1   **The consequences of polyandry for sibship structures, distributions of**

2   **relationships and relatedness, and potential for inbreeding in a wild**

3   **population**

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20

Abstract

21

22   The evolutionary benefits of simultaneous polyandry (female multiple mating within a single

23   reproductive event) remain elusive. One potential benefit could arise if polyandry alters

24   sibship structures and consequent relationships and relatedness among females'

25   descendants, and thereby intrinsically reduces future inbreeding risk (the 'indirect

26   inbreeding avoidance hypothesis'). However such effects have not been quantified in

27   naturally complex reproductive systems that also encompass iteroparity, overlapping

28   generations, sequential polyandry, and polygyny. We used long-term social and genetic

29   pedigree data from song sparrows (*Melospiza melodia*) to quantify cross-generational

30   consequences of simultaneous polyandry for offspring sibship structures and distributions of

31   relationships and relatedness among possible mates. Simultaneous polyandry decreased

32   full-sibships and increased half-sibships on average, but such effects varied among females

33   and were smaller than would occur in the absence of sequential polyandry or polygyny.

34   Further, while simultaneous polyandry decreased the overall frequencies of possible

35   matings among adult full-sibs, it increased the frequencies of possible matings among adult

36   half-sibs and more distant relatives. These results imply that the intrinsic consequences of

37   simultaneous polyandry for inbreeding risk could cause weak indirect selection on

38   polyandry, but the magnitude and direction of such effects will depend on complex

39   interactions with other mating system components and the form of inbreeding depression.

Introduction

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41 Understanding the evolutionary causes and consequences of simultaneous polyandry,

42 defined as female multiple mating within a single reproductive event, remains a central

43 challenge in evolutionary ecology (Arnqvist and Nilsson 2000; Jennions and Petrie 2000;

44 Parker and Birkhead 2013; Pizzari and Wedell 2013). One key puzzle is that direct costs of

45 multiple mating identified in diverse systems often exceed any obvious direct benefits,

46 meaning that polyandry can decrease females' own fitness (e.g., Rowe 1994; Fedorka et al.

47 2004; Cornell and Tregenza 2007; Forstmeier et al. 2014). The widespread occurrence of

48 simultaneous polyandry consequently implies that it might provide some indirect benefit,

49 manifested as increased fitness of polyandrous females' descendants rather than of the

50 polyandrous females themselves (Tregenza and Wedell 2000; Slatyer et al. 2012; Taylor et

51 al. 2014).

52   Numerous potential indirect benefits of polyandry that would be manifested as

53 increased offspring fitness have been proposed (Jennions and Petrie 2000; Slatyer et al.

54 2012). For instance, polyandrous females might produce female and/or male offspring of

55 higher additive genetic or phenotypic value for fitness (e.g. Garcia-Gonzalez and Simmons

56 2005; Forstmeier et al. 2011; Reid and Sardell 2012), or produce offspring that are less

57 inbred and hence express less inbreeding depression (Stockley et al. 1993; Tregenza and

58 Wedell 2000, 2002; Michalczyk et al. 2011; Duthie et al. 2016). However, such mechanisms

59 often require some form of active female mate choice and/or paternity allocation, which

60 may impose additional costs such as male harassment or increased risk of predation during

61 mate-searching (e.g., Rowe et al. 1994, 1998; Parker and Pizzari 2010; Duthie et al. 2016), or

62 invoke genetic constraints on female strategies (Forstmeier et al. 2011, 2014). Further,

63   empirical evidence of substantial indirect fitness benefits to polyandrous females' offspring

64   remains scant (Jennions and Petrie 2000; Arnqvist and Kirkpatrick 2005; Evans and Simmons

65   2008; Reid and Sardell 2012; Forstmeier et al. 2014; Hsu et al. 2014).

66   This situation raises the possibility that polyandry evolution might be facilitated by

67   indirect benefits manifested a further generation into the future (i.e., increased fitness of

68   polyandrous females' grandoffspring). Indeed, the 'indirect inbreeding avoidance

69   hypothesis' (IIAH, e.g., Cornell and Tregenza 2007) postulates that simultaneous polyandry

70   directly affects the distribution of paternity among population members, and thereby alters

71   inbreeding risk for polyandrous females' offspring. Specifically, when polyandry causes

72   multiple paternity, some offspring of polyandrous females are maternal half-sibs (i.e.,

73   common mother, different father), rather than full-sibs (i.e., both parents in common) as

74   would result from monandry (fig. 1A). In situations where individuals mate locally (i.e. given

75   restricted dispersal), polyandry might consequently reduce the potential (i.e., the expected

76   frequency given random mating) for full-sib inbreeding among a female's offspring (Cornell

77   and Tregenza 2007). Grandoffspring of polyandrous females would consequently be less

78   inbred than grandoffspring of monandrous females on average and, given inbreeding

79   depression in fitness, contribute more offspring (i.e., great-grandoffspring of the original

80   polyandrous female) to the population. The relative frequency of alleles underlying

81   polyandry might consequently increase across generations. Consequently, the basic IIAH

82   outlines a mechanism by which simultaneous polyandry could reduce inbreeding across

83   generations, and hence facilitate its own ongoing evolution and persistence, without

84   requiring direct inbreeding avoidance through mate choice or incurring associated costs.

85   To provide a first theoretical evaluation of the IIAH, Cornell and Tregenza (2007)

86   presented a mathematical model that considers the evolutionary dynamics of polyandry

87   resulting from reduced occurrence of full-sib inbreeding among polyandrous females'

88   offspring. They primarily considered the specific circumstance of non-overlapping,

89   alternating generations of within-brood inbreeding and complete outbreeding, such as

90   could occur in short-lived invertebrates colonizing discrete patches. Their analyses suggest

91   that the intrinsic evolutionary benefit of the IIAH process is small, as is typical for any form

92   of indirect selection (e.g., Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Arnqvist

93   and Kirkpatrick 2005), but might still act in combination with other benefits and appropriate

94   genetic architecture to facilitate ongoing polyandry evolution. However, Cornell and

95   Tregenza's (2007) specific formulation of the IIAH makes assumptions that, while sensible in

96   the context of their initial conceptual development and associated heuristic model, limit its

97   direct applicability to understanding polyandry evolution in complex natural reproductive

98   systems where polyandry and inbreeding risk co-occur.

99   First, Cornell and Tregenza's (2007) formulation of the IIAH does not explicitly

100   consider how the consequences of polyandry for the potential occurrence of inbreeding

101   might extend beyond a polyandrous female's immediate full-sib versus half-sib offspring and

102   accumulate across multiple broods and generations. In iteroparous species, individuals

103   commonly produce multiple offspring broods within and/or across years with overlapping

104   generations. In such cases, multiple full-sibs and maternal half-sibs could be produced

105   across different broods, for example where females mate with different initial (e.g., socially

106   paired) males in different reproductive events (i.e., sequential polyandry) due to mate death

107   or divorce. The set of possible mates available to a given individual offspring once they

108   reach adulthood might then include various full-sibs and half-sibs originating from current,

109   previous and subsequent broods produced by their mother. Moreover, it might also include

110   full- and half-cousins and more distant full- and half-relatives, which are themselves

111   generated across broods and generations, contingent on the degrees of simultaneous and

112   sequential polyandry enacted by each individual's female ancestors.

113   Second, Cornell and Tregenza's (2007) formulation does not explicitly consider how

114   the effects of polyandry on the frequencies of different relationships, and hence on the

115   potential for different degrees of inbreeding, depend on the overall distribution of paternity

116   within a population. Their model assumes that all polyandrous females' additional mates are

117   distinct, such that they do not sire offspring elsewhere in the population (hereafter the

118   'distinct males assumption'). Polyandry then creates maternal half-sibs rather than full-sibs

119   but does not create any paternal half-sibs (fig. 1A). The potential for full-sib mating among a

120   polyandrous female's offspring is consequently reduced, reflecting the implicit increase in

121   effective population size. However, in many natural systems males commonly sire offspring

122   of multiple polyandrous and/or monandrous females (i.e., polygyny, fig. 1B; e.g., Uller and

123   Olsson 2008; Coleman and Jones 2011; Lebigre et al. 2012; McDonald et al. 2013). Such co-

124   occurrence of polyandry and polygyny can still reduce the number of full-sibs and increase

125   the number of maternal half-sibs compared to monandry, but can also increase the number

126   of paternal half-sibs and reduce the number of unrelated individuals in the population (fig.

127   1B). Further, polyandrous females may mate with the same additional males over successive

128   reproductive events and/or allocate all paternity to their additional mate and consequently

129   produce more full-sibs and fewer half-sibs than otherwise expected (fig. 1C). By altering the

130   distribution of relationships among possible mates, such paternity allocations could reduce,

131   eliminate or even reverse the evolutionary benefit of simultaneous polyandry that the basic

132   IIAH postulates.

133   Furthermore, in populations where some degree of inbreeding is common, changes

134   in sibship structures and hence in the 'relationships' among possible mates resulting from

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135   polyandry may cause more complex changes in 'relatedness'. This is because shared

136   ancestry between a focal pair's parents can increase the pair's relatedness above that

137   expected given the same immediate relationship in an outbred population. For example, the

138   relatedness between inbred half-sibs can approach that between outbred full-sibs (Jacquard

139   1974; Lynch and Walsh 1998; Reid et al. 2016). Polyandry might therefore have less effect

140   on the distribution of relatedness among possible mates than expected given its effect on

141   the distribution of relationships.

142   Despite these possibilities, no studies have yet quantified the consequences of

143   simultaneous polyandry for the distributions of sibships, relationships, and relatedness

144   arising in natural populations. Consequently, there is no empirical basis on which to

145   consider how the evolutionary causes and consequences of simultaneous polyandry could

146   be influenced by the intrinsic effects of such polyandry on population-wide sibship or

147   relationship structures and the resulting potential for inbreeding. Such investigations are

148   particularly required for complex mating systems where iteroparity, overlapping

149   generations, and non-independent paternity within and among females' reproductive

150   events can result in complex combinations of polyandry, polygyny, and mate fidelity

151   occurring alongside inbreeding (e.g., Cockburn et al. 2003; Michalczyk et al. 2011; Culina et

152   al. 2015, Reid et al. 2015*b*).

153   Effects of simultaneous polyandry on relationships and relatedness among possible

154   mates could be quantified by experimentally enforcing polyandry or monandry across

155   multiple generations (e.g., Power and Holman 2014). However, such experiments may

156   simultaneously alter other life-history traits such as female fecundity or offspring survival

157   (e.g., Fox 1993; Fedorka and Mousseau 2002; Fisher et al. 2006; Taylor et al. 2008), thereby

158   directly altering sibship structures and relationship frequencies. Furthermore, distributions

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159   of relationships and relatedness all depend on population size and dispersal rate, on among-

160   individual variation in survival and reproductive success, and on variation in pre-

161   reproductive mortality of offspring sired by different males (e.g., Fisher et al. 2006; Gowaty

162   et al. 2010; Sardell et al. 2011; Hsu et al. 2014). The composite effects of simultaneous

163   polyandry on the potential for inbreeding could therefore be usefully quantified in free-

164   living populations where individual reproduction and offspring survival are not artificially

165   constrained.

166   One tractable approach is to utilize systems where a female's potential and realized

167   allocations of offspring paternity to initial versus additional mates can be documented

168   directly. Realized distributions of relationships and relatedness emerging from realized

169   paternity can then be compared with inferred distributions that would have emerged had all

170   a female's offspring in a given brood been sired by her initial mate (i.e., within-brood

171   monandry). Socially-monogamous species with extra-pair reproduction, and hence

172   underlying simultaneous polyandry, allow such comparisons. Here, a female's initial socially-

173   paired male can be identified from behavioral observations and realized paternity can be

174   assigned by molecular genetic analysis (e.g. Webster et al. 1995, 2007; Freeman-Gallant et

175   al. 2005; Lebigre et al. 2012). Accordingly, we used comprehensive song sparrow (*Melospiza*

176   *melodia*) pedigree data to quantify the consequences of extra-pair reproduction for sibship

177   structures and distributions of relationships and relatedness between possible mates, and

178   thereby quantify key processes that underlie the IIAH.

