group composition (monogamy or polyandry) as a categorical predictor in this model.

191   To assess whether paternal care is costly to males, we estimated a male's survival until the

192   subsequent breeding season (n = 42 males; three breeding seasons) as a function of the amount of

193   paternal effort during a breeding season. Male paternal effort was estimated as his average

194   provisioning visitation rate to all his nests during a given breeding season. We used a Cormack-Jolly-

195   Seber survival model based on our mark-recapture data to estimate the effect of paternal effort in a

196   given breeding season on his probability to survive until the next breeding season. We included the

197   average number of visits per breeding season of the male as a covariate in the model and also the

198   identity of the breeding season in order to control for any year effect that might cause biases in

199   survival. Survival was estimated in the program *MARK* (White and Burnham 1999).

200

201   **Results**

202   **General results**

203   In total, we obtained 357 hours of paternal care footage, recorded from 66 unique nesting attempts that

204   had paternity data available, attended by 42 and 36 unique males and females, respectively. Socially

205   polyandrous groups accounted for 60.6% (40/66) of nesting attempts, while monogamous pairs tended

206   the remaining 39.4% (26/66). Male number of visits increased significantly with brood size ($\beta_{(\text{slope of}}$

207    $_{\text{brood size})}$ = 0.247, 95% CI: 0.152 to 0.334). We found that co-breeding males in social polyandry made

208   on average 0.644 times significantly less ($\beta_{(\text{slope of polyandrous mating system})}$ = -0.439, 95% CI: -0.681 to -

209   0.197; Figure 1) nest visits than monogamous males after controlling for the length of the observation

210   period and brood size. Within- and between-season repeatabilities of male number of visits were

211   significantly different from 0, and moderate to high (between seasons repeatability of paternal care =

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212   0.794; Figure 2; see Table S1 in the Supporting Information for detailed results), which indicates that

213   males are likely to maintain their nest visitation rates among different breeding attempts. On average,

214   monogamous males had lower between-season repeatabilities (between seasons repeatability of

215   paternal care = 0.452) than co-breeding males (between seasons repeatability of paternal care = 0.791),

216   but there was substantial overlap of 95% CIs.

Paternal care and paternity

218   We found statistically significant evidence of a within-male effect, *i.e.* a negative relationship between

219   the proportion of extra-pair young in a brood and a male's number of visits, but only for socially

220   monogamous males (monogamy: $\beta_{(within-male\ effect)}$ = -0.732, 95% CI: -1.510 to -0.047; Figure 3). There

221   was little evidence that co-breeding males in socially polyandrous groups changed their number of

222   visits with changes in extra-group paternity (polyandry: $\beta_{(within-male\ effect)}$ = 0.592, 95% CI: -0.368 to

223   1.448; Figure 3). We found little evidence of a between-male effect of paternity on the number of

224   visits when examining the relationship across all pair broods (monogamy: $\beta_{(between-male\ effect)}$ = 0.194,

225   95% CI: -0.531 to 0.931; polyandry: $\beta_{(between-male\ effect)}$ = -0.121, 95% CI: -0.943 to 0.760).

226   We found that individual monogamous males adjusted their paternal care within-pairs (W_{mp};

227   monogamy: $\beta_{(within\ male\ within-pair\ effect)}$ = -1.169, 95% CI: -2.454 to -0.023). These males reduced their

228   visitation rate when there were more extra-pair offspring in nests of the same female partner. The

229   estimates for the parameter within males between-pairs was negative, but the 95% CI did span 0

230   (W_mB_p; monogamy: $\beta_{(within\ male\ between-pair\ effect)}$ = -0.665, 95% CI: -1.735 to 0.361).

231   In socially polyandrous groups, specifically, we found little evidence of an effect of the

232   proportion of young sired by subordinate males on the number of visits by dominant males ($\beta_{(within-pair}$

233     $_{effect)}$ = -0.346, 95% CI: -0.836 to 0.202; $\beta_{(between-pair\ effect)}$ = 0.054, 95% CI: -0.924 to 0.985).

