1   **Testing predictions of inclusive fitness theory in inbreeding relatives with**

2   **biparental care**

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35   **Abstract**

36   Inclusive fitness theory predicts that parental care will vary with relatedness between potentially

37   caring parents and offspring, potentially shaping mating system evolution. Systems with extra-

38   pair paternity (EPP), and hence variable parent-brood relatedness, provide valuable

39   opportunities to test this prediction. However, existing theoretical and empirical studies assume

40   that a focal male is either an offspring's father with no inbreeding, or is completely unrelated. We

41   highlight that this simple dichotomy does not hold given reproductive interactions among

42   relatives, complicating the effect of EPP on parent-brood relatedness yet providing new

43   opportunities to test inclusive fitness theory. Accordingly, we tested hierarchical hypotheses

44   relating parental feeding rate to parent-brood relatedness, parent kinship and inbreeding, using

45   song sparrows (*Melospiza melodia*) experiencing natural variation in relatedness. As predicted,

46   male and female feeding rates increased with relatedness to a dependent brood, even

47   controlling for brood size. Male feeding rate tended to decrease as paternity loss increased, and

48   increased with increasing kinship and hence inbreeding between socially-paired mates. We

49   thereby demonstrate that variation in a key component of parental care concurs with subtle

50   predictions from inclusive fitness theory. We additionally highlight that such effects can depend

51   on the underlying social mating system, potentially generating status-specific costs of extra-pair

52   reproduction.

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56   *Key words: extra-pair paternity, inbreeding, inclusive fitness, kinship, parental care, parent-*

57   *offspring relatedness*

1. Introduction

A central ambition in evolutionary ecology is to understand how 'altruistic' behaviours, which cost actors but benefit recipients, evolve as functions of interactions among relatives [1–4]. Parental care provided to dependent offspring represents one critically important altruistic behaviour that simultaneously emerges from, and can shape ongoing evolution of, complex reproductive strategies and mating systems. Variable parental care therefore provides one long-standing focus for developing and testing inclusive fitness theory [5].

Parental or alloparental care is typically predicted to increase with a focal adult's relatedness to dependent offspring, following the basic principle of Hamilton's rule [1,3,4,6]. Systems where relatedness between potentially caring adults and dependent offspring varies among family groups offer interesting opportunities to test this prediction, and to examine the degree to which adaptive plastic responses in parental care can arise and potentially shape mating system evolution. Such variation in adult-offspring relatedness is commonplace in socially monogamous systems with variable extra-pair paternity (EPP) [7–11]. Here, potentially caring males might not sire all offspring produced by their socially-paired female [12]. All else being equal, paternal care is then predicted to increase with a male's paternity success and resulting male-brood relatedness, defined as the total number of copies of an allele that is present in focal male i that is expected to be present in the brood (hereafter "total allelic value", TAV_i) [5,12–15]. Decreased paternal care following paternity loss can then create a cost of female extra-pair reproduction that could be sufficient to constrain the evolution of underlying polyandry [16]. Systems characterized by social monogamy, biparental care and extra-pair paternity are consequently interesting systems where evolutionary dynamics of parental care and mating system are directly intertwined, attracting substantial theory development [13,14,17–19] and empirical tests [6,20–24].

Yet, existing theoretical and empirical studies typically assume that the relatedness between a potentially caring male and a dependent offspring is either ½ or 0, meaning the male

84   is either the offspring's father with no inbreeding, or is completely unrelated [13,14,19,25,26].

85   The male's total 'relatedness' to a dependent brood, or TAV_i, is then simply $\frac{1}{2}BS \cdot P_{WPO}$ where

86   BS is brood size and P_{WPO} is the proportion of the brood that are genetic offspring of the focal

87   male (i.e., within-pair offspring, WPO). This expression reduces to $\frac{1}{2}N_{WPO}$, where N_{WPO} is the

88   number of WPO [12]. Similarly, the decrease in TAV_i to a potentially caring male resulting from

89   EPP is simply $\frac{1}{2}BS \cdot P_{EPO}$, where P_{EPO} is the proportion of the brood that are extra-pair offspring

90   (EPO, hence $P_{EPO}=1-P_{WPO}$). However, these basic premises may not hold in reality, complicating

91   the effect of EPP on parent-brood relatedness and associated optimal allocations of parental

92   care.