179   First, we quantify the degree to which extra-pair reproduction changes the

180   proportion of full-sib versus half-sib offspring produced by females over their lifetimes given

181   realized patterns of iteroparity and social pairing and repairing, and thereby quantify the

182   fundamental basis for the IIAH. We further quantify the degree to which observed changes

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183   differ from those predicted given lifelong monogamy and given the 'distinct males

184   assumption', and thereby quantify effects of sequential polyandry and polygyny on the IIAH

185   process. We additionally quantify how sibship structures differ among females' hatched and

186   adult offspring, and thereby consider the degree to which pre-reproductive mortality can

187   shape effects of extra-pair reproduction on sibship structures among breeding individuals.

188   Second, we quantify the degree to which extra-pair reproduction alters the

189   distribution of relationships among possible mates given natural iteroparity and overlapping

190   generations, and hence alters the individual and population-wide potential for inbreeding

191   between close and more distant relatives within the observed adult population.

192   Third, we quantify the degree to which extra-pair reproduction interacts with

193   inbreeding to shape the distribution of relatedness across possible mates within and across

194   categories of relationship. Through this sequence of three sets of analyses we elucidate the

195   potential overall effects of the IIAH process on the population-wide potential for inbreeding

196   in naturally complex mating systems.

197

198   **Methods**

199   *Study system*

200   A resident population of song sparrows inhabiting Mandarte Island, British Columbia,

201   Canada, has been intensively studied since 1975 (Smith et al. 2006). Each year, all breeding

202   pairs are closely monitored, all nests are located and all offspring are uniquely marked with

203   colored plastic leg bands approximately six days after hatching (Smith et al. 2006; Wilson et

204   al. 2007; Germain et al. 2015). Mandarte lies within a large song sparrow meta-population

205   and receives regular immigrants (recent mean 0.9 year^{-1}, ~75% female) that prevent the

206   mean degrees of relatedness and inbreeding from increasing (Reid et al. 2006; Wolak and

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207   Reid 2016). All immigrant breeders are mist-netted and banded soon after arriving.

208   Subsequently, the identities of all individuals alive in late April (i.e., the start of the breeding

209   season) are recorded in a comprehensive census (resighting probability > 0.99, Wilson et al.

210   2007), and the socially-paired parents that rear each brood of chicks are identified (Smith et

211   al. 2006).

212   Resulting data show that Mandarte's song sparrows typically form socially

213   monogamous breeding pairs which rear 1–4 broods of 1-4 (mean = 2.2) offspring each per

214   year (Smith et al. 2006). Both sexes can first breed aged one year, and median adult lifespan

215   is two years (maxima of eight and nine years in breeding females and males respectively,

216   Smith et al. 2006; Keller et al. 2008). Due to a typically male-biased adult sex-ratio, 10–40%

217   of males remain socially unpaired annually (Smith et al. 2006; Sardell et al. 2010; Lebigre et

218   al. 2012). Both sexes can form new social pairings within and among years following divorce

219   or death of their socially-paired mate (Smith et al. 2006; Reid et al. 2015*b*), and there is no

220   sex-biased dispersal within the study system (Arcese 1989).

221   Extra-pair reproduction is frequent: overall, 28% of hatched offspring are sired by

222   extra-pair males (Sardell et al. 2010; see also Hill et al. 2011), which is within the range

223   commonly observed in passerine birds (Griffith et al. 2002). Consequently, ~45% of broods

224   show mixed paternity, while ~10% of broods contain ≥ 2 offspring that are all sired by the

225   same extra-pair male. Population-wide extra-pair paternity is distributed across multiple

226   males rather than monopolized by few males (Reid et al. 2011a; Lebigre et al. 2012; Reid

227   and Sardell 2012).

228   Overall, this system has proved valuable for understanding variation in mating

229   strategy and fitness occurring in natural viscous meta-populations (i.e. with restricted

230   dispersal) where relatives and non-relatives interact. Specifically, previous analyses showed

231   substantial opportunity for inbreeding and inbreeding avoidance, but little evidence of

232   active inbreeding avoidance through non-random social pairing (Keller and Arcese 1998;

233   Reid et al. 2006) or non-random extra-pair reproduction (Reid et al. 2015*a,b*) with less

234   closely related mates, despite strong inbreeding depression in fitness (Keller 1998; Reid et

235   al. 2014; Nietlisbach et al. 2017). Further, female extra-pair reproduction is heritable (Reid

236   et al. 2011b) but females receive no obvious direct benefits (e.g., nuptial gifts, offspring

237   provisioning) from extra-pair males, and extra-pair reproduction can reduce offspring fitness

238   (Sardell et al. 2012; Reid and Sardell 2012). However, the potential role of the IIAH process

239   in maintaining extra-pair reproduction, and underlying simultaneous polyandry, has not

240   previously been examined.

241

242   *Social and genetic pedigrees*

243   Fully evaluating the IIAH process requires quantifying sibship structures, relationships and

244   relatedness, which can all be calculated from pedigree data linking offspring to parents. We

245   first compiled a 'social pedigree' linking all banded offspring to their observed mother and

246   her socially-paired male spanning 1975–2015 (Reid et al. 2014, 2015a,b). Since 1993, all

247   adults and banded offspring were blood sampled and genotyped at ~160 highly polymorphic

248   microsatellite loci, and all offspring were assigned to genetic sires with >99% individual-level

249   statistical confidence (Nietlisbach et al. 2015, 2017; Reid et al. 2015*a*). We then compiled a

250   'genetic pedigree' linking all banded offspring to their mother and true genetic father

251   (Sardell et al. 2010; Reid et al. 2014, 2015*a*, 2015*b*; Nietlisbach et al. 2015). We thereby

252   generated two parallel pedigrees spanning 1993–2015 that describe sibship structures and

253   the distributions of relationships and relatedness among all population members as they

254   would have been had all observed breeding pairs been monogamous within broods ('social

255   pedigree'), and given the realized pattern of extra-pair reproduction and underlying

256   polyandry ('genetic pedigree', Lebigre et al. 2012; Reid et al. 2014). Because there is no

257   extra-pair maternity (Sardell et al. 2010), the two pedigrees differ only in the paternity of

258   ~28% of individuals, and are identical in terms of individual longevity, female reproductive

259   success, and offspring survival to recruitment. Differences in sibship structure, relationships

260   and relatedness among possible mates between the two pedigrees therefore stem solely

261   from extra-pair reproduction (see Discussion).

262   To maximize use of all available pedigree data and relax the alternative assumption

263   that all 1993 breeders are unrelated, we grafted each of the 1993–2015 social and genetic

264   pedigrees onto the basal 1975–1992 social pedigree (Reid et al. 2014, 2015*a*). To minimize

265   error in estimates of relationships and relatedness stemming from inadequate pedigree

266   depth and/or remaining paternity error for some individuals hatched during 1975–1992, we

267   restricted analyses to adults alive during 2008–2015. All such individuals had genetically-

268   verified ancestors back to all great-great-grandparents, or were descendants of immigrants,

269   meaning that any error due to misassigned paternities before 1993 was trivial (Reid et al.

270   2015*a*). Immigrants are assumed to be unrelated to existing residents, and therefore to all

271   possible mates, in their arrival year (Marr et al. 2002, Reid et al. 2006, 2014, 2015*a*), and this

272   assumption is supported by comparisons among neutral microsatellite marker data (Keller

273   et al. 2001; Nietlisbach et al, unpublished data). However, immigrants could potentially

274   inbreed with their own descendants in subsequent years.

275

276   *Sibship structures*

277   To quantify the degree to which extra-pair reproduction altered the proportions of full-sibs

278   versus half-sibs that each female produced over her lifetime, we compared sibship

279   structures between the social and genetic pedigrees. We first calculated each female's total

280   lifetime number of banded offspring (j) and calculated the total number of sibships (i.e., all

281   possible full-sib and half-sib relationships, hereafter N_{sibs}) among the j offspring as

282    $N_{Sibs} = \frac{j(j-1)}{2}$. We then calculated the numbers of full-sibships and maternal half-sibships

283   among each female's offspring given the social and genetic pedigrees, and divided these

284   numbers by N_{sibs} to obtain the lifetime proportions of full-sibships (Prop$_{Full-sibs}$) and half-

285   sibships (Prop$_{Half-sibs}$) produced by each female (where Prop$_{Half-sibs}$ = 1 - Prop$_{Full-sibs}$) given each

286   pedigree. The absolute difference between each female's value of Prop$_{Full-sibs}$ given the

287   social and genetic pedigrees (i.e., Diff$_{social-gen}$ = |Prop$_{Full-sibs[social]}$ - Prop$_{Full-sibs[genetic]}$|) quantifies

288   the effect of extra-pair reproduction (i.e., simultaneous polyandry) on sibship structures

289   while fully accounting for natural patterns of variation in paternity stemming from female

290   re-pairing between broods (i.e., sequential polyandry) and repeat mating with the same

291   extra-pair male across multiple broods.

292   We then undertook analyses to explicitly quantify the combined effects of

293   simultaneous and sequential polyandry, and of polygyny, on sibship structures. First, we

294   quantified the difference between Prop$_{Full-sibs}$ given the genetic pedigree and the value of

295   Prop$_{Full-sibs}$ that would arise given strict lifelong monandry (i.e., 1.0, hence Diff$_{life\_monandry-gen}$ =

296   1.0 - Prop$_{Full-sibs[genetic]}$). Second, to quantify the degree to which observed sibship structures

297   differed from those that would have arisen in the absence of polygyny (i.e. given the

298   'distinct males assumption' that is implicit in the basic IIAH, see Introduction), we

299   additionally considered a hypothetical pedigree in which extra-pair males could sire multiple

300   offspring within a given brood but could not sire other within-pair or extra-pair offspring in

301   the population (i.e., fig. 1A). We assigned a unique sire identity to all extra-pair offspring in

302   each observed brood, maintaining the observed paternity distribution (i.e., X_i extra-pair

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303   offspring sired by male i), and then recalculated $Prop_{Full-sibs}$ and $Prop_{Half-sibs}$ for each female.

304   Finally, to elucidate mechanisms underlying observed changes in sibship structures, we also

305   calculated the total number of males that sired at least one of each female's offspring given

306   the social, genetic, and 'distinct males' pedigrees.

307   We fitted generalized linear mixed models (GLMMs) to test whether the sibship

308   structures of females' offspring (binomial error structures, with $Prop_{Full-sibs}$ and N_{sibs} as the

309   binomial numerator and denominator, respectively), or the number of different sires

310   (Poisson error structures), differed between the pedigrees. These models included fixed

311   effects of pedigree (three levels) and random female identity effects. Goodness of fit (R^2) for

312   each model was assessed by the conditional coefficient of determination (Nakagawa and

313   Schielzeth 2013). We used Tukey's post-hoc tests to evaluate pairwise differences in $Prop_{Full-sibs}$

314   and number of sires among the three pedigrees at $\alpha = 0.05$. To quantify how differences

315   in sibship structure varied with the degree to which individual females expressed extra-pair

316   reproduction, we fitted further generalized linear models (GLMs) to quantify how $Diff_{social-gen}$

317   and $Diff_{life\_monandry-gen}$ varied with whether or not any of a female's offspring were sired by an

318   extra-pair male (Supporting Information S1), or with the overall proportion of their lifetime

319   offspring that were sired by an extra-pair male. These GLMs had binomial error structures,

320   with $Diff_{social-gen}$ and $Diff_{life\_monandry-gen}$ as respective binomial numerators, and N_{sibs} as the

321   binomial denominator. There was little over-dispersion in our dataset beyond that

322   accounted for by the fitted models.

