

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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15 **Key words:** extra-pair reproduction, inbreeding avoidance, kinship, monogamy, polyandry,
16 relatedness

17 Short title: Polyandry and potential for inbreeding

18 Manuscript type: Article

19 Supplementary Material: Supporting Information S1-S6

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21

Abstract

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.

40

Introduction

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 IAH 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 IAH 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 IAH 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

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

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 rearing, and thereby quantify the
182 fundamental basis for the IIAH. We further quantify the degree to which observed changes

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

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. 2011*a*; 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 IAH 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 IAH 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, 2015*a,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

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 $N_{\text{sibs}} = \frac{j(j-1)}{2}$. 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 ($\text{Prop}_{\text{Full-sibs}}$) and half-
285 sibships ($\text{Prop}_{\text{Half-sibs}}$) produced by each female (where $\text{Prop}_{\text{Half-sibs}} = 1 - \text{Prop}_{\text{Full-sibs}}$) given each
286 pedigree. The absolute difference between each female's value of $\text{Prop}_{\text{Full-sibs}}$ given the
287 social and genetic pedigrees (i.e., $\text{Diff}_{\text{social-gen}} = |\text{Prop}_{\text{Full-sibs}[\text{social}]} - \text{Prop}_{\text{Full-sibs}[\text{genetic}]}|$) 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 $\text{Prop}_{\text{Full-sibs}}$ given the genetic pedigree and the value of
295 $\text{Prop}_{\text{Full-sibs}}$ that would arise given strict lifelong monandry (i.e., 1.0, hence $\text{Diff}_{\text{lifelong-monandry-gen}} =$
296 $1.0 - \text{Prop}_{\text{Full-sibs}[\text{genetic}]}$). 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

303 offspring sired by male i), and then recalculated $\text{Prop}_{\text{Full-sibs}}$ and $\text{Prop}_{\text{Half-sibs}}$ 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 $\text{Prop}_{\text{Full-sibs}}$ 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 $\text{Prop}_{\text{Full-}}$
314 sibs 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 $\text{Diff}_{\text{social-gen}}$
317 and $\text{Diff}_{\text{life_monandry-gen}}$ 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 $\text{Diff}_{\text{social-gen}}$ and $\text{Diff}_{\text{life_monandry-gen}}$ 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

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 $N_{\text{sibs}} = 0$), 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 $26.9 \pm 8.8\text{SD}$ females [range 13–38] and $35.1 \pm 10.5\text{SD}$ 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-

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 $\pm 1SD$.

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 $\sim 26\%$ 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

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 $\text{Prop}_{\text{Full-sibs}}$ given the genetic pedigree, illustrating that
424 polyandry can increase rather than decrease full sibships (fig. 2B). Indeed, mean $\text{Diff}_{\text{social-gen}}$
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., $\text{Diff}_{\text{social-gen}}$ 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 $\text{Diff}_{\text{life_monandry-gen}}$, 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 $\text{Prop}_{\text{Full-sibs}}$ given the ‘distinct males’
434 pedigree than given the genetic pedigree and no females had higher $\text{Prop}_{\text{Full-sibs}}$ (fig. 2B),
435 creating a mean reduction in $\text{Prop}_{\text{Full-sibs}}$ 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 $\text{Prop}_{\text{Full-sibs}}$ 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 $\text{Prop}_{\text{Full-sibs}}$ was slightly higher for recruited offspring than for
452 banded offspring across all three pedigrees (table 1D,F), but mean $\text{Prop}_{\text{Full-sibs}}$ 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 $\text{Prop}_{\text{Full-sibs}}$ given the genetic pedigree,
455 while 51% (19/37) had no change and one female had higher $\text{Prop}_{\text{Full-sibs}}$ (fig. 2D). $\text{Diff}_{\text{social-gen}}$
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 $\text{Prop}_{\text{Full-sibs}}$ 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

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

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

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

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 ($\text{Prop}_{\text{Full-sibs}}$)
568 and increase the mean proportion of maternal half-sibships ($\text{Prop}_{\text{Half-sibs}}$) 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 $\text{Prop}_{\text{Full-sibs}}$ (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 re-pairing 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 $\text{Prop}_{\text{Full-sibs}}$ 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, $\text{Prop}_{\text{Full-sibs}}$ 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, *Parus ater*, Schmolle 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.