93   Specifically, many populations and mating systems foster reproductive interactions

94   among multiple relatives, including active or passive inbreeding and different forms of kin-

95   structured reproductive groups or neighbourhoods [9–11,27,28]. Such systems can generate

96   more subtle forms of variation in adult-offspring relatedness than a simple 'parent or not'

97   dichotomy. Specifically, a focal male i that fails to sire an offspring of his socially-paired female j

98   could still be related to that EPO, and hence accrue some inclusive fitness benefit of paternal

99   care, if he is related to the EPO's mother (i.e., his socially-paired female) by coefficient of kinship

100   $k_{ij}>0$, and/or to the EPO's genetic father (i.e., his socially-paired female's extra-pair mate q) by

101   $k_{iq}>0$ [12,29] (ESM Appendix S1). Quantitatively, a male's relatedness to an EPO that he did not

102   sire but could rear is $r_{iEPO} = k_{ij} + k_{iq}$ [12]. Further, the general expressions for relatedness

103   between a focal male and female and their WPO are $r_{iWPO} = \frac{1}{2} + k_{ij} + \frac{1}{2}f_i$ and $r_{jWPO} = \frac{1}{2} + k_{ij} + \frac{1}{2}f_j$

104   respectively, where f_i and f_j are these parents' own coefficients of inbreeding [12,30] (ESM

105   Appendix S1). Similarly, a female's relatedness to its EPO is $r_{jEPO} = \frac{1}{2} + k_{jq} + \frac{1}{2}f_j$, where k_{jq} is the

106   coefficient of kinship between j and q. These expressions show that a focal parent can be

107   considerably more closely related to its offspring than the basic value of $\frac{1}{2}$ when it is related to

108   its mate ($k_{ij}>0$ or $k_{jq}>0$) and/or is inbred itself ($f_i>0$ or $f_j>0$), and hence given inbreeding in the

109   current and/or previous generation [12,31–33]. Consequently, the total relatedness between a

110   potentially caring male and a focal dependent brood, TAV_i, is most generally calculated as the

111   sum of r_{iWPO} or r_{iEPO} across all WPO and EPO within the brood respectively, whereas TAV_j for a

112   female is the sum of r_{jWPO} and r_{jEPO} across all these offspring [12] (ESM Appendix S1). TAV for a

113   focal brood can therefore differ between paired males and females, and can substantially

114   exceed the typically assumed basic values of $\frac{1}{2}N_{WPO}$ and $\frac{1}{2}BS$ respectively [12]. Further,

115   because a potentially caring male's relatedness to an EPO may not be zero, the decrease in

116   TAV_i resulting from EPP no longer simply equals $\frac{1}{2}BS \cdot P_{EPO}$. Rather, this difference (hereafter

117   "lost allelic value", LAV) can be calculated as $LAV=PAV-TAV_i$, where PAV is the "potential allelic

118   value" of the brood to the male if he had sired the entire brood (ESM Appendix S1). Subtle

119   patterns of adaptive variation in the degree of parental care might then be predicted, such that

120   paternal care might increase more tightly with increasing TAV than with BS, and decrease with

121   increasing LAV (and P_{EPO}, Table 1), reflecting the fundamental premise that care should be

122   adjusted in proportion to relatedness to dependent offspring. Such subtle modulation of parental

123   care might then further affect mating system dynamics emerging among interacting relatives

124   [13,14,18,19].

125   Additionally, recent advances in inclusive fitness theory predict that the kinship k_{ij}

126   between paired parents will directly influence optimal parental investment [31]. Specifically, if

127   parental care, which forms a component of parental investment, can ameliorate inbreeding

128   depression in offspring viability, then the optimal degree of care is predicted to increase with

129   increasing k_{ij} [31]. In contrast, under these circumstances, optimal care is not predicted to vary

130   directly and adaptively with f_i or f_j [31], but could potentially show inbreeding depression if inbred

131   parents are resource constrained. Consequently k_{ij} and f_i or f_j, which constitute the fundamental

132   underlying elements that determine parent-offspring relatedness and hence shape TAV and

133   LAV, are predicted to have different direct effects on parental care [31]. However, the resulting

134   suite of predictions regarding variation in parental care in relation to TAV, LAV, k_{ij}, f_i and f_j (Table

135   1) has not been tested in any system.