323   All the above analyses were implemented across each female's offspring that

324   survived to banding, and across offspring that survived to age one year (recruits). These two

325   sets of analyses respectively elucidate the direct primary effects of the distribution of

326   paternity on sibship structures, and elucidate the net effects of this distribution coupled

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327   with pre-reproductive mortality on realized sibship structures among (potentially)

328   reproductive adults. Females that were still alive in 2016, or that produced ≤1 banded or ≤1

329   recruited offspring (meaning that N_{sibs} = 0), were excluded from the respective analyses.

330   Analyses for banded offspring were also repeated across the subset of females that

331   produced ≥2 recruited offspring, thereby allowing direct comparison across offspring stages

332   within females (Supporting Information S2). While our primary analyses focused on sibship

333   structures among females' offspring, further analyses demonstrated similar structures

334   among males' offspring (Supporting Information S3).

335

336   *Distribution of relationships among possible mates*

337   We next quantified how changes in sibship structures resulting from extra-pair reproduction

338   translated into cross-generational differences in relationships among possible mates within

339   the observed adult population, and hence affected the potential for inbreeding. We used

340   annual censuses of all adults alive in each year during 2008–2015 (annual means of

341   26.9±8.8SD females [range 13–38] and 35.1±10.5SD males [range 20–56]) to generate all

342   possible female-male pairs that could possibly have mated in each year, assuming no mating

343   constraints (hereafter 'all possible matings'). Since we analyzed relationships from the

344   female perspective the assumption of no constraints is reasonable; due to extra-pair

345   reproduction any adult female could possibly mate with any adult male in the population.

346   We compared the frequencies of all possible matings for each adult female in each

347   year that comprised key relationships given the social and genetic pedigrees. These

348   relationships comprised: fathers, full-brothers, and sons (1st degree relatives); grandfathers,

349   uncles, half-brothers, double first cousins (i.e., both parents of each mating individual are

350   full-sibs), nephews, and grandsons (2nd degree relatives); and great-grandfathers, single first

351 cousins, and great-grandsons (3rd degree relatives). We also considered half-uncles, half-

352 single first cousins (i.e., one parent of each mating individual is a half-sib), and half-nephews

353 (4th degree relatives) and thereby quantified effects of extra-pair reproduction (and

354 consequent production of half-sibs rather than full-sibs) on possible matings that would

355 otherwise have involved 3rd degree relatives. Matings involving immigrants were defined as

356 'unrelated' except where immigrants could mate with their own descendants. All possible

357 matings that did not fall into any of the above categories were considered 'more distantly

358 related'. If a possible mating fell into multiple categories (e.g., one case where a possible

359 mate was both a female's son and grandson [i.e., the progeny of a female mating with

360 another son]) it was allocated to the closer relationship. These full- and half-relationships

361 provide a mechanistic link between the generation of half-sibs caused by polyandry, and

362 resulting cross-sex relationships among possible mates.

363   We used Wilcoxon matched pair tests to evaluate whether the lifetime number of

364 possible matings between individual adult females and available adult males in each

365 relationship category differed between the genetic versus social pedigrees. While changes in

366 some relationships given the genetic pedigree may be counted in multiple years (if both the

367 female and possible mate survive across years), these represent separate potential

368 opportunities for inbreeding given random mating, and were thus retained. Although each

369 female has exactly one father in each pedigree, changes in assigned father between the two

370 pedigrees could change whether or not a female's assigned father is still alive in certain

371 years and hence available as a possible mate. Since there is no extra-pair maternity, the

372 number of possible female-son matings cannot change between the two pedigrees.

373 However, such matings were counted to provide a complete summary of possible matings

374 among 1st degree relatives.

375

376   *Distribution of relatedness among possible mates*

377   Given the occurrence of ancestral inbreeding in a population, sibship structures resulting

378   from polyandry, and consequent frequencies of relationships between possible mates, do

379   not translate directly into fixed degrees of relatedness. Hence, to quantify how polyandry

380   translates into quantitative differences in relatedness among possible mates, we used

381   standard pedigree algorithms (Lange 1997) to calculate the coefficient of kinship (k)

382   between all adult females and all available adult males given the social (k_{SOC}) and genetic

383   (k_{GEN}) pedigrees. The coefficient k measures the probability that two homologous alleles

384   sampled from two individuals will be identical by descent relative to the pedigree baseline,

385   and equals the coefficient of inbreeding (f) of resulting offspring (Jacquard 1974; Lynch and

386   Walsh 1998; Reid et al. 2016).

387   We quantified differences in k between each individual adult female and her lifetime

388   set of possible mates given the genetic and social pedigrees in three ways. First, to retain

389   the mechanistic links with relationships and underlying sibship structures, we quantified the

390   differences in each female's mean k_{SOC} and k_{GEN} with all possible mates that were identified

391   as 1st, 2nd, 3rd, and 4th degree relatives, or as more distantly related or unrelated, given the

392   social pedigree. Second, to quantify the effect of extra-pair production on the k between

393   each possible female-male pair, we calculated the difference in k for each possible mating as

394     $k_{DIFF} = k_{GEN} - k_{SOC}$, calculated mean k_{DIFF} for each individual female, and quantified the

395   proportion of females for whom mean k_{DIFF} increased, decreased, or did not change given

396   the genetic versus social pedigrees. Finally, we quantified the degree to which extra-pair

397   reproduction altered the overall potential for inbreeding across the whole population. To do

398   so, we pooled all possible matings during 2008–2015 and used a two-sample Anderson-

                                                                                                                    17

399   Darling test to test whether the shapes of the continuous distributions of k_{GEN} and k_{SOC}

400   differed significantly (using 10,000 resampling permutations).

401   Analyses were run in R version 3.2.2 (R Development Core Team 2015) using

402   packages *MasterBayes*, *nadiv*, *lme4*, *kinship2*, and *kSamples* (Hadfield et al. 2006; Wolak

403   2012; Sinnwell et al. 2014; Bates et al. 2015; Scholz and Zhu 2015). Raw means are reported

404   ±1SD.

405

406   **Results**

407   *Sibship structure of banded offspring*

408   A total of 98 female song sparrows alive during 2008–2015 produced at least two banded

409   offspring over their lifetime (mean 11.4±10.6; median 7–8, range 2–60), and hence at least

410   one sibship. Table 1A,B summarizes the number of sires and Prop$_{Full-sibs}$ among these

411   females' lifetime banded offspring given the social, genetic and 'distinct males' pedigrees.

412   Given the social pedigree, the mean number of sires per female was 1.9, and mean

413   Prop$_{Full-sibs}$ was 0.74 (table 1A,B; fig. 2A,B). Thus, even without considering extra-pair

414   reproduction (i.e., simultaneous polyandry), the occurrence of re-pairing between breeding

415   events (i.e., sequential polyandry), meant that the mean proportion of full-sibships among

416   females' banded offspring was on average ~26% less than expected under lifelong

417   monandry (i.e., 1.0).

418   Given the genetic pedigree, the mean number of sires per female was 2.9, equating

419   to a mean increase of 1.0 sire per female compared to the social pedigree (table 1A; fig. 2A).

420   Consequently, as might be expected, Prop$_{Full-sibs}$ among the banded offspring of most

421   females (60%; 59/98) was lower given the genetic pedigree than given the social pedigree

18

422   (table 1B; fig. 2B). However, for 38% (37/98) of females there was no change, and 2% (2/98)

423   of females actually had higher $Prop_{Full-sibs}$ given the genetic pedigree, illustrating that

424   polyandry can increase rather than decrease full sibships (fig. 2B). Indeed, mean $Diff_{social-gen}$

425   was greater in females where at least one offspring was sired by an extra-pair male, but

426   greatest in females with intermediate proportions of extra-pair offspring (fig. 3A; Supporting

427   Information S1). However, the realized effects of extra-pair reproduction on sibship

428   structure (i.e., $Diff_{social-gen}$ fig. 3A) were smaller, due to sequential polyandry, than would be

429   observed had all females been strictly monandrous throughout their lifetimes (i.e.,

430   $Diff_{life\_monandry-gen,}$ fig. 3B).

431   As expected, the number of sires per female was greatest given the 'distinct males'

432   pedigree (fig. 2A), but in fact did not differ significantly from the genetic pedigree (table 1A).

433   However, most females (69%, 68/98) had even lower $Prop_{Full-sibs}$ given the 'distinct males'

434   pedigree than given the genetic pedigree and no females had higher $Prop_{Full-sibs}$ (fig. 2B),

435   creating a mean reduction in $Prop_{Full-sibs}$ of ~8% relative to the genetic pedigree (table 1B).

436   Thus, while female song sparrows would produce offspring with similar numbers of males

437   given the 'distinct males assumption' as in reality (i.e., given the genetic pedigree), they

438   would produce fewer full-sibships.

439

440   *Sibship structure of recruited offspring*

441   A total of 37 females produced at least two recruited offspring over their lifetime (mean

442   4.2±3.0; median 3, range 2–13). Across these females, the numbers of males that sired

443   banded offspring was consistently higher and $Prop_{Full-sibs}$ were consistently lower than across

444   the full set of 98 females (table 1A,B vs C,D). This is because females that produced ≥2

445   recruits typically produced numerous banded offspring spanning multiple broods. However,

446   the patterns of differences between the pedigrees mirrored those estimated across all 98

447   females (Tukey tests, table 1A,B vs C,D).

448   Comparisons within the 37 females showed that the mean number of sires

449   decreased between banded and recruited offspring, as might be expected given offspring

450   mortality, and hence no longer differed as substantially among the three pedigrees (table

451   1C,E). Meanwhile, mean $Prop_{Full-sibs}$ was slightly higher for recruited offspring than for

452   banded offspring across all three pedigrees (table 1D,F), but mean $Prop_{Full-sibs}$ among

453   recruited offspring was again lower given the genetic versus social pedigrees (table 1F). At

454   the individual level, 46% (17/37) of females had lower $Prop_{Full-sibs}$ given the genetic pedigree,

455   while 51% (19/37) had no change and one female had higher $Prop_{Full-sibs}$ (fig. 2D). $Diff_{social-gen}$

456   was again greater in females with intermediate proportions of extra-pair offspring (fig. 3C),

457   and the effects of extra-pair reproduction on recruit sibship structure were smaller than

458   would be observed given lifelong monandry (fig. 3D, Supporting Information S1). Finally, the

459   difference in $Prop_{Full-sibs}$ given the genetic versus 'distinct males' pedigrees was no longer

460   significant across recruited offspring (Tukey test, table 1F; fig. 2D). Thus, while patterns in

461   the effects of extra-pair mating on sibship structure were qualitatively similar among

462   banded and recruited offspring, these effects were more pronounced among banded

463   offspring, suggesting that early offspring mortality can reduce or alter the effects of

464   polyandry on sibship structures.

465

466   *Distribution of relationships among possible mates*

467   There was a total of 8028 possible matings between adult females and adult males that

468   were alive in each year during 2008–2015, spanning 114 females and 144 males. On

469   average, there were 0.6 fewer possible matings between individual focal females and their

20

470   full-brothers given the genetic versus social pedigrees, but 1.6 more possible matings with

471   half-brothers (table 2). However the distributions of the within-female differences in the

472   numbers of full- and half-brothers between the two pedigrees spanned zero, showing that

473   some females had more full-brothers and/or fewer half-brothers given the genetic pedigree

474   (table 2; fig. 4). This illustrates that patterns of extra-pair reproduction enacted by some

475   female's ancestors increased rather than decreased the number of possible matings

476   between focal females and full-brothers versus half-brothers.