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

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. 2015a).
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

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

690 We thank the Tsawout and Tseycum First Nations for access to Mandarte Island, Pirmin
691 Nietlisbach, Lukas Keller, Greta Bocedi, Brad Duthie, and Matthew Wolak for helpful
692 discussions, and the European Research Council, National Sciences and Engineering
693 Research Council of Canada, and Swiss National Science Foundation for funding. Field data
694 collected following UBC Animal Care Committee (A07-0309) and Environment Canada
695 (Master banding permit 10596) guidelines. All data from this publication will be archived in
696 the Dryad Digital Repository (*doi* upon acceptance).

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 ($\text{Prop}_{\text{Full-sibs}}$) 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 (\pm SD)	Median (Range)	df	R ²	Estimate (\pm 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

931 **Table 2:** Mean \pm 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)
1 st 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)
2 nd 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)
3 rd 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)
4 th 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)

941 **Table 3:** Mean \pm 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)
1 st degree ($n = 378$, ♀ = 104)	0.314 \pm 0.034 (0.261–0.472)	0.263 \pm 0.067 (0.031–0.368)	-0.051\pm0.07 (-0.301–0.062)	5.7 (<0.001)
2 nd degree ($n = 453$, ♀ = 99)	0.197 \pm 0.032 (0.147–0.361)	0.157 \pm 0.042 (0.03–0.338)	-0.041\pm0.045 (-0.165–0.128)	7.2 (<0.001)
3 rd degree ($n = 297$, ♀ = 78)	0.141 \pm 0.026 (0.094–0.255)	0.112 \pm 0.029 (0.057–0.198)	-0.033\pm0.031 (-0.14–0.063)	6.7 (<0.001)
4 th degree ($n = 629$, ♀ = 97)	0.125 \pm 0.022 (0.084–0.174)	0.108 \pm 0.032 (0.031–0.179)	-0.017\pm0.026 (-0.099–0.06)	4.3 (<0.001)
More distant ($n = 5463$, ♀ = 110)	0.087 \pm 0.017 (0.034–0.119)	0.088 \pm 0.018 (0.041–0.122)	+0.001 \pm 0.011 (-0.023–0.039)	0.2 (0.84)
Unrelated ($n = 808$, ♀ = 114)	0.000 \pm 0.000 --	0.000 \pm 0.000 --	0.00 \pm 0.00 --	0.0 (1.00)

951

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 ($\text{Prop}_{\text{Full-sibs}}$) and half-sibships ($\text{Prop}_{\text{Half-sibs}}$), where

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 $\text{Prop}_{\text{Full-sibs}}$ given (A and
980 C) the genetic versus social pedigrees ($\text{Diff}_{\text{social-gen}}$), and (B and D) the genetic pedigree versus
981 strict lifelong monandry ($\text{Diff}_{\text{lifelong-monandry-gen}}$) 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

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).