234   Additionally, the proportion of young sired by subordinate males had little effect on their own number

235   of nest visits in socially polyandrous groups ($\beta_{(within-pair\ effect)}$ = -0.177, 95% CI: -0.921 to 0.589; $\beta_{(between-}$

236     $_{pair\ effect)}$ = -0.674, 95% CI: -3.475 to 2.186). Finally, there was little evidence of a difference in the

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237   number of nest visits by subordinate co-breeding males in social polyandry when they gained paternity

238   or not in a brood ($\beta_{(intercept)}$ = 0.864, 95% CI: 0.509 to 1.291; $\beta_{(gained\ paternity)}$ = -0.085, 95% CI: -0.532 to

239   0.381).

240   **Paternal care: its benefits to offspring and its costs to paternal males**

241   We found evidence that increments in male relative participation to total nest visitation increased

242   fledging success in monogamous broods ($\beta_{(scaled\ proportion\ male\ nest\ visits)}$ = 1.942, 95% CI: 0.139 to 3.846;

243   Figure 4), but not in polyandrous broods ($\beta_{(scaled\ proportion\ male\ nest\ visits)}$ = 0.526, 95% CI: -0.572 to 1.844).

244   There was little evidence that a male's paternal effort influenced his own survival until the next

245   breeding season (mean male survival = 0.892, 95% CI: 0.776 to 0.990; $\beta_{(paternal\ effort)}$ = -0.146, 95% CI:

246   -1.069 to 0.796).

247   **Discussion**

248   In this study, we tested whether dunnock males reduce their paternal care (*i.e.*, certainty of paternity

249   hypothesis) or not when their paternity decreases. We used a dataset with repeated observations and

250   genetic paternity in order to address this question. Our results corroborate the certainty of paternity

251   hypothesis, but only partially. We found evidence that socially monogamous males reduced paternal

252   care when they lost paternity to extra-pair sires. Nevertheless, such an effect only occurred when

253   investigating the certainty of paternity hypothesis between broods of the same breeding pair (within-

254   male within-pair effect). We found little evidence of a between-pair effect. Below we discuss some of

255   the implications of our findings.

256   Our results indicate that when within-male paternal care adjustment occurs – in socially

257   monogamous males –, it is likely in response to changes in the extra-pair behaviour of their female

258   partners. Which in turn suggests that socially monogamous males may be able to use information to

259   determine how much to invest in a brood. Our findings are in contrast with predictions from a sealed-

260   bid model (Houston and Davies 1985), in which paternal care levels would be optimized over

261   evolutionary time. Yet, we did not find evidence that co-breeding males in socially polyandrous

262   groups adjust their levels of care. This evidence from co-breeding males is in line with predictions

263   from a sealed-bid model. Combined, the findings of adjustment of paternal care in socially

264   monogamous males, and lack of adjustment in co-breeding males – in the same population – provide

265   an interesting case about the organization of parental care with regards to behavioural flexibility. Our

266   study indicates that the ability to adjust paternal provisioning behaviour is modulated by the breeding

267   status of male dunnocks (see Holtmann et al. 2015 for more details about breeding status).

268   Interestingly, our observations lead to a situation analogous to the "negotiation continuum" over the

269   supply of provisioning behaviour (Hinde and Kilner 2007) in within-population context.

270   In addition to the within-male within-pair adjustment of paternal care exhibited by socially

271   monogamous males, we found that these males' relative participation in nest visitation has an

272   important effect on fledging success. The combination of these two findings indicates that when

273   socially monogamous females engage in extra-pair behaviour, they put their own broods at risk.

274   Recently, Schroeder et al. (2016) found that male house sparrows adjust their levels of paternal care in

275   relation to cuckoldry. However, differently from our study, Schroeder et al. (2016) found that the

276   adjustment occurred when males changed partners that consistently differed in their levels of

277   cuckoldry. Yet, what both studies have in common is evidence that males adjust care when cuckold,

278   leading to costs to females (this study). Our findings, along with studies that have shown that females

279   suffer indirect costs when producing extra-pair offspring (Hsu et al. 2015) call for further theoretical

280   investigations of female infidelity.