477   On average, there were also fewer possible matings between females and their full

478   uncles, nephews, double first-cousins and single first-cousins given the genetic versus social

479   pedigree and correspondingly increased numbers of possible matings with half-uncles and

480   half-single first cousins (but little change in the number of possible matings with half-

481   nephews, table 2). However, the distributions of the within-female differences again

482   spanned zero, especially for half-single first cousins (fig. 4). There was consequently

483   substantial among-individual variation in the consequences of extra-pair reproduction for

484   the risk of inbreeding with 3rd versus 4th degree relatives.

485   As expected there was no change in the number of possible female-son matings

486   given the genetic versus social pedigrees, and only small average changes in the numbers of

487   possible matings with fathers, grandfathers, grandsons, great-grandfathers and great-

488   grandsons (table 2) with little variation among individuals (fig. 4). Furthermore, there was

489   little or no change in the number of possible matings between females and more distant

490   relatives or completely unrelated males, respectively (table 2).

491   Overall, the individual-level differences in the distribution of relatives available as

492   possible mates translated into substantial population-level differences: extra-pair

493   reproduction meant that, across the population, adult females had 40% fewer possible

494   matings with full-brothers, 166% more possible matings with half-brothers, and 85% more

495   possible matings with 4th degree relatives than with analogous 2nd and 3rd degree relatives

496   (Supporting Information S4).

497

498   *Distribution of relatedness among possible mates*

499   Due to variation in inbreeding among females' ancestors, there was substantial among-

500   individual variation in the mean kinship (k) between adult females and their possible mates

501   that were identified as 1st, 2nd, 3rd or 4th degree relatives given the social pedigree (fig. 5A–

502   D), particularly for 1st and 2nd degree relatives. Of the females that had ≥1 possible mate

503   that was identified as a 1st, 2nd, 3rd or 4th degree relative given the social pedigree most, but

504   not all, had lower mean k with these same sets of possible mates given the genetic pedigree

505   (fig. 5A–D). Across females, mean k_{GEN} was significantly lower than mean k_{SOC} for all four

506   categories of relative, but the magnitude of the difference was smallest for 4th degree

507   relatives (table 3). Conversely, mean k_{SOC} and mean k_{GEN} did not differ across females'

508   possible mates that were identified as more distant relatives given the social pedigree (table

509   3; fig. 5E). Because newly arrived immigrants were the only individuals that were completely

510   unrelated to their possible mates, mean k_{SOC} and mean k_{GEN} were identical across individuals

511   that were identified as non-relatives in the social pedigree (table 3; fig. 5F).

512   Of the 114 females, 71% (81) had negative values of mean k_{DIFF} across all possible

513   matings given the genetic pedigree versus the social pedigree, while 25% (29) had positive

514   values of mean k_{DIFF}, and 4% (4) had no change in mean k_{DIFF} (three female immigrants that

515   were alive in only one year, and one female immigrant whose only possible matings with

516   relatives were with sons or grandsons). Grand mean k_{DIFF} across all possible matings for

517   individual females was -0.007 ±0.01 (median -0.008, range -0.035–0.017), showing that, on

22

518   average, females were slightly less related to all possible mates given the genetic pedigree

519   than given the social pedigree.

520   However, across all pooled possible matings for all females, the distributions of k_{GEN}

521   and k_{SOC} were significantly different (two-sample Anderson-Darling test, AD = 28.27, T =

522   35.79, p < 0.001). This difference arose because the distribution of k_{GEN} included fewer

523   possible matings at higher k (fig. 6, black bars), but more possible matings at lower but non-

524   zero k (fig. 6, white bars), than the distribution of k_{SOC}. There was again no difference in the

525   number of possible matings among unrelated individuals (i.e., k = 0, fig. 6). Thus, the main

526   effects of extra-pair mating were not in altering mean relatedness among potential mates

527   but in altering the distribution of relatedness, such that females were less likely to mate at

528   intermediate and higher levels of k (i.e., with closely related males) and more likely to mate

529   at lower, but non-zero, levels of k (i.e., with more distantly related males).

530

531   **Discussion**

532   Simultaneous polyandry is widely hypothesized to have evolved to facilitate inbreeding

533   avoidance in populations where relatives interact and inbreeding depression is strong (e.g.,

534   Stockley et al. 1993; Tregenza and Wedell 2000; Michalczyk et al. 2011; Duthie et al. 2016;

535   Bocedi and Reid 2017). Consequently, numerous empirical studies on diverse systems have

536   tested whether polyandrous females avoid inbreeding by expressing pre-copulatory and/or

537   post-copulatory choice for less closely related mates (Tregenza and Wedell 2002; Firman

538   and Simmons 2008; Brouwer et al. 2011; Reid et al. 2015a). However, no studies have

539   quantified the degree to which intrinsic effects of polyandry on sibship structures might

540   indirectly reduce inbreeding risk (i.e., the 'indirect inbreeding avoidance hypothesis', IIAH) in

541   systems experiencing natural variation in polyandry, polygyny and paternity within and

23

542   across overlapping generations. Accordingly, we compared long-term social and genetic

543   pedigree data from free-living song sparrows to examine the consequences of extra-pair

544   paternity, and hence of underlying simultaneous polyandry, for sibship structures and

545   resulting distributions of relationships and relatedness. Further, by comparing observed

546   patterns to those that would have arisen given lifelong monandry (i.e., no simultaneous or

547   sequential polyandry) or given simultaneous polyandry but no resulting polygyny (i.e., the

548   'distinct males assumption'), we isolated effects of major components of the complex

549   overall natural mating system on sibship structures.

550   Comparisons between social and genetic pedigrees have previously been used to

551   quantify effects of extra-pair reproduction on the variance in male reproductive success and

552   hence on effective population size and the opportunity for selection (Webster et al. 1995,

553   2007; Freeman-Gallant et al. 2005; Lebigre et al. 2012). Such effects are often small,

554   including in song sparrows (Lebigre et al. 2012, see also Karl 2008). However, such results do

555   not preclude the possibility that extra-pair reproduction could affect individual-level

556   inbreeding risk. This is because the same overall variance in male reproductive success, but

557   very different sibship structures and distributions of relationships and relatedness, can arise

558   if individual males sire several offspring of one female (i.e., generating full-sibs) or sire one

559   offspring of several females (i.e., generating paternal half-sibs).

560

561   *Sibship structures*

562   It may seem inevitable that extra-pair reproduction will reduce full-sibships, as assumed by

563   the basic IIAH, and by Cornell and Tregenza's (2007) initial theoretical model. However our

564   analyses illustrate that such effects arising within a natural mating system are not so

565   straightforward. Comparison of the social and genetic song sparrow pedigrees showed that

24

566   extra-pair reproduction did indeed increase the mean number of different males that sired

567   individual females' offspring and hence reduce the mean proportion of full-sibships ($Prop_{Full\text{-}sibs}$)

568   and increase the mean proportion of maternal half-sibships ($Prop_{Half\text{-}sibs}$) among females'

569   lifetime banded offspring. However, such means mask substantial among-female variation,

570   including cases where extra-pair reproduction increased rather than reduced $Prop_{Full\text{-}sibs}$ (fig.

571   2B). Such patterns can result from non-independent extra-pair paternity when females

572   produce numerous extra-pair offspring with the same male across broods (as indicated by

573   fig. 3A,C), and/or if a female's extra-pair male from one brood becomes her socially-paired

574   male for another brood (or vice versa). Further, comparisons with the hypothetical

575   occurrence of lifelong monogamy showed that the occurrence of social re-pairing across

576   breeding attempts (i.e., sequential polyandry) already reduced the effects of simultaneous

577   polyandry on sibship structures by ~26%. Selection for simultaneous polyandry stemming

578   from the IIAH process might consequently be weaker given iteroparity and associated

579   repairing than given semelparity and/or strict lifelong monogamy. Comparison with the

580   hypothetical 'distinct males' pedigree showed that 68% of females would have had lower

581     $Prop_{Full\text{-}sibs}$ among their banded offspring in the absence of polygyny than given the observed

582   pattern of polygyny defined by the genetic pedigree (fig. 2B). This implies that Cornell and

583   Tregenza's (2007) theoretical formulation of the IIAH might overestimate indirect selection

584   on polyandry arising in polygynandrous systems.

585   While simultaneous polyandry can clearly affect the sibship structure of females'

586   conceived offspring, its consequences for inbreeding risk (and other kin interactions

587   including kin cooperation and competition) ultimately depend on its effects on the sibship

588   structure of offspring that survive to life-history stages when key interactions occur. In song

589   sparrows, further comparisons of the genetic and social pedigrees showed that the effects

590   of extra-pair reproduction on sibship structures were qualitatively similar, but subtly

591   different, across recruited versus banded offspring (fig. 2). Most notably, Prop$_{Full-sibs}$ for

592   recruits no longer differed between the genetic and 'distinct males' pedigrees (table 1B,D vs

593   F). These patterns imply that theoretical predictions regarding indirect selection on

594   polyandry might, in some instances, be relatively robust to an assumption of no polygyny.

595   However, such inferences from observed genetic and social pedigrees require the

596   additional, and commonly violated, assumption that offspring survival to recruitment does

597   not depend on paternity. In song sparrows, female extra-pair offspring are less likely to

598   recruit than female within-pair offspring reared in the same brood (i.e., maternal half-

599   sisters, Sardell et al. 2011), and extra-pair offspring of both sexes have lower survival and/or

600   reproductive success than within-pair offspring in other passerine birds (e.g., house

601   sparrows, *Passer domesticus*, Hsu et al. 2014; coal tit, *Periparus ater*, Schmoll et al. 2009).

602   Any small reduction in inbreeding among polyandrous females' offspring might therefore be

603   further reduced by stochastic and/or deterministic variation in survival of offspring sired by

604   different males. The ultimate consequences of polyandry for the expected frequency of

605   close inbreeding and consequent fitness among descendants of polyandrous females in

606   natural populations may therefore be smaller than predicted by models that do not consider

607   differential offspring survival (e.g., Cornell and Tregenza 2007), and estimated in laboratory

608   populations where variation in survival may be minimized (e.g., Power and Holman 2014).

609   Future theoretical and empirical studies considering the evolutionary causes and

610   consequences of polyandry arising through its effects on sibship structures should therefore

611   consider such effects within the context of the overall mating system, including natural

612   variation in paternity arising through sequences of polygyny and mate fidelity, re-pairing

613   due to divorce and mate death, as well as differential offspring survival.

26

614

615   *Distributions of relationships and relatedness*

616   The effects of simultaneous polyandry on sibship structures among recruited offspring are

617   likely to alter the frequencies of diverse types of half-relatives versus full-relatives spanning

618   multiple (overlapping) generations, thereby altering any individual's overall potential for

619   inbreeding or interacting with different types of relatives. The form and magnitude of

620   indirect selection on polyandry stemming from the IIAH process might then differ from that

621   predicted in restricted situations with within-brood mating and non-overlapping

622   generations (e.g., Cornell and Tregenza 2007). Indeed, our comparisons of the social and

623   genetic pedigrees of female and male song sparrows that survived to adulthood showed

624   that ancestral extra-pair reproduction generally reduced the potential for inbreeding among

625   different degrees of full-relatives, and increased the potential for inbreeding among more

626   distant half-relatives. However, this change was not consistent across all individual females

627   and types of relationship (table 2, fig. 4, Supporting Information S4). Similarly, simultaneous

628   polyandry reduced the mean kinship (k) between adult females and their possible mates,

629   most notably with available adult males that would otherwise have been 1st degree relatives

630   (fig. 5). However, the overall conclusions remained unchanged when all possible matings

631   among 1st degree relatives were excluded (Supporting Information S5), thereby considering

632   a scenario where individuals actively avoid inbreeding with 1st degree relatives, as could be

633   achieved through some form of active or passive kin discrimination (e.g., Stow and Sunnucks

634   2004; Gerlach and Lysiak 2006; Archie et al. 2007; Brouwer et al. 2011; Ihle and Forstmeier

635   2013). Overall, the individual-level differences in relatedness among possible mates

636   stemming from simultaneous polyandry resulted in fewer possible matings at intermediate

27

637   and higher *k* (i.e., among closely related pairs), and more possible matings at lower but non-

638   zero *k* (fig. 6).