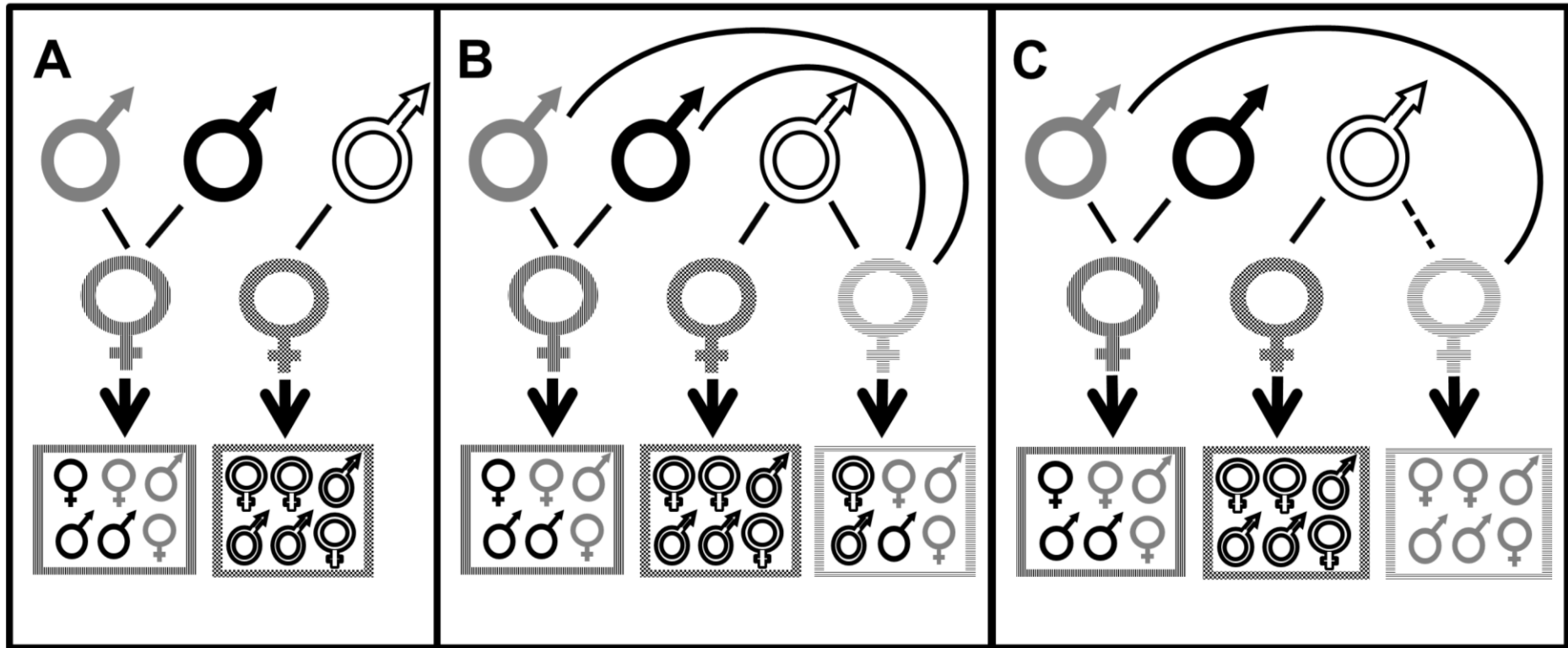
1006

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 \times 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