281   Interestingly, our results do not bear similarities to another dunnock study. Davies et al.

282   (1992) did not find evidence that the experimental removal (and subsequent loss of paternity to extra-

283   pair males) of monogamous males from their territories during the mating period—before egg-

284   laying—altered their provisioning behaviour. A simple explanation for the divergence between the

285   results could be the fact that only two monogamous males were experimentally removed in Davies et

286   al. (1992) during the period before laying. It is likely that such a small sample size would not be

287   sufficient to detect an effect. Moreover, as we have shown in our study, the reduction in paternal care

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288   was only observed within-males within-pairs, thus, Davies et al. (1992) would not have been able to

289   detect the effect under their experimental design.

290   Contrary to Burke et al. (1989), which reported that polyandrous males that gained paternity

291   in their broods (dominant vs. subordinate males) were more likely to feed offspring than males that did

292   not gain paternity, we found little evidence that polyandrous males adjusted their levels of care in

293   relation to loss of paternity to both subordinate and extra-group males. Furthermore, the repeatability

294   of paternal care was high among co-breeding males in socially polyandrous groups, indicating that

295   males consistently provided similar levels of care in different breeding attempts. Given the previous

296   findings and the biology of dunnocks, we found our results to be unexpected. We could simply

297   attribute the discrepancy to differences in demography, and ecology between the two populations (our

298   study vs. the Cambridge study). Nevertheless, we expected that co-breeding male dunnocks would be

299   able to assess their risk of being cuckolded (i.e. having information on female promiscuity), because

300   of the high levels of mate guarding in this species (see Davies 1992). Possibly, males have information

301   about the risk of being cuckolded, but lack the ability to recognize their own offspring in a brood.

302   Thus, adjustment of paternal care could be maladaptive, because males would reduce care to their own

303   young, thus directly decreasing their own fitness. Nevertheless, our results of lack of adjustment and

304   high repeatability among co-breeding males are consistent with the prediction of the sealed-bid

305   hypothesis (Houston and Davies 1985) that 'negotiation' over how much care to provide occurs over

306   evolutionary time (Houston and Davies 1985) (e.g., Schwagmeyer et al. 2002; Nakagawa et al. 2007).

307   Under this scenario, changes in paternity between breeding attempts of a male should not influence

308   how much care he provides.

309   Similarly to dunnocks, in the reed bunting, *Emberiza schoeniclus*, an early study found

310   evidence for the certainty of paternity hypothesis (Dixon et al. 1994), whereas a more recent

311   investigation did not (Bouwman 2005). In the latest reed bunting study (Bouwman 2005), the authors

312   discussed three assumptions from theoretical models that need to be met in order for males to adjust

313   care in relation to paternity. Succinctly (refer to Bouwman et al. 2005 for a detailed discussion), these

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314   assumptions are that: i) levels of paternity need to vary between breeding attempts of a male; ii) males

315   should be able to assess their share of paternity through behavioural cues (e.g., absence of female

316   during her fertile period or number of intruding males); and iii) the benefits of reducing care should

317   outweigh the costs. The first assumption is not contentious throughout most studies, as levels of

318   paternity vary considerably among broods (reviewed in Griffith et al. 2002). However, evidence

319   supporting the other two assumptions is debatable. Our findings suggest that under some

320   circumstances (social monogamy, within-pair effect), males adjust their paternal care when paternity

321   is lost to extra-pair sires. These results indicate that these males may use cues provided by females to

322   adjust the amount of care provided. However, it is worth noting that the within-pair reduction of care

323   could also be triggered by other factors associated with the identity of individual females, such as their

324   breeding condition, which could affect her share of parental care towards the brood. Disentangling the

325   effects of factors associated with female identity from variation in extra-pair paternity would yield

326   interesting insights into the mechanisms that cause males to reduce their paternal care. The third

327   assumption that males should benefit from reducing their care can also be questioned. Our results

328   suggest that males do not suffer mortality costs of providing paternal care. This finding is in

329   agreement with a recent meta-analysis that has shown that in birds, males do not gain benefits in terms

330   of their own survival to the next breeding season when paternal effort is experimentally reduced

331   (Santos and Nakagawa 2012; but see Magrath and Komdeur 2003 for a discussion of benefits in terms

332   of additional mating opportunities).