639   Such conclusions rely on the implicit assumptions of our study design that mating

640   decisions and recruitment are unaffected by pedigree structure, and hence that there is no

641   active inbreeding avoidance or differential survival by within-pair versus extra-pair offspring.

642   Indeed, previous analyses showed that song sparrows do not actively avoid inbreeding

643   through social pairing or extra-pair reproduction (Keller and Arcese 1998; Reid et al. 2015*a*).

644   However, to further consider the implications of such assumptions, we conducted additional

645   analyses to quantify effects of polyandry on relatedness within a single cohort (Supporting

646   Information S6). Such analyses have the advantage that they do not require any

647   assumptions regarding patterns of mating or survival in the absence of extra-pair

648   reproduction, but the disadvantage that they eliminate effects of polyandry on relatedness

649   generated across multiple (overlapping) generations. These analyses also showed reduced

650   potential for close inbreeding ($k \geq 0.25$) given the genetic versus social pedigrees, but no

651   reduction in more distant inbreeding ($0.03125 \leq k < 0.25$, Supporting Information S6). These

652   supporting results illustrate that overall effects of polyandry in reducing the potential for

653   inbreeding at intermediate *k* accumulate across generations, meaning that exact

654   quantitative outcomes could be influenced by patterns of differential survival of within-pair

655   versus extra-pair offspring.

656

657   *Implications*

658   Our results imply that the magnitude and direction of indirect selection on simultaneous

659   polyandry stemming from the intrinsic consequences of such polyandry for distributions of *k*

660   among females' offspring, and hence grand-offspring *f,* will depend on the shape of the

28

661 relationship between fitness and f (i.e., the form of inbreeding depression). Given

662 multiplicative effects of deleterious recessive alleles, inbreeding depression is expected to

663 be log-linear, such that the reduction in fitness decreases with increasing f (fig. 7, Morton et

664 al. 1956; Charlesworth and Charlesworth 1987; Charlesworth and Willis 2009). Counter-

665 intuitively, under these conditions, polyandry might in fact cause a net decrease in mean

666 fitness, even though it slightly reduces mean grand-offspring f. Intrinsic indirect selection on

667 polyandry stemming from 'indirect inbreeding avoidance' might then impede rather than

668 facilitate polyandry evolution. However, given epistatic or threshold effects, inbreeding

669 depression could be weak up to some value of f above which fitness decreases markedly

670 (e.g., fig. 7, Charlesworth and Willis 2009). Given such threshold effects, the long-term

671 relative frequency of alleles underlying polyandry could then increase due to the reduced

672 frequency of matings among close relatives and the resulting net increase in mean offspring

673 fitness that would arise despite an increased frequency of matings among more distant

674 relatives.

675   The form of inbreeding depression is very difficult to quantify in natural populations,

676 not least because close inbreeding often occurs infrequently and may be more likely in high-

677 fitness lineages where more relatives are available for mating, meaning that phenotypic

678 effects of inbreeding could be confounded with environmental and/or additive genetic

679 effects (Reid et al. 2008). Experimental assessments of the shape of inbreeding depression

680 across ranges of f relevant to animal mating systems are also scarce, because most

681 experimental studies consider restricted inbred groups generated through one or multiple

682 generations of sib-sib mating (Charlesworth and Charlesworth 1987; Keller and Waller 2002;

683 Charlesworth and Willis 2009). Full quantitative, mechanistic evaluation of the 'indirect

684 inbreeding avoidance' process in driving or impeding polyandry evolution will therefore

685 require information on distributions of sibships, relationships and relatedness arising within

686 complex natural mating systems to be coupled with detailed experimental assessments of

687 the form of inbreeding depression arising across appropriate ranges of f.

688

689 **Acknowledgments**

697

698 **Supplementary Material**

699 **Supporting Information S1:** Quantifying the combined effects of simultaneous and

700 sequential polyandry on sibship structures

701 **Supporting Information S2:** Sibship structure among banded offspring of females that

702 produced recruits

703 **Supporting Information S3:** Sibship structure among males' banded and recruited offspring

704 **Supporting Information S4:** Population-wide effects of polyandry on the distribution of

705 relatedness

706 **Supporting Information S5:** Distribution of relatedness excluding all 1st degree relatives

707 **Supporting Information S6:** Distribution of relatedness within cohorts

708

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916   **Table 1:** Summary statistics (left panel) and generalized linear mixed models (right panel)

917   estimating differences in the number of males that sired a female's offspring, and the

918   proportion of full-sibships (Prop$_{\text{Full-sibs}}$) among females' offspring given the social, genetic

919   and 'distinct males' pedigrees. Focal females and offspring comprise (A and B) banded

920   offspring of all females that produced ≥2 banded offspring (i.e., ≥1 sibship, *n* =98 females),

921   and (C and D) banded offspring and (E and F) recruited offspring of females that produced

922   ≥2 recruited offspring (*n* =37 females). Raw means are presented ± 1 standard deviation

923   (SD). Models assumed (A,C,E) Poisson or (B,D,F) binomial error structures. Estimated

924   pedigree effects (on latent scales) are differences from the intercept (social pedigree) and

925   are presented ±1 standard error (SE), *df* is the residual degrees of freedom, R^2 is the

926   conditional coefficient of determination, and *Z* and *p* values are presented for each fixed

927   effect level where the social pedigree represents the intercept. 'Tukey' summarizes a Tukey

928   post-hoc test assessing differences among pedigrees, where different lower case letters

929   (a,b,c) represent groups with significantly different means.

Response variable	Pedigree	Mean (±SD)	Median (Range)	df	R^2	Estimate (±SE)	Z	p	Tukey
Banded offspring – Full Dataset									
A) Number of males	Social	1.9 (1.2)	1 (1–6)	290	0.52	0.45 (0.10)			a
	Genetic	2.9 (2.1)	2 (1–10)			0.45 (0.09)	4.8	<0.001	b,c
	Distinct males	3.5 (2.9)	2 (1–14)			0.63 (0.09)	7.0	<0.001	c
B) Prop$_{Full-sibs}$	Social	0.74 (0.31)	1.00 (0.15–1.00)	290	0.61	1.36 (0.24)			a
	Genetic	0.53 (0.34)	0.40 (0.00–1.00)			-0.58 (0.03)	18.6	<0.001	b
	Distinct males	0.49 (0.35)	0.33 (0.00–1.00)			-0.77 (0.03)	24.1	<0.001	c
Banded offspring – Restricted dataset									
C) Number of males	Social	2.7 (1.5)	2 (1–6)	107	0.56	0.86 (0.13)			a
	Genetic	4.3 (2.5)	4 (1–10)			0.48 (0.13)	3.8	<0.001	b,c
	Distinct males	5.2 (3.2)	5 (1–14)			0.68 (0.12)	5.6	<0.001	c
D) Prop$_{Full-sibs}$	Social	0.56 (0.32)	0.46 (0.15–1.00)	107	0.33	0.08 (0.20)			a
	Genetic	0.40 (0.28)	0.30 (0.10–1.00)			-0.52 (0.03)	15.1	<0.001	b
	Distinct males	0.34 (0.25)	0.25 (0.05–1.00)			-0.66 (0.04)	19.0	<0.001	c
Recruited offspring									
E) Number of males	Social	1.6 (0.6)	2 (1–3)	107	0.18	0.43 (0.14)			a
	Genetic	2.2 (1.2)	2 (1–7)			0.31 (0.17)	1.9	0.06	a
	Distinct males	2.3 (1.3)	2 (1–7)			0.37 (0.17)	2.2	0.03	a
F) Prop$_{Full-sibs}$	Social	0.67 (0.37)	0.85 (0.00–1.00)	107	0.37	0.82 (0.27)			a
	Genetic	0.47 (0.37)	0.40 (0.00–1.00)			-0.96 (0.14)	7.0	<0.001	b,c
	Distinct males	0.43 (0.38)	0.33 (0.00–1.00)			-1.06 (0.14)	7.6	<0.001	c

930

931 **Table 2:** Mean ±SD (and range) of the number of lifetime possible matings for individual

932 adult female song sparrows at 15 specified relationships, and with more distant related and

933 unrelated individual adult males, given the social and genetic pedigrees. The mean

934 difference shows the mean decrease (negative values) or increase (positive values) in the

935 number of possible matings at each relationship level given the genetic versus social

936 pedigrees across 114 individual adult females. Full distributions of the differences are shown

937 in fig. 4. *Z* and *p* denote the Wilcoxon rank sum test statistic value and associated *p* value.

938 Relationships where numbers of possible matings decreased or increased significantly given

939 the genetic pedigree are highlighted in bold.

Relationship		Social pedigree	Genetic pedigree	Mean Difference	*Z (p)*
1st degree	Father	0.92 ±0.88 (0–5)	0.85 ±0.88 (0–5)	-0.07 ±0.47 (-2–1)	0.7 (0.49)
	Full-brother	1.50 ±1.86 (0–9)	0.90 ±1.33 (0–6)	**-0.60 ±1.05 (-6–1)**	**2.9 (0.004)**
	Son	0.90 ±1.85 (0–11)	0.90 ±1.85 (0–11)	0.00 ±0.00 (0–0)	0.0 (1.00)
2nd degree	Grandfather	0.40 ±0.74 (0–4)	0.35 ±0.60 (0–2)	-0.05 ±0.65 (-4–2)	0.2 (0.84)
	Uncle	0.78 ±1.17 (0–5)	0.39 ±0.88 (0–5)	**-0.39 ±0.75 (-4–1)**	**3.4 (<0.001)**
	Half-brother	0.96 ±1.71 (0–10)	2.54 ±2.87 (0–12)	**+1.59 ±2.17 (-1–11)**	**5.7 (<0.001)**
	Double first cousin	0.07 ±0.42 (0–3)	0.00 ±0.00 --	-0.07 ±0.42 (-3–0)	2.0 (0.05)
	Nephew	1.39 ±2.97 (0–14)	0.65 ±1.74 (0–12)	**-0.75 ±2.12 (-14–1)**	**2.2 (0.03)**
	Grandson	0.37±1.20 (0–7)	0.39 ±1.48 (0–12)	+0.02 ±0.59 (-2–5)	0.4 (0.69)
3rd degree	Great-grandfather	0.17 ±0.46 (0–2)	0.15 ±0.55 (0–3)	-0.02 ±0.69 (-2–3)	1.0 (0.32)
	Single first cousin	2.33 ±2.87 (0–16)	0.76 ±1.77 (0–15)	**-1.57 ±2.44 (-13–2)**	**5.5 (<0.001)**
	Great-grandson	0.11 ±0.72 (0–7)	0.12 ±0.81 (0–7)	+0.02 ±0.19 (0–2)	0.0 (0.99)
4th Degree	Half-uncle	1.08 ±1. 75 (0–8)	2.00 ±2.30 (0–10)	**+0.92 ±2.09 (-6–6)**	**3.6 (<0.001)**
	Half-single first cousin	2.46 ±3.17 (0–17)	5.39 ±6.44 (0–35)	**+2.94 ±5.53 (-13–28)**	**4.1 (<0.001)**
	Half-nephew	1.98 ±4.29 (0–23)	2.82 ±5.46 (0–32)	+0.84 ±4.63 (-16–24)	1.0 (0.33)
More distant		47.92 ±35.06 (0–207)	45.11±35.06 (0–182)	-2.81 ±7.65 (-29–20)	0.6 (0.52)
Unrelated		7.09 ±24.49 (1–261)	7.09 ±24.49 (1–261)	0.00 ±0.00 (0–0)	0.0 (1.00)

940

941 **Table 3:** Mean ±SD (and range) pairwise coefficient of kinship (k) between individual adult

942 female song sparrows and all possible adult male mates that were classified as 1st, 2nd, 3rd or

943 4th degree relatives, or as more distant relatives or as unrelated given the social pedigree,

944 with k calculated from the social pedigree (k_{SOC}) or genetic pedigree (k_{GEN}). n and ♀

945 respectively represent the numbers of possible matings and individual females in each

946 category. Mean difference denotes the mean decrease (negative values) or increase

947 (positive values) in mean k for individual females given the genetic versus social pedigrees

948 (i.e., k_{GEN} - k_{SOC}). Z and p denote the Wilcoxon rank sum test statistic value and associated p

949 value. Degrees of relationship where mean k decreased significantly are highlighted in bold.