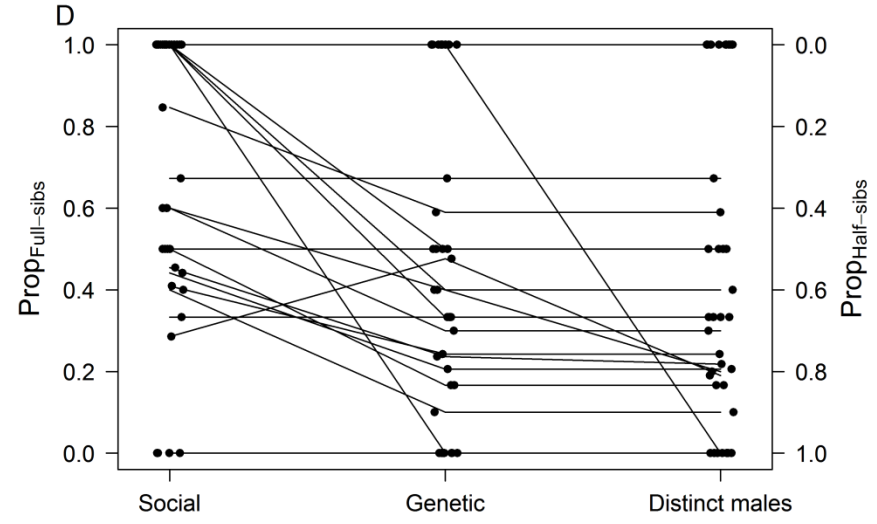
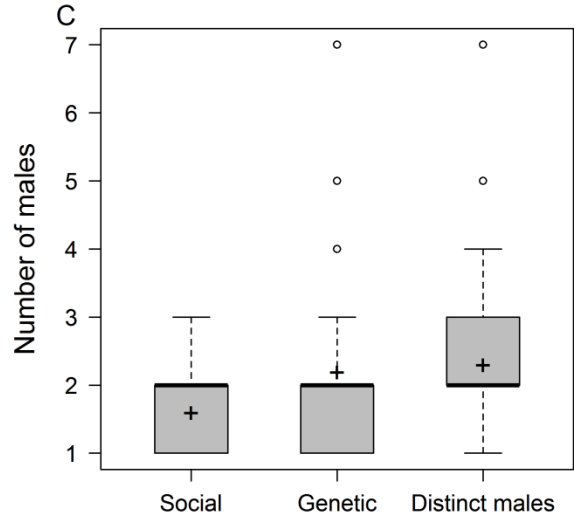
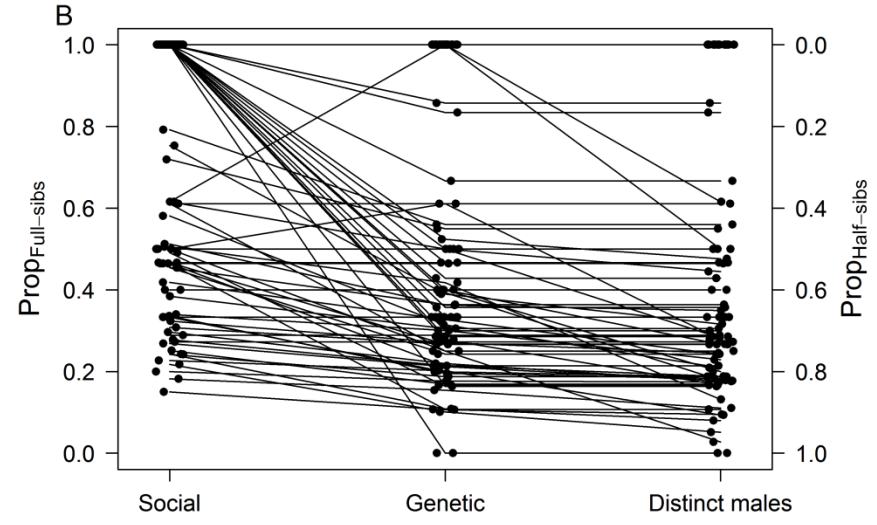
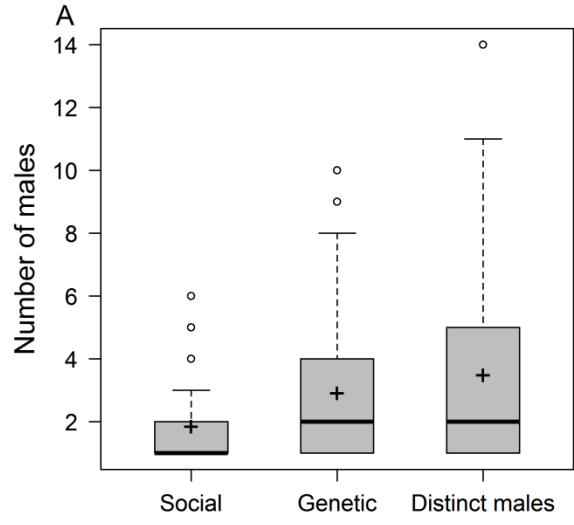
1019 **Figure 7:** Conceptualization of potential relationships between mean fitness (scaled relative
1020 to an outbred individual) and individual coefficient of inbreeding (f). Such relationships