136   We recorded rates at which adults provisioned broods of dependent offspring (hereafter

137   "feeding rates") as a measure of parental care in a song sparrow (*Melospiza melodia*) population

138   where BS, EPP, k_{ij}, f_i and f_j and hence TAV and LAV vary substantially among individuals and

139   breeding attempts [12,31], and tested three sets of hypotheses and associated predictions

140   (Table 1). First, we tested whether female and male feeding rates increased with increasing total

141   relatedness to their brood, measured as TAV_i or TAV_j. Since TAV is intrinsically positively

142   correlated with BS overall but can vary within levels of BS (ESM Appendix S1, S4), we further

143   tested whether feeding rates increased with TAV after controlling for BS. Second, we tested

144   whether male feeding rates decreased with increasing LAV (or P_{EPO}), and hence with the value

145   of offspring lost though EPP. Third, we focussed on the fundamental underlying elements and

146   tested whether male and female feeding rates increased with increasing k_{ij} but not with

147   increasing f_i or f_j as predicted by inclusive fitness theory [31]. While the focal song sparrows are

148   typically socially monogamous, some are socially polygynous (i.e., one male simultaneously

149   socially paired with ≥ 2 females), and paternal care can be differentially allocated to offspring of

150   different females [5,34–36]. We therefore additionally tested whether parental feeding rate

151   varied with social status, and whether TAV, LAV, k_{ij}, f_i and f_j interacted with social status to

152   shape patterns of parental care arising given complex reproductive interactions among relatives.

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154   **2. Methods**

155   **(a) Study system**

156   Testing the focal predictions (Table 1) requires quantifying the degree of parental care

157   expressed across family groups comprising social parents and WPO and/or EPO with known

158   parental k_{ij}, k_{iq}, k_{jq}, f_i and f_j. These data are available from a resident, pedigreed, population of

159   song sparrows on Mandarte Island, BC, Canada [37].

160   On Mandarte, both song sparrow sexes can breed from age one year, and pairs typically

161   rear 2–3 broods of 1–4 nestlings during April–July each year. Each year since 1975, all

162   territories were mapped, all nests were monitored, and all nestlings and any immigrants were

163   uniquely colour-ringed [35,36,38]. The socially-paired adults attending each nest were identified

164   and sexes were attributed from observed reproductive behaviour (male song, female

165   incubation), allowing identification of socially monogamous and polygynous breeding pairs

166   [35,36,38]. Genetic parentage analyses demonstrated 28% EPP (affecting 44% of broods), but

167   no extra-pair maternity [39] (ESM Appendix S2). Mandarte is part of a large meta-population [38]

168   and the small local population size (mean 33.5 adult females, range 4–72), plus occasional

169   immigrants (mean ~ 0.9/year) generates substantial variation in k and f [12].

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171   **(b) Parental feeding rates**

172   As a measure of parental care, we recorded parental feeding rates defined as the number of

173   provisioning visits made to a focal nest per hour by each socially-paired parent (ESM Appendix

174   S2). The dataset totalled 337 1-hr observation 'sessions' spanning the 12-day nestling period at

175   138 different nests (38, 46 and 44 in 2003, 2007 and 2008 respectively), with a median of 2

176   sessions/nest (range: 1–7). Nests attended by socially monogamous pairings were defined as

177   "monogamous" (N=79). We defined each polygynous male's first hatched nest among broadly

178   concurrent attempts as "primary polygynous" (N=30), and his second or third concurrent nest as

179   "secondary polygynous" (N=29). Since females did not always pair with the same male across

180   nesting attempts, and some females bred in multiple years, the 138 nests were attended by 65

181   and 54 different females and males respectively (generating 75 different pairings).

182

183   **(c) Statistical analyses**

184   We used standard pedigree algorithms to compute each individual's f_i or f_j, and k_{ij}, k_{iq} and k_{jq}

185   between individuals, and hence calculate relatedness between each focal parent and each

186   nestling they reared. Male TAV (TAV$_i$), female TAV (TAV$_j$) and LAV were then calculated for

187   each brood (ESM Appendix S1). We fitted linear mixed effects models (LMMs) to test specified

188   hypotheses relating male and female feeding rates to the focal variables (Table 1).