950

Relationship given social pedigree	k_{SOC}	k_{GEN}	Mean difference	Z (p)
1st degree (n = 378, ♀ = 104)	0.314±0.034 (0.261–0.472)	0.263±0.067 (0.031–0.368)	**-0.051±0.07** **(-0.301–0.062)**	**5.7** **(<0.001)**
2nd degree (n = 453, ♀ = 99)	0.197±0.032 (0.147–0.361)	0.157±0.042 (0.03–0.338)	**-0.041±0.045** **(-0.165–0.128)**	**7.2** **(<0.001)**
3rd degree (n = 297, ♀ = 78)	0.141±0.026 (0.094–0.255)	0.112±0.029 (0.057–0.198)	**-0.033±0.031** **(-0.14–0.063)**	**6.7** **(<0.001)**
4th degree (n = 629, ♀ = 97)	0.125±0.022 (0.084–0.174)	0.108±0.032 (0.031–0.179)	**-0.017±0.026** **(-0.099–0.06)**	**4.3** **(<0.001)**
More distant (n = 5463, ♀ = 110)	0.087±0.017 (0.034–0.119)	0.088±0.018 (0.041–0.122)	+0.001±0.011 (-0.023–0.039)	0.2 (0.84)
Unrelated (n = 808, ♀ = 114)	0.000±0.000 --	0.000±0.000 --	0.00±0.00 --	0.0 (1.00)

951

42

952   **Figure 1:** Conceptualized mating systems with simultaneous polyandry and (A) distinct

953   males across females ('distinct males assumption'); (B) common males across females (i.e.,

954   polygyny) with independent paternity; and (C) common males across females and non-

955   independent (i.e., skewed) paternity. Top female and male symbols depict breeding females

956   and their mate(s) (connected by black lines). Boxed females and males depict resulting

957   offspring from each mating, where box edge patterns match offspring to their mother, and

958   individual shading match offspring to their father. In (A), a polyandrous female's (vertical

959   stripes) offspring have the same mother (i.e., enclosed within vertical striped box), but only

960   some have the same father (i.e., are full-sibs rather than maternal half-sibs; matching grey

961   or black shading). A monandrous female's (checkered box) offspring all have the same

962   mother and father. In (B), the same males can mate with multiple polyandrous and/or

963   monandrous females, creating more offspring that have the same father (i.e., paternal half-

964   sibs), and fewer unrelated offspring that share neither parent. In (C), a polyandrous female

965   (horizontal stripes) mates with an initial male (connected by dashed line) but all of her

966   offspring are sired by the same additional male, resulting in full-sib offspring (as for A).

967

968   **Figure 2**: The numbers of different males that sired female song sparrows' (A) banded and

969   (C) recruited offspring, and the sibship structures of females' (B) banded and (D) recruited

970   offspring given the social pedigree ('Social'), genetic pedigree ('Genetic'), and 'distinct

971   males' pedigree ('Distinct males'). In (A) and (C), box lines represent the median, upper and

972   lower quartiles, whiskers demarcate 1.5× the interquartile range, and '+' shows the mean. In

973   (B) and (D), the left and right axes respectively show the proportions of sibships among each

974   female's offspring that are full-sibships ($Prop_{Full-sibs}$) and half-sibships ($Prop_{Half-sibs}$), where

43

975   points denote individual females (jittered for clarity), and lines join observations for

976   individual females given the three pedigrees.

977

978   **Figure 3:** Relationships between the proportion of a female's lifetime offspring that were

979   extra-pair offspring (Proportion EPO) and the absolute difference in $Prop_{Full\text{-}sibs}$ given (A and

980   C) the genetic versus social pedigrees ($Diff_{social\text{-}gen}$), and (B and D) the genetic pedigree versus

981   strict lifelong monandry ($Diff_{life\_monandry\text{-}gen}$) for (A and B) banded and (C and D) recruited

982   offspring. Predictions (black lines) and confidence intervals (grey bands) are from

983   generalized linear models (Supporting Information S1).

984

985   **Figure 4:** Distributions of the difference in the number of possible matings at each focal

986   relationship level (listed in table 2) across 114 individual adult females given the genetic

987   versus social pedigrees. Negative and positive values respectively indicate decreases and

988   increases in the number of possible matings with available adult males at each relationship

989   level. White bars denote lineal relatives (where little difference in the number of possible

990   matings is expected), black bars denote relationship levels where the mean increase or

991   decrease in the number of possible matings differed significantly from zero (table 2), and

992   grey bars denote all other non-lineal relationship levels. Two relationship levels ('son' and

993   'unrelated') are not depicted because the difference in the number of matings between the

994   social and genetic pedigrees was uniformly zero (table 2).

995

44

996   **Figure 5:** Mean coefficient of kinship (k) between individual adult female song sparrows and

997   all possible adult male mates that were identified in the social pedigree as 1st, 2nd, 3rd or 4th

998   degree relatives, or as more distant relatives or as unrelated, where k is calculated given the

999   social pedigree ('Social') or genetic pedigree ('Genetic'). Note that y-axis scales differ among

1000   rows of panels. Points denote individual females (jittered for clarity), and lines join

1001   observations for individual females given the two pedigrees. Of the females that had ≥1

1002   possible mate that was identified as a 1st, 2nd, 3rd or 4th degree relative given the social

1003   pedigree most, but not all, had lower mean k with these same sets of possible mates given

1004   the genetic pedigree (80% [83/104], 84% [83/99], 87% [68/78] and 73% [71/97] of females

1005   respectively).

1006

1007   **Figure 6:** Overall distributions of pairwise coefficients of kinship across all possible matings

1008   between adult female and male song sparrows, calculated from the social pedigree (black

1009   bars) or genetic pedigree (white bars), with grey bars denoting overlap between the two

1010   distributions. Dotted, dashed, and dot-dashed lines depict kinship values equivalent to first

1011   cousin (0.0625), half-sib (0.125), and full-sib (0.25) matings, respectively. Box plots further

1012   visualize the distribution of k given each pedigree, where box lines represent the median,

1013   upper and lower quartiles, whiskers demarcate 1.5× the interquartile range, and '+'

1014   represents the mean. Mean k_{SOC} was 0.101±0.069 (median 0.914, range 0.000–0.472) and

1015   mean k_{GEN} was 0.094±0.065 (median 0.087, range 0.00–0.421), corresponding to a small but

1016   statistically significant mean decrease of -0.006±0.040 (median -0.003, range -0.301–0.251,

1017   Wilcoxon signed rank test: Z = 18.95, p < 0.001).

1018

1019   **Figure 7:** Conceptualization of potential relationships between mean fitness (scaled relative

1020   to an outbred individual) and individual coefficient of inbreeding (f). Such relationships

1021   could be linear (white circles), concave (i.e., log-linear, given multiplicative allelic effects,

1022   grey circles), convex (given epistasis, black circles), or follow a threshold pattern (diamonds).

1023   Points denote x-axis intervals of 0.01 to depict the effects of different shapes of inbreeding

1024   depression on equal scales. Note that concave and convex forms of inbreeding depression

1025   are often depicted on a log scale (i.e., log-fitness) such that log-linear effects appear linear

1026   (e.g., Charlesworth and Willis 2009). Each series of points is meant to convey qualitative