333   In conclusion, our results show that males are able to adjust their paternal contribution, but

334   only under specific conditions. Monogamous males adjust their paternal investment within-pairs, and

335   this may have important fitness consequences to the extra-pair offspring, as the amount of paternal

336   care provided is associated with fledging success. Co-breeding males in socially polyandrous groups

337   did not adjust their levels of paternal care according to variation in paternity. Taken together, our

338   results raise the question of what causes socially monogamous—but not co-breeding males in social

339   polyandry—to adjust paternal care when paternity changes when paired to the same female. Finally,

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340   females in social monogamy that engage in extra-pair behaviour face important fitness costs, as their

341   partners' reduction in care has negative consequences to nestling fledging success.

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Acknowledgements

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476

477 **Supporting information**

478 **Supporting information S1** Supplementary methods, tables and figures.

479

480 **Data accessibility**

481 Data used in this manuscript will be made available in the fig**share** repository upon acceptance of the
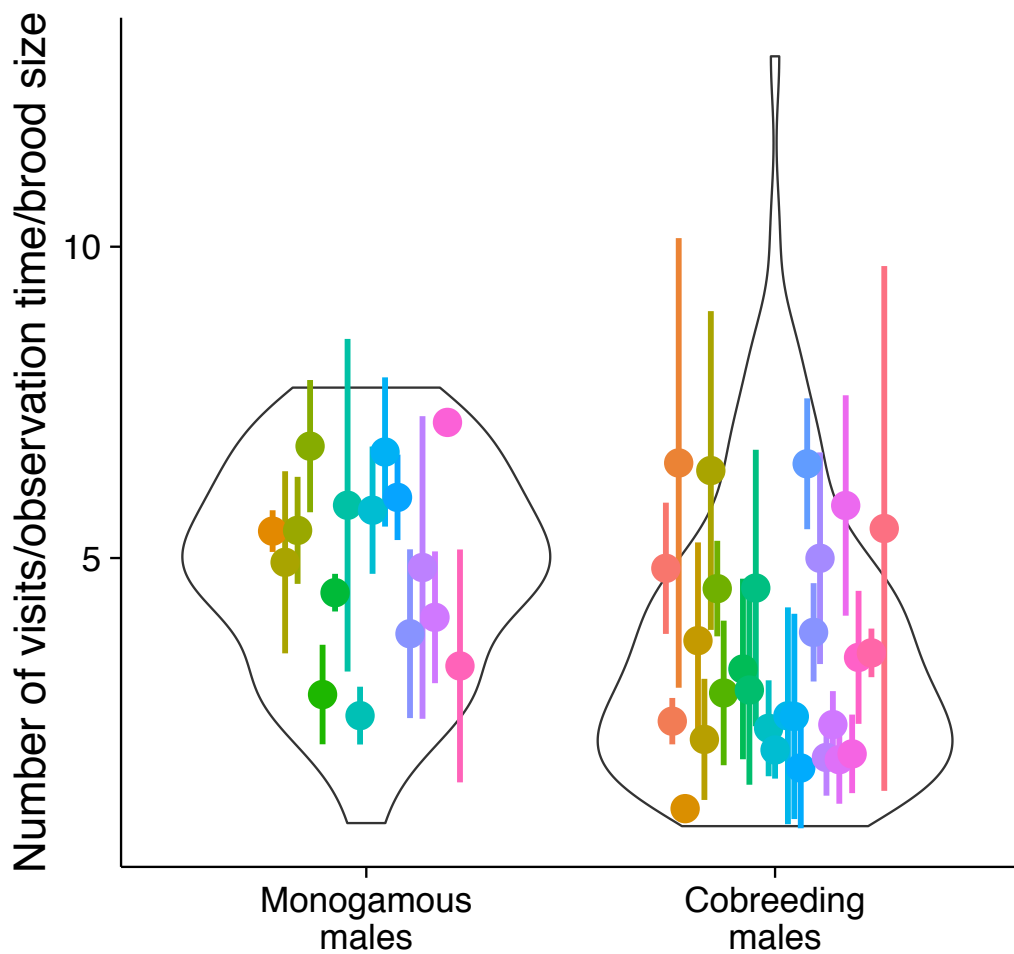
482 paper.

483

484 **Author contributions**

485 ESAS conceived the study; ESAS and SN designed the study; ESAS collected the data, conducted

486 laboratory analyses and analysed the data; ESAS and SN wrote and edited the manuscript.