189   In general, feeding rates often vary with multiple non-focal variables, including nestling

190   age [40,41], time of season and day [42], mate behaviour [43,44], and social status [35]. We

191   therefore used a comparative modelling approach, and compared a null LMM that included

192   baseline effects on feeding rate to LMMs that additionally included each focal variable. Baseline

193   effects comprised nestling age (days after hatch, continuous variable), nest lay date (continuous

194   variable), time of day (morning or afternoon, two-level factor), and nest social status

195   (monogamous, primary polygynous or secondary polygynous three-level factor). Since effects on

196   male and female feeding rates were modeled separately but experimental, empirical and

197   theoretical studies suggest that a focal individual's behaviour might be influenced by its mate's

198   behaviour [43,45,46], each null LMM also included the focal individual's mate's simultaneously

199   observed feeding rate (as a continuous covariate) and interactions with social status. However,

200   key model results remained quantitatively similar when mate feeding rate was removed.

201   First, to test the prediction that parental feeding rates increased with increasing TAV

202   more than with BS (Table 1) we compared support for LMMs that additionally included TAV or

203   BS versus the null LMM. Here, TAV and BS were modelled as continuous covariates, therefore

204   adding one parameter to the null model. We then z-standardized TAV within each level of BS

205   (i.e., $TAV_Z = (TAV - \mu_{TAV})/\sigma_{TAV}$, where μ_{TAV} and σ_{TAV} are the mean and standard deviation of TAV

206   within each BS) and compared LMMs that included additive and interactive effects of TAV_Z and

207   BS (as a four-level factor) to models that did not include TAV_z.

208   Second, to test the prediction that male but not female feeding rate decreased with

209   increasing LAV (or P_{EPO}; Table 1) we compared LMMs that additionally included each of these

210   covariates to the null LMM. Third, to test the predictions that parental feeding rates would

211   increase with increasing k_{ij}, but not vary with f_i and f_j, we compared LMMs that included each of

212   these three covariates to the null LMM. These LMMs additionally included BS (as a continuous

213   covariate). Finally, we expected male feeding rates to be lower at secondary polygynous nests,

214   while female feeding rates could be higher if they compensated [43,44], implying that both

215   sexes' feeding rates might depend on social status. Consequently, we additionally fitted LMMs

216   that included 2-way interactions between nest social status and each focal variable.

217   LMMs assumed Gaussian distributions for feeding rates. All continuous variables within

218   interaction terms were centered to minimize multicollinearity and aid model convergence. To

219   account for non-independence across multiple observation sessions of the same nest and

220   parents, random individual identity, social mate identity, and nest identity effects were included

221   in all LMMs. We used Akaike information criterion, corrected for small sample sizes (AIC_c), to

222   assess whether LMMs that included each focal predictor variable were better supported than the

223   null LMM and/or than their competing predictor (e.g., TAV vs BS), defined as a difference in AIC_c

224   (ΔAIC_c) equalling or exceeding two units [47].

225   All models were fitted using R 3.1.1 [48] with packages lme4 [49], lmerTest [50] and

226   MuMIn [51]. Raw means are presented ± 1 standard deviation (SD). Full distributions of all

227   variables, and relationships between feeding rate and null variables, are in ESM Appendix S3.

228   LMM results are presented as standardized estimates (regression slope β) ± 1 standard error

229   (SE). Estimates and SEs for factor levels not in interactions (i.e., brood size, time of day, and

230   social status) are presented as least square means. Full details of all LMMs are in ESM

231   Appendix S6. Data are available from the Dryad Digital Repository

232   https:doi.org/10.5061/dryad.1zcrdfnf.

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234   **3. Results**

235   **(a) Baseline effects of sex and social status**

236   Across all observation sessions, mean female and male feeding rates were 6.4±4.1 and 4.2±3.4

237   trips/hour, respectively. Males had lower mean feeding rates at secondary polygynous nests

238   (1.4±2.3) than at primary polygynous (4.7±3.8) or monogamous nests (5.1±3.1), while females

239   had higher mean feeding rates at secondary polygynous nests (9.1±4.9) than at primary

240   polygynous (6.4±3.6) or monogamous nests (5.4±3.4; ESM Appendix S3, S6). Male and female

241   feeding rates were positively correlated at primary polygynous and monogamous nests (Pearson

242   correlation coefficient: r_p=0.40, 0.44 respectively), but weakly negatively correlated at secondary

243   polygynous nests (r_p=-0.10; ESM Appendix S3). Secondary females therefore partially

244   compensated for lower feeding rates of their socially polygynous mates.