1021 could be linear (white circles), concave (i.e., log-linear, given multiplicative allelic effects,
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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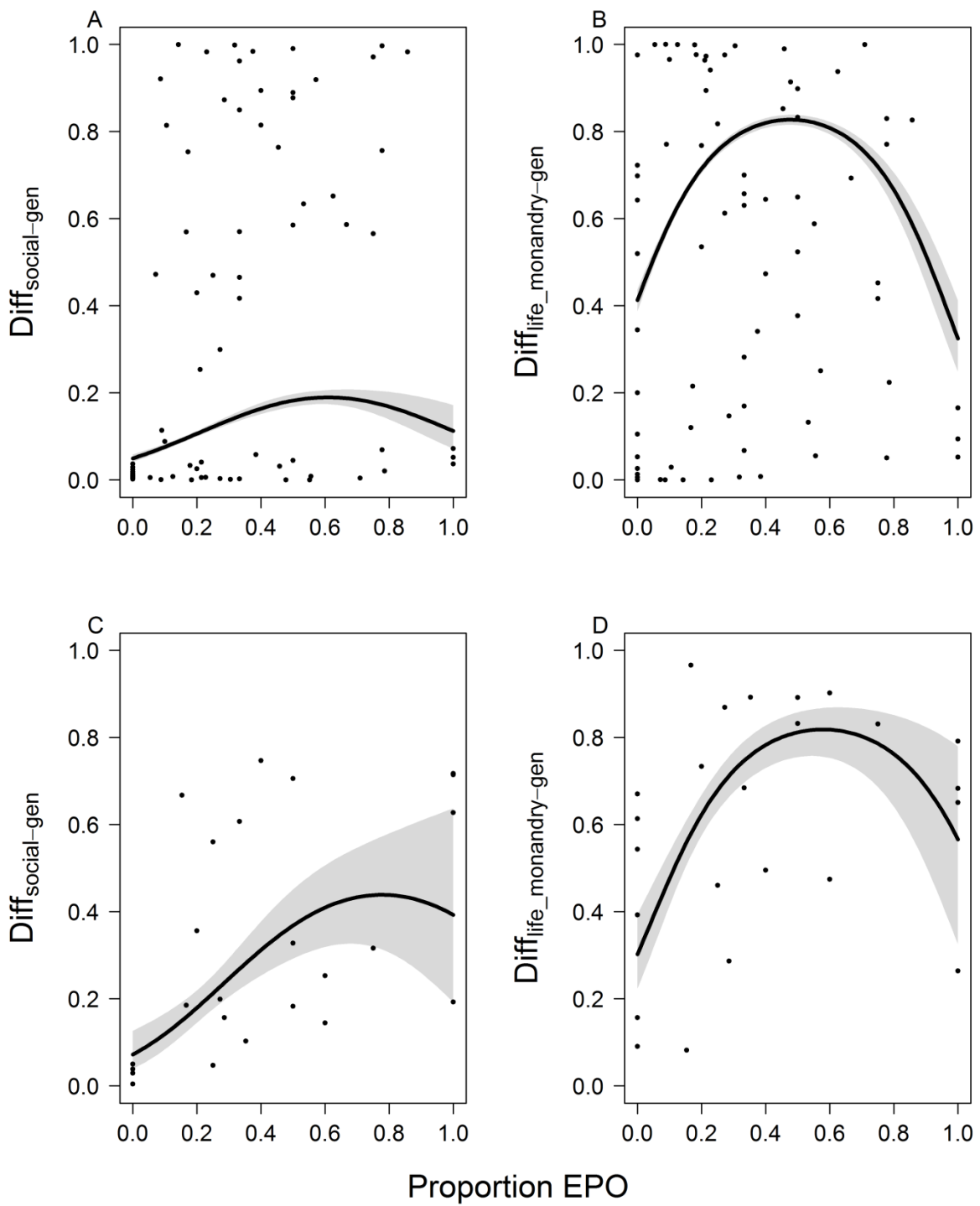
1030 **Figure 1**



