The consequences of polyandry for sibship structures, distributions of relationships and relatedness, and potential for inbreeding in a wild population

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Abstract

The evolutionary benefits of simultaneous polyandry, defined as female multiple mating within a single reproductive event, remain elusive. One potential benefit could arise if polyandry alters sibship structures and consequent relationships and relatedness among females' descendants, and thereby intrinsically reduces future inbreeding risk (the 'indirect inbreeding avoidance hypothesis'). However such effects have not been quantified in naturally complex reproductive systems that also encompass iteroparity, overlapping generations, sequential polyandry, and polygyny. We used long-term social and genetic pedigree data from song sparrows (*Melospiza melodia*) to quantify cross-generational consequences of simultaneous polyandry for offspring sibship structures and distributions of relationships and relatedness among possible mates. Simultaneous polyandry decreased full-sibships and increased half-sibships on average, but such effects varied among females and were smaller than would occur in the absence of sequential polyandry or polygyny. Further, while simultaneous polyandry decreased the overall frequencies of possible matings among close relatives, it increased the frequencies of possible matings among distant relatives. These results imply that the intrinsic consequences of simultaneous polyandry for inbreeding risk could cause weak indirect selection on polyandry, but the magnitude and direction of such effects will depend on complex interactions with other mating system components and the form of inbreeding depression.

Introduction

Understanding the evolutionary causes and consequences of simultaneous polyandry, defined as female multiple mating within a single reproductive event, remains a central challenge in evolutionary ecology (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Parker and Birkhead 2013; Pizzari and Wedell 2013). One key puzzle is that direct costs of multiple mating identified in diverse systems often exceed any obvious direct benefits that increase polyandrous females' fitness (e.g., Rowe 1994; Fedorka et al. 2004; Cornell and Tregenza 2007; Forstmeier et al. 2014). The widespread occurrence of simultaneous polyandry consequently suggests that it might provide some indirect benefit, manifested as increased fitness of polyandrous females' descendants rather than of the polyandrous females themselves (Tregenza and Wedell 2000; Slatyer et al. 2012; Taylor et al. 2014).

Numerous potential indirect benefits of polyandry that would be manifested as increased offspring fitness have been proposed (Jennions and Petrie 2000; Slatyer et al. 2012). For instance, polyandrous females could mate with additional males of higher additive genetic value for fitness and hence produce fitter offspring (Garcia-Gonzalez and Simmons 2005; Reid and Sardell 2012), or mate with less closely related males (i.e., inbreeding avoidance) and thereby produce outbred offspring that express less inbreeding depression (Stockley et al. 1993; Tregenza and Wedell 2000, 2002; Michalczyk et al. 2011; Duthie et al. 2016). However, such mechanisms often require some form of active female mate choice and/or paternity allocation, which may impose further costs (e.g., Parker and Pizzari 2010; Duthie et al. 2016). Further, empirical evidence of substantial indirect fitness benefits to polyandrous females' offspring remains scant (Jennions and Petrie 2000;

62 Arnqvist and Kirkpatrick 2005; Evans and Simmons 2008; Reid and Sardell 2012; Forstmeier
63 et al. 2014; Hsu et al. 2014).

64 This situation raises the possibility that evolution of simultaneous polyandry might
65 be facilitated by indirect benefits that are manifested a further generation into the future
66 (i.e., increased fitness of polyandrous females' grandoffspring). Here, we first summarize a
67 general hypothesis for how such extended indirect benefits might result from cross-
68 generational consequences of polyandry for individual and population-wide inbreeding: the
69 'indirect inbreeding avoidance hypothesis' (IIAH, e.g., Cornell and Tregenza 2007). We then
70 use comprehensive pedigree data from socially monogamous but genetically polyandrous
71 song sparrows (*Melospiza melodia*) to examine the possible magnitude of such effects
72 arising in a naturally complex mating system. We thereby provide a conceptual and
73 empirical basis for considering how intrinsic indirect effects of simultaneous polyandry
74 might potentially facilitate its own evolution, and also shape the wider evolutionary
75 consequences of interactions among relatives.

76

77 *The 'Indirect Inbreeding Avoidance Hypothesis' for polyandry evolution*

78 The IIAH postulates that the occurrence of simultaneous polyandry intrinsically affects the
79 distributions of paternity, relationships and relatedness among population members, and
80 thereby alters inbreeding risk for polyandrous females' offspring. The basic hypothesis
81 states that, when simultaneous polyandry causes some degree of multiple paternity, it
82 alters sibship structures such that some offspring of polyandrous females are maternal half-
83 sibs (i.e., common mother, different father), rather than full-sibs (i.e., both parents in
84 common) as would result from monandry (fig. 1A). In situations where individuals mate
85 locally, polyandry might consequently reduce the potential (i.e., the expected frequency

given random mating) for full-sib inbreeding among a female's offspring (Cornell and Tregenza 2007). Grandoffspring of polyandrous females would consequently be less inbred than grandoffspring of monandrous females on average and, given inbreeding depression in fitness, contribute more offspring (i.e., great-grandoffspring of the original polyandrous female) to the population. The relative frequency of alleles underlying polyandry might consequently increase across generations, facilitating ongoing evolution and persistence of simultaneous polyandry.