245

246   **(b) Brood size (BS) and total allelic value (TAV)**

247   Models for sex-specific feeding rates that additionally included BS (continuous variable) were

248   substantially better supported than the null LMM for females (ΔAIC_c=-11.1), but only slightly

249   better supported for males (ΔAIC_c=-0.7). These LMMs showed that feeding rate increased with

250   increasing BS in females (β=0.87±0.23), and tended to do so in males (β=0.38±0.21; ESM

251   Appendix S3, S6).

252   As expected, TAV_i and TAV_j were strongly but not perfectly positively correlated across

253   the 139 observed broods (r_p=0.75), and TAV was positively correlated with BS in both sexes

254   (males: r_p=0.54; females: r_p=0.76; ESM Appendix S4, S6). However, both TAV_i and TAV_j varied

255   considerably within levels of BS, reflecting underlying variation in P_{EPO}, k_{ij}, k_{iq}, k_{jq}, f_i and f_j (ESM

256   Appendix S4). LMMs that included brood TAV were much better supported than the null LMM for

257   both sexes (males: ΔAIC_c=-5.1, females: ΔAIC_c=-14.9), showing that feeding rate increased with

258   TAV in both sexes (Fig 1). Importantly, LMMs that included TAV were better supported than

259   competing LMMs that included BS for males (ΔAIC_c=-4.3) and females (ΔAIC_c=-3.8, ESM

260   Appendix S6). Consequently, as predicted, male and female feeding rates were better explained

261   by increasing TAV than by increasing BS.

262   Furthermore, models that included standardized TAV within brood size (TAV_z) were

263   better supported than the null LMM (without BS) for females (ΔAIC_c=-2.9) and males (ΔAIC_c =-

264   2.6). Models that included TAV_z and BS were also better supported than the null with BS for

265   females (ΔAIC_c=-3.0) and males (ΔAIC_c=-2.5; ESM Appendix S6). Feeding rates therefore

266   increased with TAV_z within broods of each size (Fig 1). LMMs that additionally included TAV_z by

267   BS interactions were marginally better supported than the null model (males: ΔAIC_c=-1.3,

268   females: ΔAIC_c=-2.1), but less well supported than models without interactions (males:

269   ΔAIC_c=2.0, females: ΔAIC_c=2.1). Meanwhile, LMMs that included TAV_z by social status

270   interactions were marginally better supported than the null model for males (ΔAIC_c=-1.7), and

271   slightly less well supported for females (ΔAIC_c=+0.6). Overall, these results show that, in

272   accordance with the prediction (Table1), increased TAV was associated with increased parental

273   feeding rates (Fig 1).

274

275   **(c) Lost allelic value (LAV)**

276   Across all nests, P_{EPO} varied between 0.00 and 1.00 (mean: 0.27±0.35), and LAV varied

277   between 0.000 and 1.913 (mean: 0.208±0.373). As expected, LAV was positively correlated with

278   P_{EPO} across all 138 focal broods (r_p=0.89; ESM Appendix S5). Yet, some broods had low LAV

279   relative to P_{EPO}, reflecting cases where cuckolded males were closely related to EPO (ESM

280   Appendix S5). P_{EPO}, and hence LAV, varied with social status. Specifically, primary polygynous

281   nests had higher P_{EPO} than monogamous nests (0.33±0.30 versus 0.21±0.30; β=0.12±0.04,

282   85%CI: 0.06–0.19) and secondary polygynous nests (0.24±0.30; β=-0.10±0.45, 85%CI: -0.19–

283   0.004), while monogamous and secondary polygynous nests were similar (β=0.03±0.45, 85%CI:

284   -0.06–0.11; Appendix S6).

285   Models for sex-specific feeding rates that included LAV were slightly better supported

286   than the null LMM (including BS as a covariate) for males (ΔAIC_c=-1.9), but less well supported

287   for females (ΔAIC_c=+1.7). As predicted, male feeding rate tended to decrease with increasing

288   LAV, but female feeding rate did not (Fig 2). LMMs that additionally included LAV by social

289   status interactions were slightly less well supported than the null LMM for males (ΔAIC_c=+1.0),

290   but indicated that males at primary polygynous nests showed the greatest reduction in feeding

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291   rate with increasing LAV (Fig 2; ESM Appendix S6). There was no support for LMMs that

292   included a LAV by social status interaction in females (ΔAIC_c=+7.9; Fig 2; ESM Appendix S6).