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1032 **Figure 2**

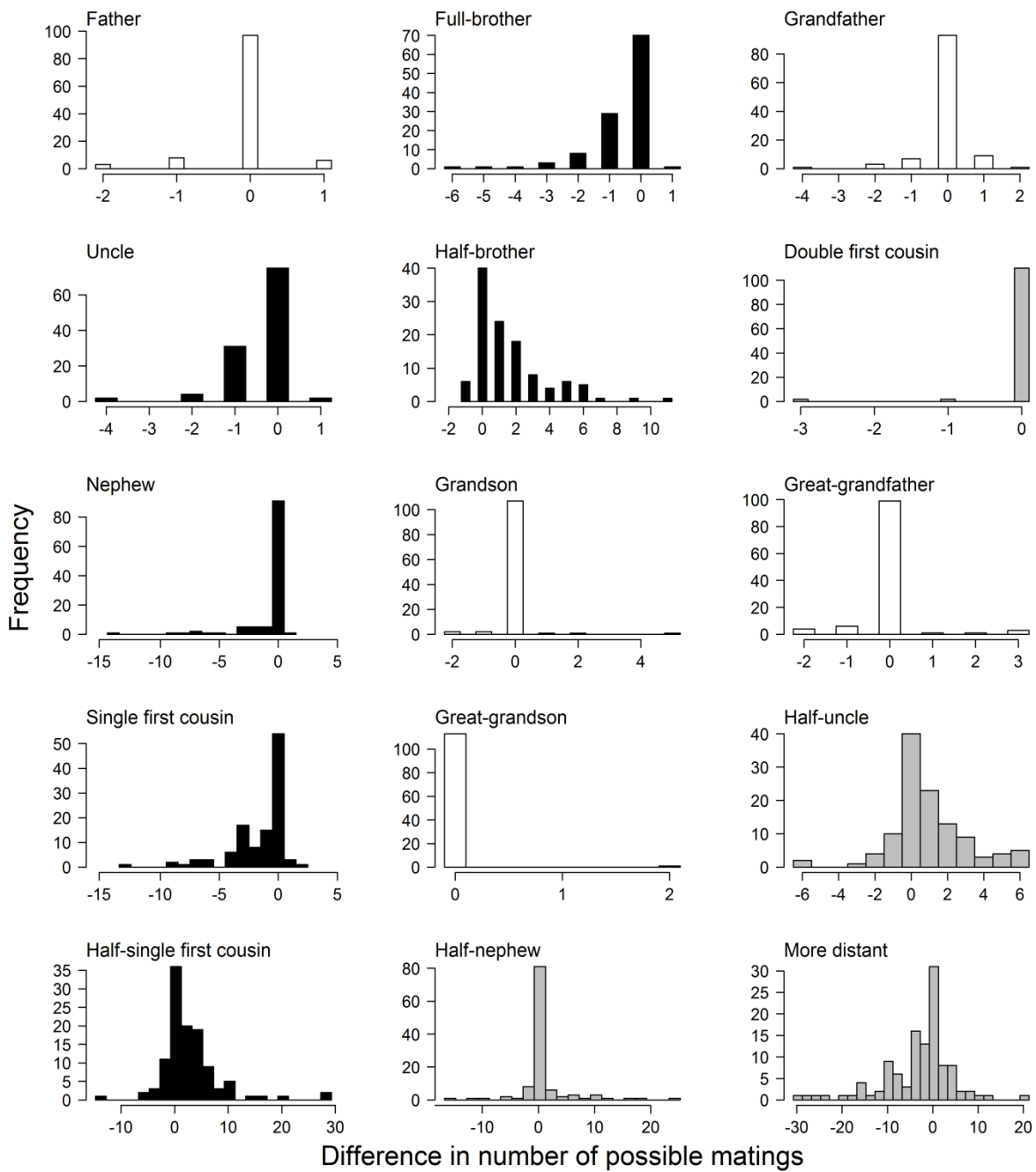
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1035 **Figure 3**