As with any hypothesis explaining mating system evolution as a function of inbreeding avoidance, the IIAH assumes that mating individuals experience some risk of inbreeding, and that inbreeding reduces offspring fitness (i.e., inbreeding depression, Charlesworth and Willis 2009; Szulkin et al. 2013). Indeed, it is increasingly clear that mating individuals do commonly encounter different degrees of relatives in diverse systems, due to small population size, limited dispersal (i.e., high population viscosity), or co-dispersal of kin groups within larger populations (Sharp et al. 2008; Busch et al. 2009; Hatchwell 2010; O'Leary et al. 2013; While et al. 2014; Blyton et al. 2015), while inbreeding depression is widespread and can be severe (Crnokrak and Roff 1999; Keller and Waller 2002; O'Grady et al. 2006). Evolution of some form of inbreeding avoidance, mediated by pre- and/or post-copulatory female choice for less closely related mates, is consequently widely postulated (Tregenza and Wedell 2000; Szulkin et al. 2013), but could be impeded by individuals' inabilities to discriminate relatives and direct costs of mate choice (Duthie and Reid 2016; Duthie et al. 2016). In contrast, the IIAH postulates that simultaneous polyandry could intrinsically reduce inbreeding across generations without requiring mate choice or kin discrimination or incurring associated costs. Further, by affecting sibship structures, polyandry might also shape other evolutionary processes stemming from interactions

among close relatives in small or viscous populations, including kin cooperation and competition, and resulting kin selection on social behavior and dispersal (e.g., Queller 1994; Gandon 1999; Perrin and Mazalov 2000; Evans and Kelley 2008; Hatchwell 2010; Díaz-Muñoz 2011).

Like any form of indirect selection, effects of the IIAH process are likely to be weak, but could still act alongside multiple other direct and indirect costs and benefits to facilitate or hinder polyandry evolution (e.g., Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Arnqvist and Kirkpatrick 2005). Theoretical and empirical studies are therefore required to quantify such effects. In a first theoretical evaluation of the IIAH, Cornell and Tregenza (2007) presented a mathematical model that considers the evolutionary dynamics of polyandry resulting from the occurrence of half-sib rather than full-sib inbreeding among polyandrous females' offspring. They primarily considered the specific restricted circumstance of non-overlapping, alternating generations of within-brood inbreeding and complete outbreeding, such as could occur in short-lived invertebrates colonizing discrete patches. Their analyses suggest that the intrinsic evolutionary benefit of polyandry stemming solely from reduced full-sib inbreeding is indeed small but might, in combination with other benefits and appropriate genetic architecture, facilitate ongoing polyandry evolution. However, Cornell and Tregenza's (2007) specific formulation of the IIAH makes assumptions that, while sensible in the context of their initial conceptual development and associated heuristic model, limit its direct applicability to understanding polyandry evolution in complex natural reproductive systems where polyandry and inbreeding risk co-occur.

First, Cornell and Tregenza's (2007) formulation of the IIAH does not explicitly consider how the consequences of polyandry for the distributions of relationships and relatedness among possible mates, and the resulting potential for different degrees of

134 inbreeding, might extend beyond a polyandrous female's immediate full-sib versus half-sib
135 offspring and accumulate across multiple broods and generations. This issue is particularly
136 relevant for iteroparous species where individuals produce multiple broods of offspring
137 within and/or across years with overlapping generations. In such cases, multiple full-sibs and
138 maternal half-sibs could be produced across different broods, for example where females
139 mate with different initial males in different reproductive events (i.e., sequential polyandry)
140 due to mate death or divorce. The set of possible mates available to any individual offspring
141 at any point in time might then include various full-sibs and half-sibs originating from
142 current, previous and subsequent broods produced by their mother. Moreover, it might also
143 include full- and half-cousins and more distant full- and half-relatives, which are themselves
144 generated across broods and generations, contingent on the degrees of simultaneous and
145 sequential polyandry enacted by each individual's female ancestors.