293   Since LAV and P_{EPO} were correlated, conclusions were very similar for models that included

294   P_{EPO} rather than LAV as the focal variable (ESM Appendix S5, S6).

295

296   **(d) Kinship (k) and inbreeding (f) coefficients**

297   Individuals' coefficients of kinship with their social mates (k_{ij}) varied between 0.000 and 0.301

298   (mean: 0.087±0.055). Models for sex-specific feeding rates that included k_{ij} were better

299   supported than the null LMM (including BS) for males (ΔAIC_c=-4.4), but less well supported for

300   females (ΔAIC_c=+2.0; ESM Appendix S6). Males in pairs with higher k_{ij} had higher feeding rates

301   but females did not (Fig 3). LMMs that additionally included k_{ij} by social status interactions were

302   similarly supported as the null LMM for males (ΔAIC_c=-0.7), but suggest that feeding rate tended

303   to increase most markedly with increasing k_{ij} at primary polygynous nests (Fig 3). Such models

304   were less well supported for females (ΔAIC_c=+1.8), but suggest that females at secondary

305   polygynous nests had lower feeding rates increasing k_{ij} (Fig 3).

306   Individuals' coefficients of inbreeding (f) varied between 0 and 0.164 (mean:

307   0.057±0.035) for males and 0 and 0.181 (mean: 0.057±0.039) for females. LMMs that included f_i

308   were marginally less well supported than the null LMM (including BS) for males (ΔAIC_c=+1.0),

309   and females (ΔAIC_c=+1.5; ESM Appendix S6). Overall, feeding rates did not vary markedly with

310   f_i in either sex (Fig 3). However, LMMs that additionally included f_i by social status interactions

311   were slightly better supported than the null LMM in males (ΔAIC_c=-1.6) but not females

312   (ΔAIC_c=+4.3). Male feeding rates tended to increase with increasing f_i at primary polygynous

313   nests, decrease with increasing f_i at secondary polygynous nests, and did not vary with f_i at

314   monogamous nests (Fig 3). Such patterns were not evident in females across social statuses

315   (Fig 3).

316

4. Discussion

Patterns of variation in parental feeding rates observed in song sparrows experiencing considerable natural variation in parent-brood relatedness, resulting from combinations of extra-pair paternity, mate kinship and individual coefficient of inbreeding, broadly concurred with key predictions of inclusive fitness theory (Table 1). A key result is that feeding rates of both sexes increased with increasing total allelic value (TAV) of the dependent brood, even after controlling for brood size (TAV_z; Fig 1). Males and females consequently fed broods more often per hour as the expected number of identical-by-descent allele copies increased, to degrees that would generate notable increases in the total feeds received by highly related broods over the full nesting period (Fig 1). These results support the central premise of existing models of optimal parental effort and investment that consider brood size [52] and relatedness [25], but provide conceptual and empirical advances by encompassing complex variation in relatedness arising from reproductive interactions among relatives [12].

Variation in brood TAV from the perspective of a potentially caring male partly reflects variation in paternity loss (proportion of offspring that are extra-pair; P_{EPO}) and kinship with his socially-paired female (k_{ij}) and her extra-pair male(s) (k_{iq}) and resulting lost allelic value (LAV). Our analyses provide some support for the prediction that male feeding rate will decrease with increasing LAV, and with increasing P_{EPO} itself, and hence that males that lose relatedness to a dependent brood due to EPP provide less care. This concurs with some [6,13–15,23,53], but not all [6,15,53], previous empirical studies that tested whether paternal care decreases with increasing P_{EPO}. However, our results highlight that key patterns of variation in paternal care might also depend on the social mating system. In particular, the negative effect of LAV on male feeding rate tended to be strongest at primary polygynous nests, perhaps reflecting the higher mean P_{EPO} in these nests. Overall, these results support the hypothesis that female extra-pair reproduction can incur a cost in the form of reduced paternal care, potentially selecting against underlying polyandry [16,36], but imply that such costs might depend on social status [35].

13

343   Variation in TAV also reflects variation in kinship between socially-paired mates (k_{ij}), and

344   inclusive fitness theory predicts that optimal paternal care, interpreted as a component of

345   parental investment, should increase with increasing k_{ij} [31]. Our results strongly support this

346   prediction for males (Fig 3), translating into substantial increases in the number of paternal feeds

347   received by inbred broods. Such increases might yield an evolutionary benefit of inbreeding, or

348   at least negate the underlying evolutionary cost [54]. This is because inbreeding increases

349   parent-offspring relatedness and hence propagation of identical-by-descent allele copies (given

350   no 'opportunity cost' of lost outbred matings), but may also cause inbreeding depression in

351   resulting offspring [32]. However, this cost can be negated if inbreeding parents can ameliorate

352   inbreeding depression in resulting offspring through increased parental care [55]. This may be

353   the case for song sparrows, since inbreeding depression in nestling survival from hatching to

354   independence from parental care is weak [56], and inbreeding parents rear larger broods [57].