1027   patterns of inbreeding depression and not quantitative values, and so are jittered for clarity.
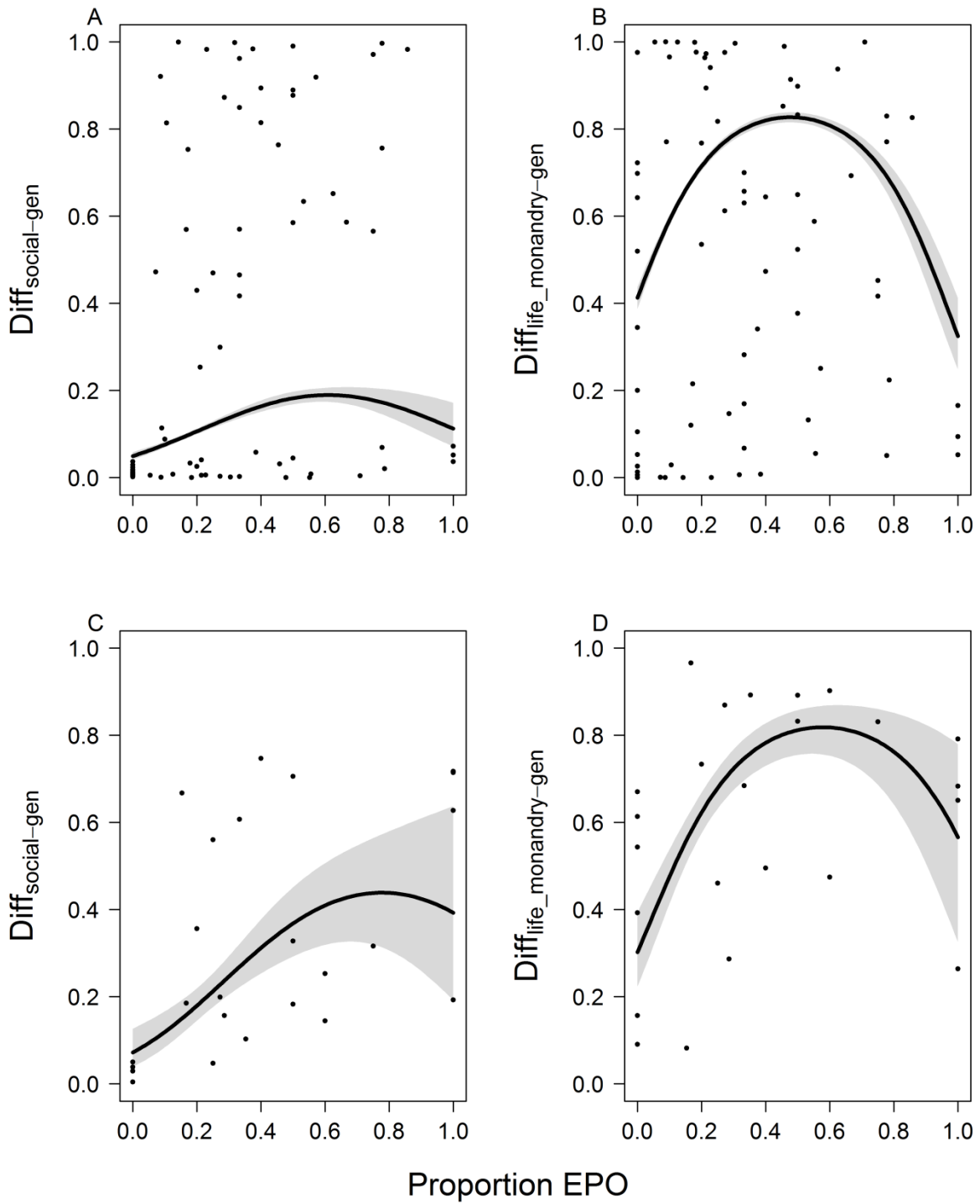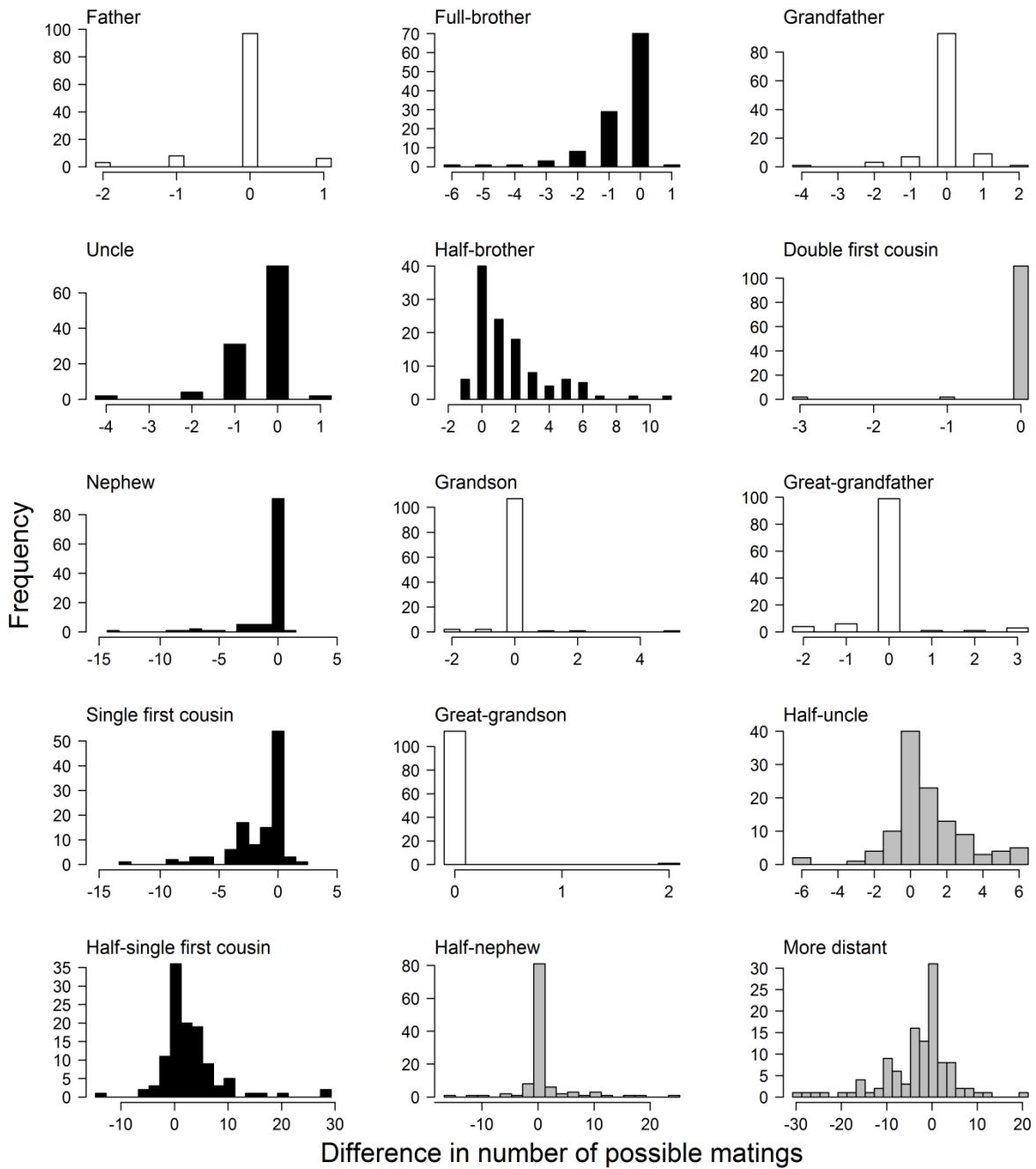
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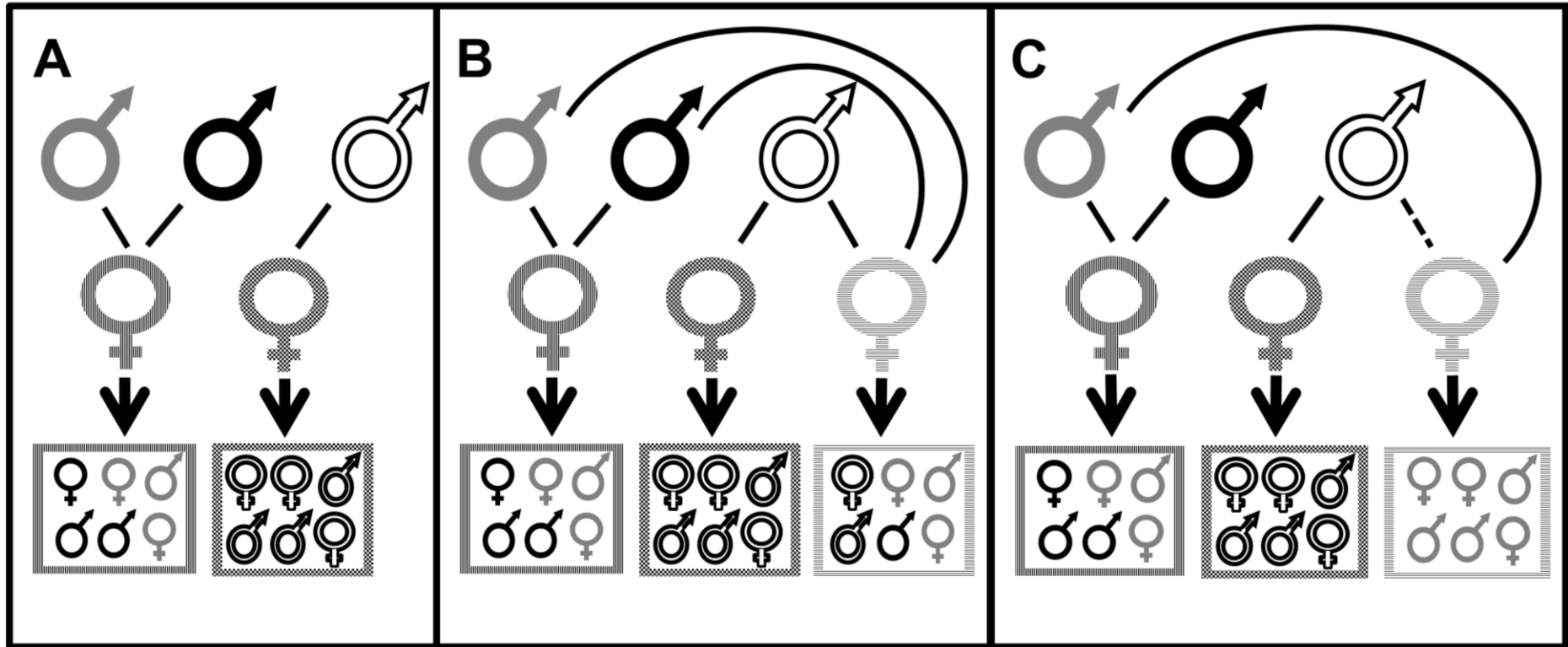
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1030   **Figure 1**
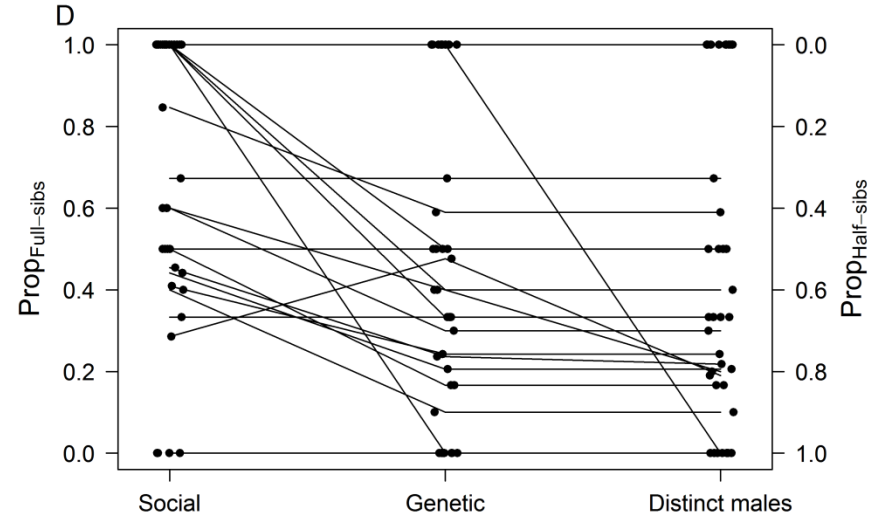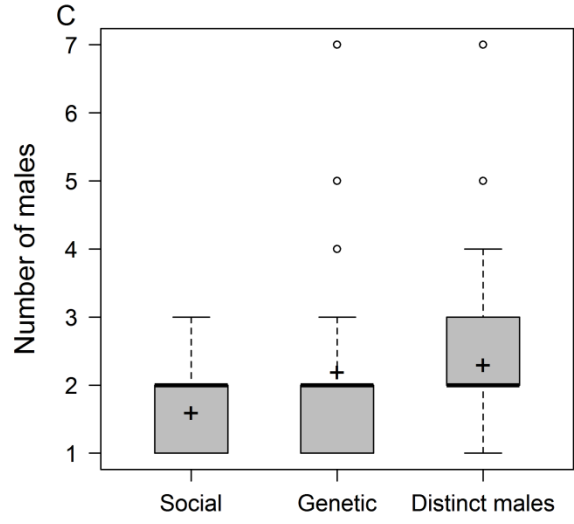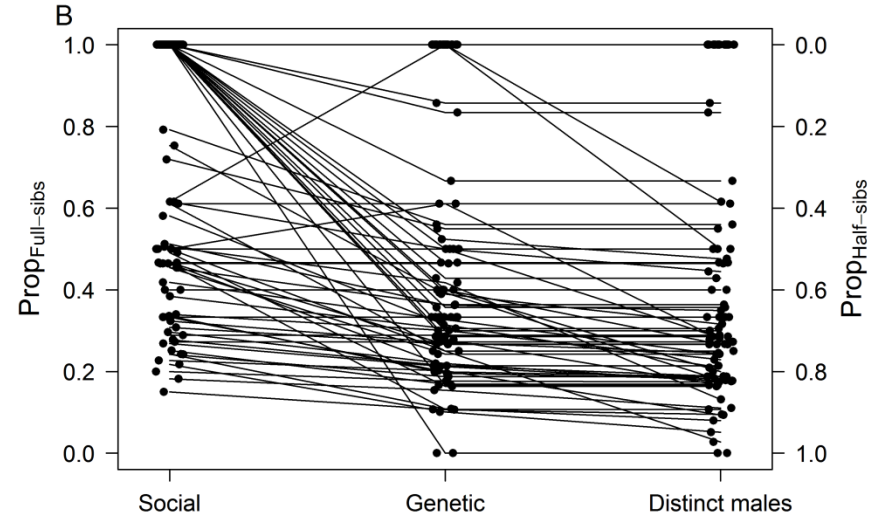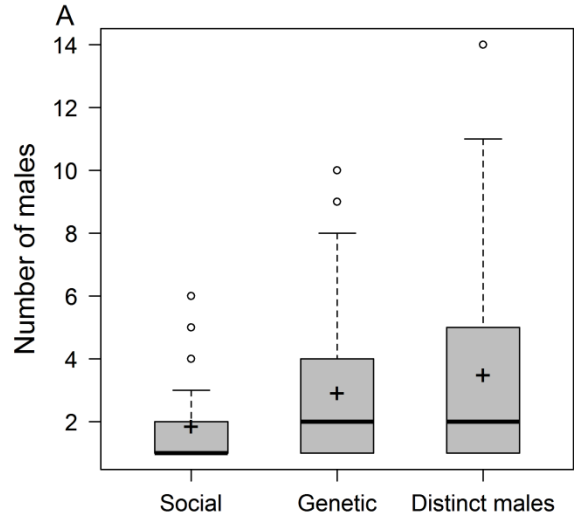
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Figure 2