146 Second, Cornell and Tregenza's (2007) formulation does not explicitly consider how
147 the effects of polyandry on the frequencies of different relationships, and hence on the
148 potential for different degrees of inbreeding, depend on the overall distribution of paternity
149 within a population. Their model assumes that all polyandrous females' additional mates are
150 distinct, such that they do not sire offspring elsewhere in the population (hereafter the
151 'distinct males assumption'). Polyandry then creates maternal half-sibs rather than full-sibs
152 but does not create any paternal half-sibs (fig. 1A). The potential for full-sib mating among a
153 polyandrous female's offspring is consequently reduced, reflecting the implicit increase in
154 effective population size. However, the distinct males assumption is unlikely to hold in
155 nature. Indeed, males commonly sire offspring of multiple polyandrous females and can also
156 be the sole mate of monandrous females (i.e., polygyny, fig. 1B; e.g., Uller and Olsson 2008;
157 Coleman and Jones 2011; Lebigre et al. 2012; McDonald et al. 2013). Such co-occurrence of

158 polyandry and polygyny can still reduce the number of full-sibs and increase the number of
159 maternal half-sibs compared to monandry, but can also increase the number of paternal
160 half-sibs and reduce the proportion of individuals in the population that are unrelated (fig.
161 1B). Further, polyandrous females may mate with the same additional males over successive
162 reproductive events and/or allocate all paternity to their additional mate, and hence could
163 produce more full-sibs and fewer half-sibs than otherwise expected, thereby reducing,
164 eliminating or even reversing the evolutionary benefit of simultaneous polyandry that the
165 basic IIAH postulates (fig. 1C).

166 However, despite these conflicting possibilities and their broad implications for
167 diverse forms of inbreeding avoidance and other kin interactions, no empirical studies have
168 yet quantified the consequences of simultaneous polyandry for the frequencies of different
169 relationships arising in populations with iteroparity, overlapping generations, and complex
170 patterns of non-independent paternity within and among a female's reproductive events.
171 Consequently, even though complex combinations of polyandry, polygyny and mate fidelity
172 and divorce widely occur alongside inbreeding (e.g., Cockburn et al. 2003; Michalczyk et al.
173 2011; Culina et al. 2015), there is no general empirical basis on which to consider how the
174 evolutionary causes and consequences of simultaneous polyandry could be influenced by
175 the intrinsic effects of such polyandry on population-wide sibship or relationship structures
176 and the resulting potential for inbreeding.

177 Furthermore, in populations where some degree of inbreeding is common, changes
178 in the 'relationships' among possible mates resulting from polyandry may cause more
179 complex changes in 'relatedness'. This is because shared ancestry between a focal pair's
180 parents can increase the pair's relatedness above that expected given the same immediate
181 relationship in an outbred population. For example, the relatedness between inbred half-

sibs can approach that between outbred full-sibs (Jacquard 1974; Lynch and Walsh 1998; Reid et al. 2016). Polyandry might therefore have less effect on the distribution of relatedness among possible mates than expected given its effect on the distribution of relationships. Studies that quantify the effects of simultaneous polyandry on distributions of relatedness alongside distributions of discrete relationships among possible mates are therefore required.

Evaluating the basis of the 'Indirect Inbreeding Avoidance Hypothesis'

The effects of simultaneous polyandry on sibship structures and distributions of relationships and relatedness among possible mates could be quantified by comparing populations where polyandry or monandry is experimentally enforced across multiple generations (e.g., Power and Holman 2014). However, such experiments may simultaneously alter other life-history traits in females and offspring, including survival and fecundity (e.g., Fox 1993; Fedorka and Mousseau 2002; Fisher et al. 2006; Taylor et al. 2008), thereby directly altering sibship structures and relationship frequencies. Furthermore, sibship structures and distributions of relationships and relatedness all depend on population size and viscosity, and on among-individual variation in survival and reproductive success, and on variation in pre-reproductive mortality of offspring sired by different males (e.g., Fisher et al. 2006; Gowaty et al. 2010; Sardell et al. 2011; Hsu et al. 2014). The composite effects of simultaneous polyandry on sibship structures and distributions of relationships and relatedness would therefore be usefully quantified in free-living populations where individual reproductive strategies and offspring survival are not artificially constrained.

205 One tractable approach is to utilize systems where a female's potential and realized
206 allocations of offspring paternity to initial versus additional mates can be documented
207 directly. Realized distributions of relationships and relatedness emerging from realized
208 paternity can then be compared with inferred distributions that would have emerged had all
209 a female's offspring in a given brood been sired by her initial mate (i.e., within-brood
210 monandry). Socially-monogamous species with extra-pair reproduction, and hence
211 underlying simultaneous polyandry, allow such comparisons. Here, a female's initial socially-
212 paired male can be identified from behavioral observations and realized paternity can be
213 assigned by molecular genetic analysis. Such systems have been used to compare the
214 variance in inferred (i.e., 'social') and realized (i.e., 'genetic') male reproductive success, and
215 thereby quantify the consequences of extra-pair reproduction for effective population size
216 and opportunity for selection (Webster et al. 1995, 2007; Freeman-Gallant et al. 2005;
217 Lebigre et al. 2012; Schlicht and Kempenaers 2013). However, similar within-system paired-
218 comparison approaches have not been used to quantify the consequences of extra-pair
219 reproduction for sibship structures and distributions of relationships and relatedness, or
220 hence for individual potential for inbreeding. Such studies ideally require complete data on
221 the social pairings and realized paternity of all population members across multiple years
222 and generations.