355   Consequently, there is weak selection against inbreeding despite strong inbreeding depression

356   in individual fitness, and no evidence for active inbreeding avoidance through either social

357   pairing or extra-pair reproduction [56,58]. In contrast, female song sparrows tended to decrease

358   their feeding rate with increasing k_{ij}, perhaps reflecting a response to substantially increased

359   male feeding rate. But, generally, it is unclear if increased levels of male care would be strong

360   enough to substantially decrease inbreeding depression. Indeed, additional male care did not

361   decrease inbreeding depression in burying beetles (*Nicrophorus vespilloides*) [59]. However, our

362   results add to several recent experimental studies on diverse taxa suggesting parents mated to

363   kin may adjust reproductive strategies to reduce inbreeding depression, for example by reducing

364   their clutch size in burying beetles [60], gaining alloparental care from helpers in red-winged

365   fairy-wrens (*Malurus elegans*) [61], providing increased levels of prenatal maternal provisioning

366   in Japanese Quail (*Coturnix japonica*) [62], adopting group living and maternal care in social

367   spiders (*Anelosimus cf. jucundus*) [63], or more cooperative parental behaviour in an African

368   cichlid (*Pelvicachromis taeniatus*) [28]. Yet, to our knowledge, no previous studies have directly

14

369   examined how mate kinship influences parental care in wild non-cooperative breeding species.

370   Since inbreeding occurs in many species [e.g. 27,55,62,64] such effects warrant wider attention

371   in the context of inclusive fitness theory [1]. In our system, and others, this could potentially

372   include examining female responses to kinship with their extra-pair mates (k_{jq}).

373   Our results also broadly concur with the prediction that overall feeding rates should not

374   vary with a parent's own f_i, insofar as such null predictions can be rigorously tested. These

375   results can also be interpreted to provide no overall evidence of direct inbreeding depression in

376   parental feeding rates. The few previous studies quantifying inbreeding effects on parental care

377   all compared highly inbred (e.g. $f≥0.25$) to outbred parents in captivity. Inbred versus outbred

378   prairie voles (*Microtus ochrogaster)* and burying beetles did not differ in multiple parental

379   behaviours [65,66], whereas inbred female zebra finches (*Taeniopygia guttata*) incubated less

380   than outbred females [67]. However, in song sparrows, the effects of f_i on parental feeding rate

381   appear to vary strongly with social status: male feeding rate increased markedly with increasing

382   f_i at primary polygynous nests but decreased at secondary polygynous nests, perhaps reflecting

383   re-allocation of parental investment among broods by more inbred males. Future studies should

384   further examine how effects of f on key parental behaviours are shaped by the social mating

385   system.

386   Parental feeding rate is one key component of parental care that may be positively or

387   negatively correlated with other components. Consequently, the degree to which variation in

388   feeding rate captures variation in overall care, or in parental investment strictly defined [5,34], is

389   unknown. Nevertheless, our results are striking in showing that one major component of care

390   does vary with subtle variation in relatedness in accordance with inclusive fitness theory (Table

391   1), especially in males. This raises interesting questions regarding how such outcomes could

392   arise. Our results are inevitably correlative and hence cannot prove causal effects; but any

393   experimental manipulation of such effects in free-living populations would be exceptionally

394   challenging, and our analyses controlled for key potentially confounding variables that are

395   known to affect feeding rates. The observed increases in parental feeding rates with increasing

396   TAV$_z$ may therefore imply that song sparrows can respond to direct or indirect cues of

397   relatedness. Some mechanisms by which this could be achieved have previously been identified

398   in song sparrows. Specifically, preen wax composition, male song repertoire size, and

399   demographic status have been shown to indicate relatedness [68–70], but of course other

400   mechanisms, such as differential offspring behaviour, might also be involved.

401

402

403   **Ethics**

404   This research was approved by the University of British Columbia's Animal Care Committee.

405

406   **Data accessibility**

407   Data are deposited in Dryad https:doi.org/10.5061/dryad.1zcrdfnf.

408   R code supporting this article has been uploaded as part of the electronic supplementary

409   material.