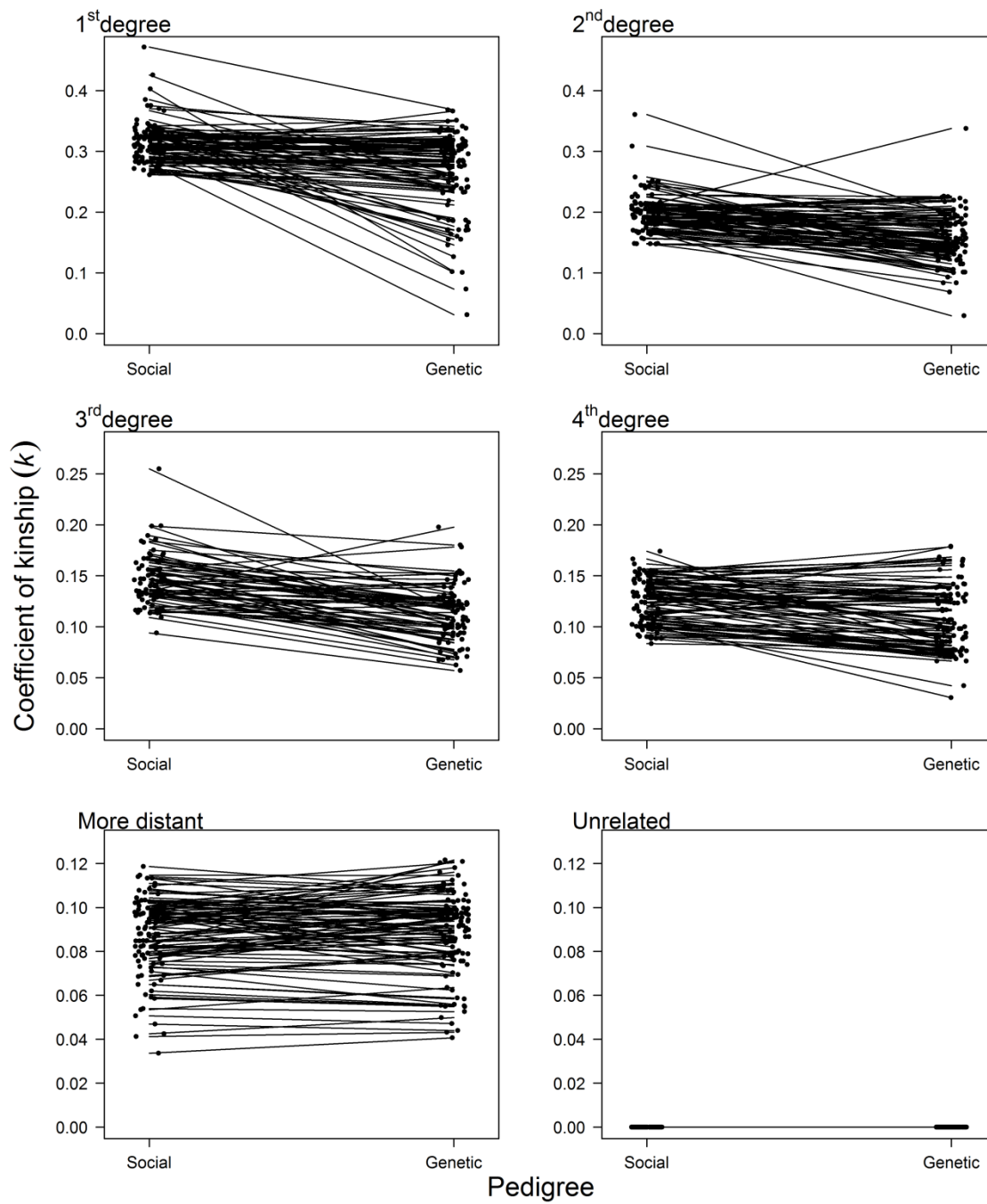
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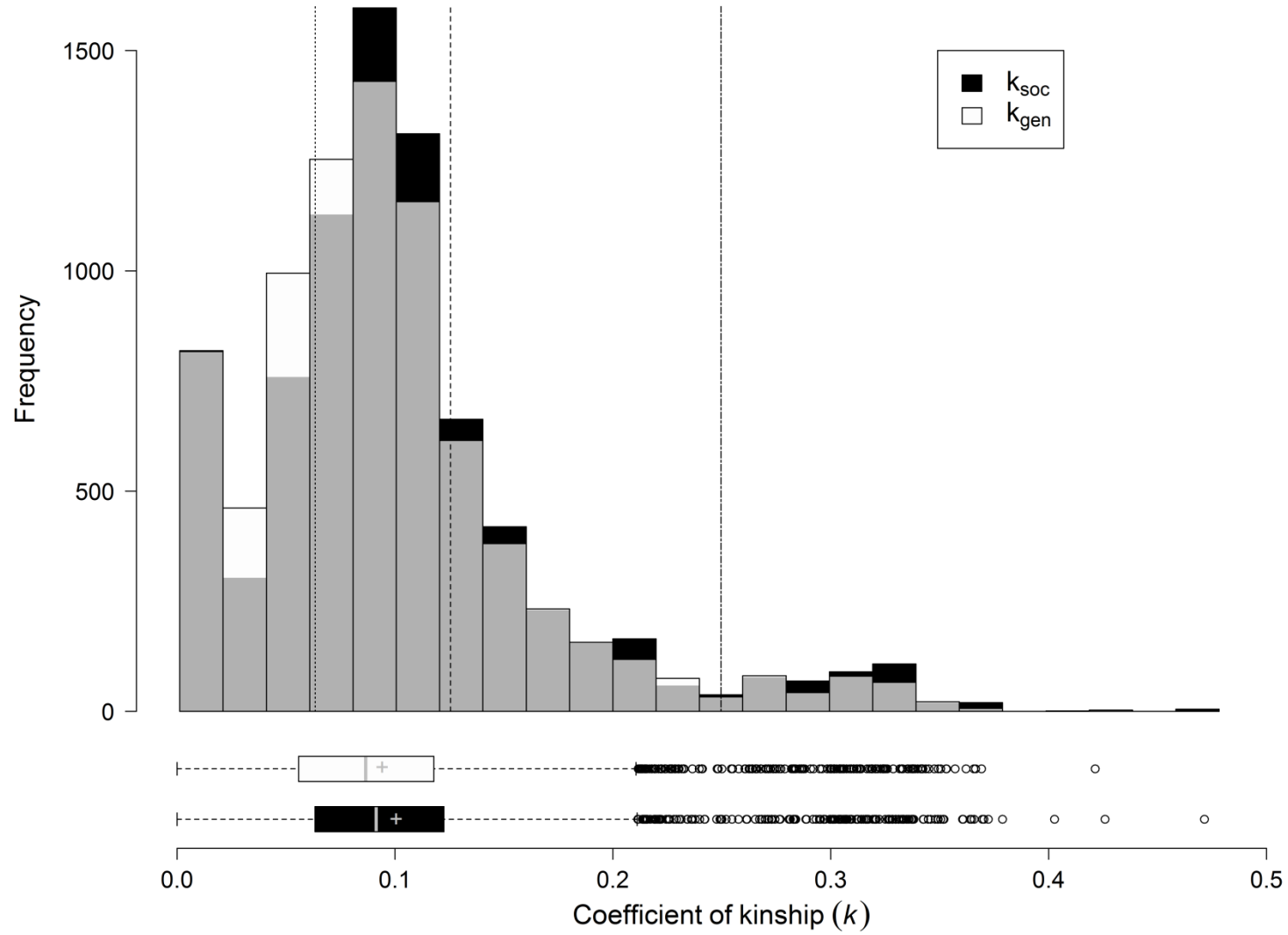
1038 **Figure 4**