487

488   **Figures**

489   **Figure 1**

490

491   **Fig. 1** Number of nest visits by the duration of the parental care observation period made by
492   monogamous, and co-breeding males in social polyandry (the y-axis is presented for visualization
493   purpose; we used raw count data in our statistical models). Dots represent the mean number of visits
494   per observation for each male (vertical bars are ± 1 SD; each male is coloured with a different shade).
495   The envelopes show the density of the data for each male mating category.

496

497 **Figure 2**
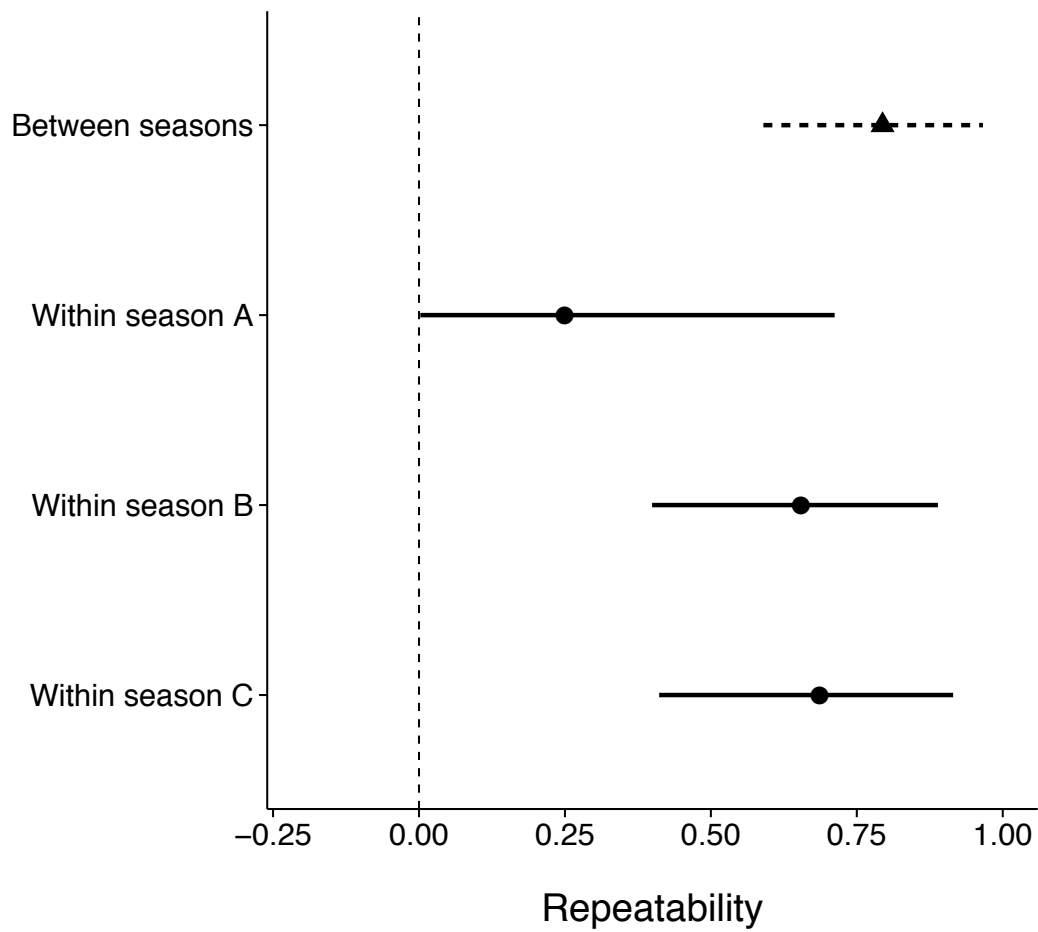
498

499 **Fig. 2** Within- and between-season repeatability estimates of the number of visits to a nest by male
500 dunnocks. Point estimates represent posterior mean repeatabilities and horizontal bars are the 95%
501 credible intervals. Estimates with 95% credible intervals that do not touch or overlap the vertical
502 dashed line (0) are significantly repeatable. Season A: 2009–2010 (n = 28); season B: 2010–2011 (n =
503 79); and season C: 2011–2012 (n = 51).