410

411   **Author contributions.**

412   E.A.G. and J.M.R. designed the research and wrote the manuscript. E.A.G. analysed the data.

413   All other authors conducted key fieldwork and contributed to manuscript editing.

414

415   **Competing interests**

416   We declare no competing interests.

417

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Table 1. Summary of key focal variables and predictions based on underlying kin selection and inclusive fitness theory. Subscripts i and j refer to a socially-paired male and female respectively, and q refers to the female's extra-pair mate. Individuals i and j could produce within-pair offspring (WPO), while individuals j and q could produce extra-pair offspring (EPO) through extra-pair paternity (EPP). Full details of metric calculations are in ESM Appendix S1.

Hypothesis set	Focal variables	Predicted response by males	Predicted response by females
1A	Brood total allelic value (TAV)	Paternal feeding rate will increase with increasing TAV more tightly than with increasing BS.	Maternal feeding rate will increase with increasing TAV more tightly than with increasing BS.
1B	Brood total allelic value (TAV) controlling for brood size (BS)	Paternal feeding rate will increase with increasing TAV after controlling for BS.	Maternal feeding rate will increase with increasing TAV after controlling for BS.
2	Lost allelic value (LAV) and paternity loss (P_{EPO})	Paternal feeding rate will decrease with increasing LAV and P_{EPO}.	Maternal feeding rate will not vary directly with LAV or P_{EPO}.
3A	Coefficient of kinship between mates (k_{ij})	Paternal feeding rate will increase with increasing k_{ij}.	Maternal feeding rate will increase with increasing k_{ij}.

| 3B | Individual's own coefficient of inbreeding (f) | Paternal feeding rate will not vary with f_i. | Maternal feeding rate will not vary with f_j. |

Figure Captions:

Figure 1. Relationships between male and female song sparrow parental feeding rates and (a, b) brood total allelic value (TAV_i and TAV_j) and (c, d) standardized TAV within each level of brood size (TAV_{iz} and TAV_{jz}). Points represent observation sessions. Colours denote different brood sizes (1: black; 2: green; 3: yellow; 4: blue). Lines show predicted regressions of feeding rates on TAV or TAV_z. Regression slopes are presented as β estimates ±1 standard error (full details in ESM Appendix S6).

Figure 2. Relationships between (a) male and (b) female song sparrow parental feeding rates (trips/hr) and lost allelic value (LAV). Colours indicate nest social status (monogamous (M): blue; primary polygynous (PP): purple; secondary polygynous (SP): yellow). Points represent observation sessions. Lines show predicted regressions of feeding rate on LAV overall (black), and for each social status. Regression slopes are presented as standardized β estimates ±1 standard error from models that included a standardized LAV by social status interaction and represent the absolute slope (non-contrast) of the relationship. Y-axes are on different scales for males and females.

Figure 3. Relationships between male and female song sparrow parental feeding rates and (a, b) pair coefficient of kinship (k_{ij}) and (c, d) individual coefficient of inbreeding (f_i or f_j). Colours indicate nest social status (monogamous (M): blue; primary polygynous (PP): purple; secondary polygynous (SP): yellow). Points represent observation sessions. Lines show predicted regressions of feeding rate on k_{ij}, f_i or f_j. Regression slopes are presented as standardized β estimates ±1 standard error from LMMs that included a standardized focal variable by social status interaction and represent the absolute slope (non-contrast) of the relationship. Y-axes are on different scales for males and female

29

(a) social status

- monogamous
- primary polygynous
- secondary polygynous

M = -0.2±0.3
PP = -0.7±0.3
SP = 0.03±0.5

male feeding rate (trips/hr)

(b)

M = 0.3±0.5
PP = 0.1±0.5
SP = 0.4±0.7

female feeding rate (trips/hr)

lost allelic value (LAV)

social status

(a)

M: 0.5±0.2
PP: 1.0±0.4
SP: 0.01±0.4

- monogamous
- primary polygynous
- secondary polygynous

(b)

M: 0.1±0.3
PP: -0.3±0.6
SP: -1.3±0.7

(c)

M: 0.3±0.2
PP: 1.4±0.6
SP: -0.8±0.6

(d)

M: 0.4±0.3
PP: -0.5±0.6
SP: -0.03±0.5