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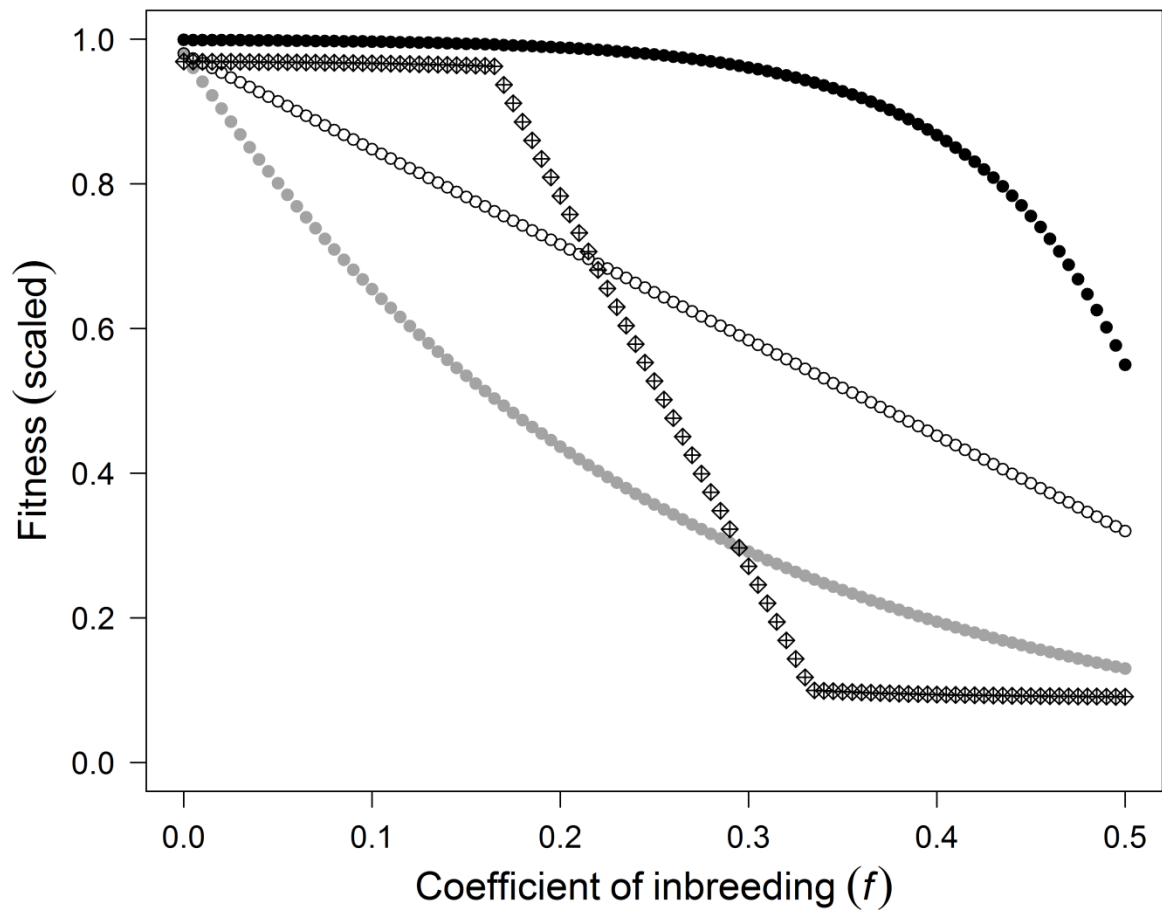
1041 **Figure 5**



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1043 **Figure 6**

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1046 **Figure 7**