504

505   **Figure 3**
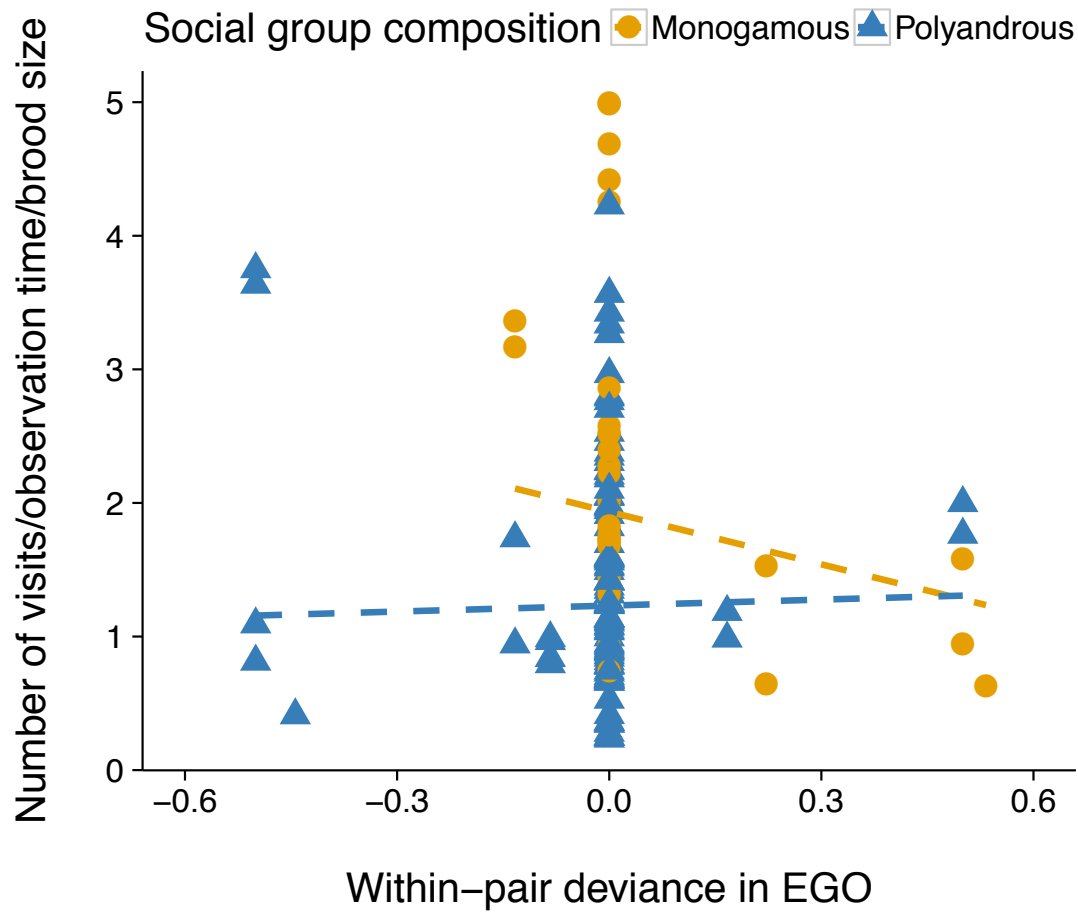
506

507   **Fig. 3** Relationship between the within-pair deviance in the proportion of extra-group offspring (EGO)
508   in broods and male number of visits to a nest. All male-female pairs that did not show variance
509   between breeding attempts in the proportion of extra-group offspring are spread vertically at $x = 0$.
510   Orange and blue symbols and lines represent males in socially monogamous (n = 46 observations) and
511   socially polyandrous (n = 112 observations) groups, respectively. Lines represent predicted results
512   from Poisson Bayesian mixed model with *Male identity* and *Nest identity* as random effects (posterior
513   means and 95% CI): 0.172 (0.082 to 0.293) and 0.027 (0.0003 to 0.073), respectively.