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1034
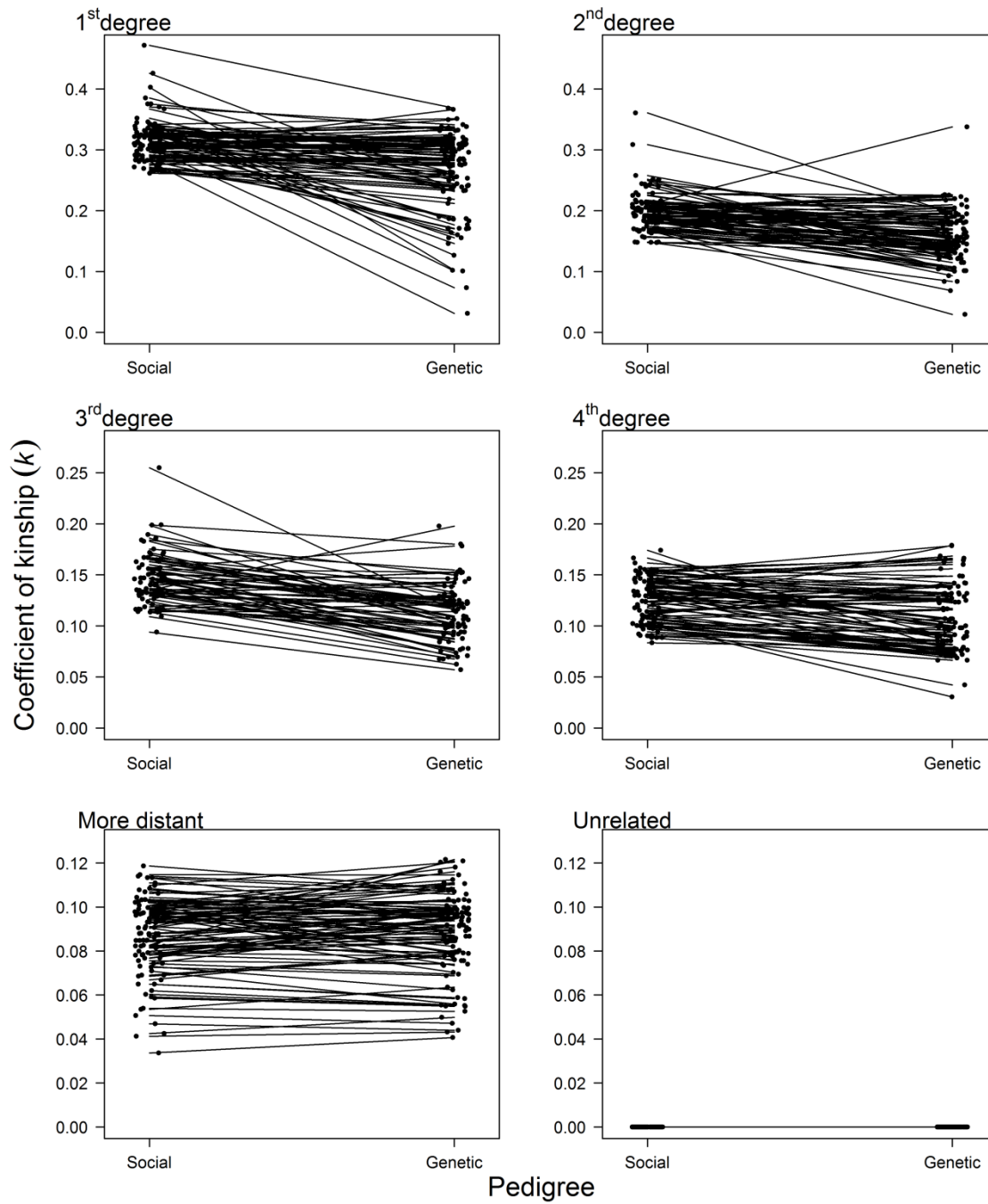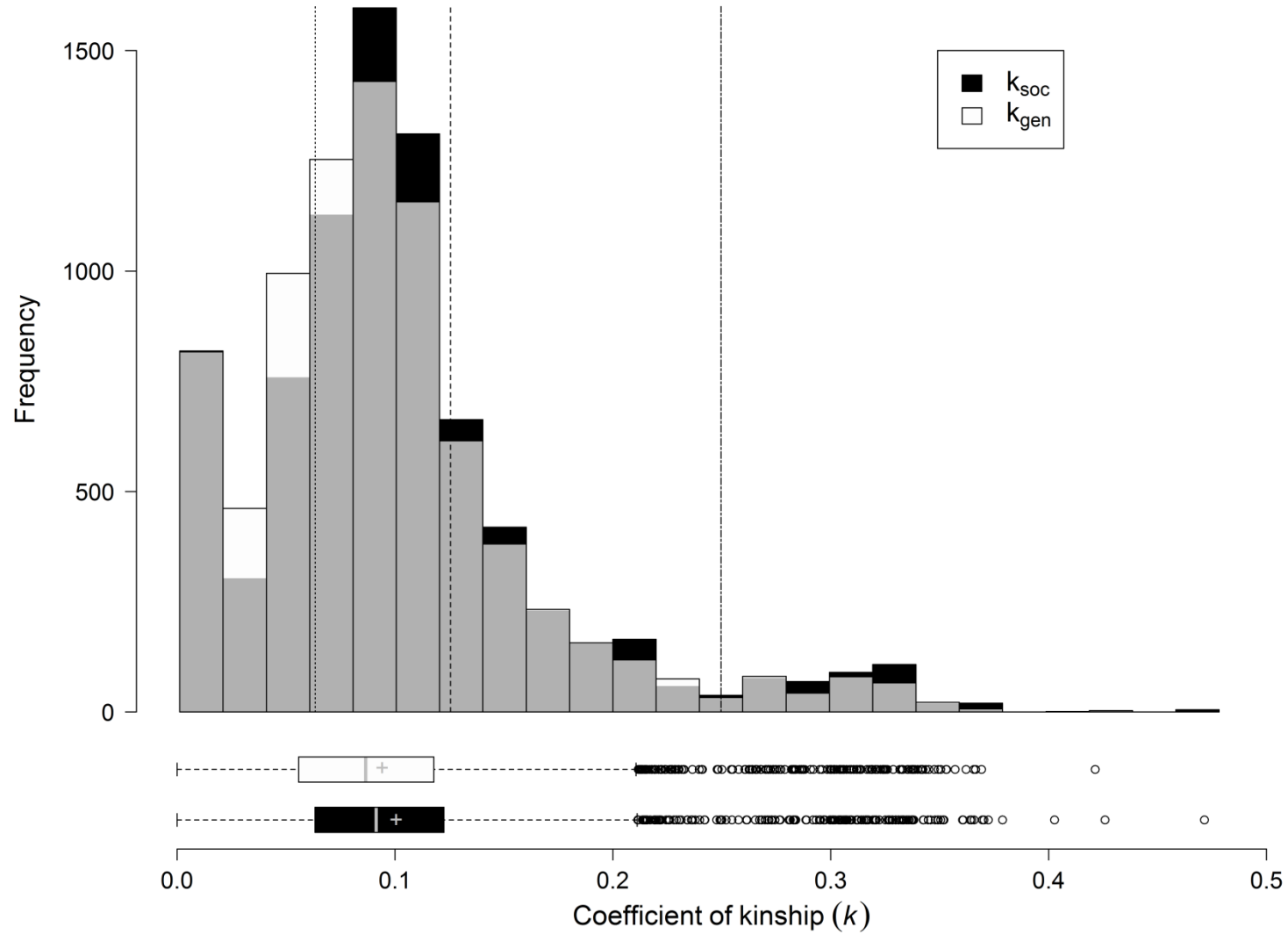
1035 **Figure 3**

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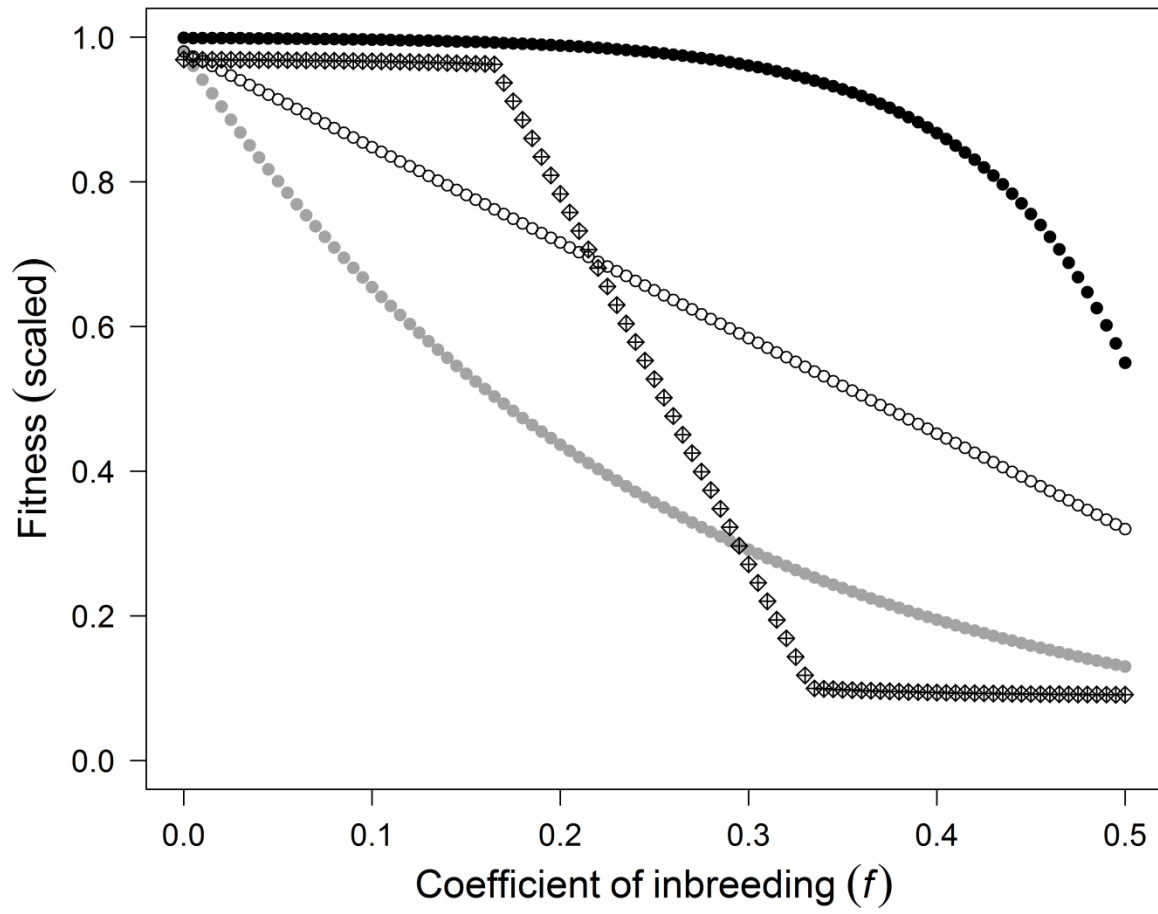1037

1038   **Figure 4**

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1041   **Figure 5**

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1043 **Figure 6**

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1045

1046   **Figure 7**