514

515 **Figure 4**
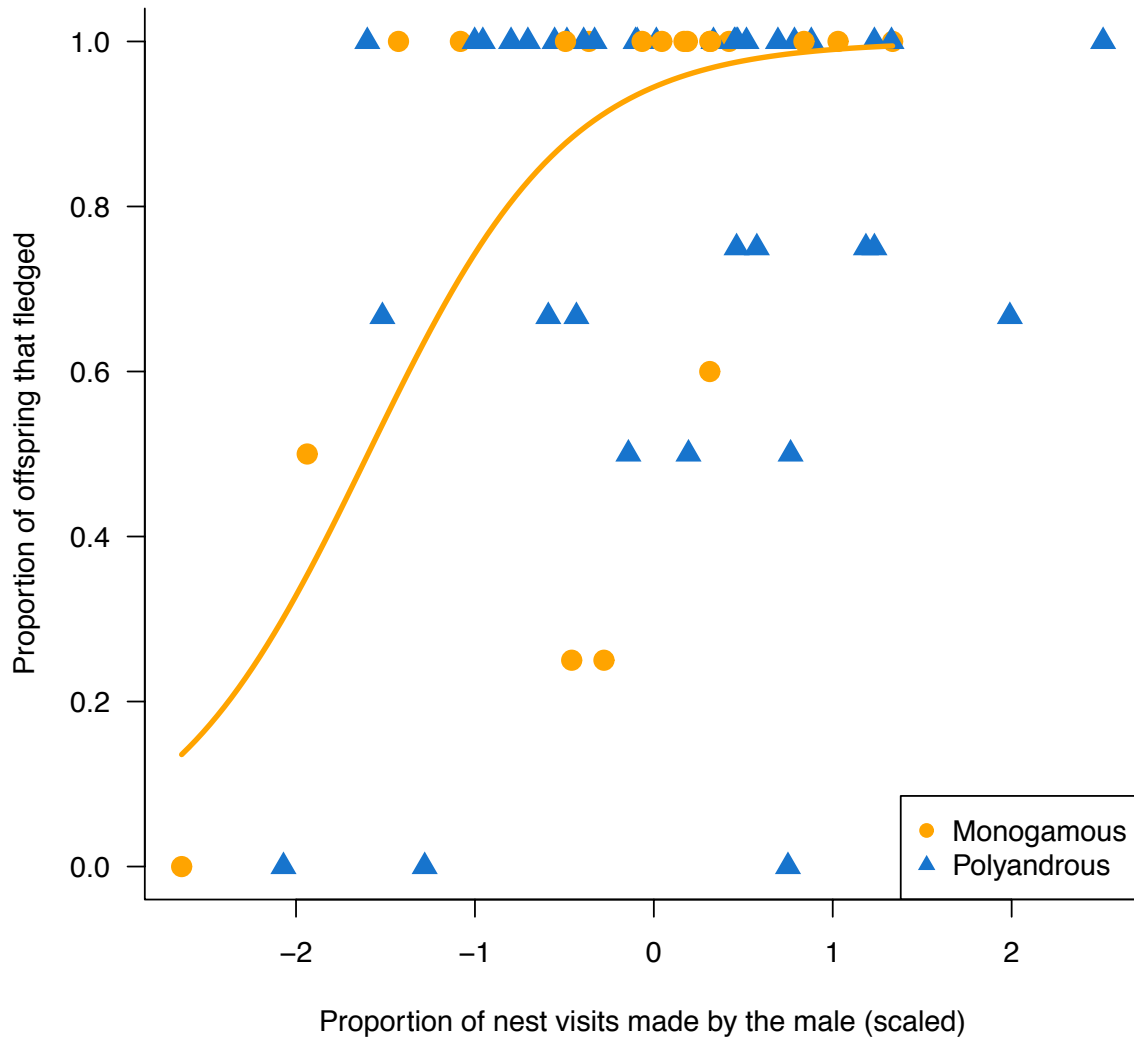
516

517 **Fig. 4** Relationship between the proportion of male visits to a nest (relative participation to total nest
518 visitation; scaled and centred) and the proportion of young that fledged. Orange and blue symbols
519 represent males in socially monogamous (n = 19 observations) and socially polyandrous (n = 37
520 observations) groups, respectively. The orange line represents predicted results from a binomial
521 Bayesian model for monogamous males.