223 We used comprehensive song sparrow pedigree data to quantify the consequences
224 of extra-pair reproduction for sibship structures and distributions of relationships and
225 relatedness between possible mates, and thereby quantify key processes that underlie the
226 general 'indirect inbreeding avoidance hypothesis' for polyandry. First, we quantify the
227 degree to which extra-pair reproduction changes the proportion of full-sib versus half-sib
228 offspring produced by females over their lifetimes given realized patterns of iteroparity and

social pairing. We further quantify the degree to which observed changes differ from those predicted given lifelong monogamy and given the 'distinct males assumption' (i.e., extra-pair sires differ among females' broods), and thereby consider effects of sequential polyandry and polygyny. We additionally quantify the degree to which sibship structures differ among females' hatched and adult offspring, and thereby illustrate the degree to which pre-reproductive mortality can shape effects of extra-pair reproduction on sibship structures among breeding individuals. Second, we quantify the degree to which extra-pair reproduction alters the distribution of relationships among possible mates given natural iteroparity and overlapping generations, and hence alters the individual and population-wide potential for inbreeding between close and more distant relatives. Third, we quantify the degree to which extra-pair reproduction interacts with inbreeding to shape the distribution of relatedness within and across categories of relationship. Overall, we thereby evaluate the degree to which simultaneous polyandry can affect sibship structures and the resulting population-wide potential for inbreeding, and for other interactions among disparate co-existing relatives.

Methods

Study system

A resident population of song sparrows inhabiting Mandarte Island, British Columbia, Canada, has been intensively studied since 1975 (Smith et al. 2006). The focal population lies within a large meta-population and receives regular immigrants (recently mean 0.9 $year^{-1}$) that prevent the mean degrees of relatedness and inbreeding from increasing (Wolak and Reid 2016). This system has therefore proved a valuable model for understanding evolutionary processes occurring in natural viscous meta-populations where relatives and

253 non-relatives interact, including the occurrence and fitness consequences of inbreeding and
254 inbreeding avoidance (Keller and Arcese 1998; Reid et al. 2006, 2015a,b) and the heritability
255 and fitness consequences of polyandry and resulting extra-pair reproduction (Reid et al.
256 2011*a*, 2011*b*; Lebigre et al. 2012).

257 Song sparrows in the focal population typically form socially monogamous breeding
258 pairs which jointly defend territories and rear 1–4 broods of offspring per year (Smith et al.
259 2006). Both sexes can first breed aged one year, and median adult lifespan is two years
260 (maxima of eight and nine years in breeding females and males respectively, Smith et al.
261 2006; Keller et al. 2008). Due to a typically male-biased adult sex-ratio, 10–40% of males
262 remain socially unpaired annually (Smith et al. 2006; Sardell et al. 2010; Lebigre et al. 2012).
263 Extra-pair reproduction is frequent: 28% of hatched offspring are sired by extra-pair males
264 (i.e., males other than a female's initial socially-paired male, Sardell et al. 2010; see also Hill
265 et al. 2011), which is within the range commonly observed in passerine birds (Griffith et al.
266 2002). Both socially-paired and unpaired males can sire extra-pair offspring, and both sexes
267 form new social pairings within and among years following divorce or death of their socially-
268 paired mate (Smith et al. 2006; Reid et al. 2015*b*). Females receive no obvious direct
269 benefits (e.g., nuptial gifts, offspring provisioning) from extra-pair males.

270 Each year, all pairs are closely monitored, all nests are located and all offspring are
271 uniquely marked with colored plastic leg bands approximately six days post-hatch (Smith et
272 al. 2006; Wilson et al. 2007; Germain et al. 2015). Immigrant breeders are mist-netted and
273 banded soon after arrival. The identities of all individuals alive in late April (i.e., the start of
274 the breeding season) are recorded in a comprehensive census (resighting probability > 0.99,
275 Wilson et al. 2007), and all socially-paired parents that rear each brood of chicks are
276 identified.

Social and genetic pedigrees

Sibship structures, relationships and relatedness can all be calculated from pedigree data, which link offspring to parents. We first compiled a 'social pedigree' linking all banded offspring to their observed mother and her socially-paired male spanning 1975–2015 (Reid et al. 2014, 2015a,b). Since 1993, all adults and banded offspring were blood sampled and genotyped at ~160 highly polymorphic microsatellite loci, and all offspring were assigned to genetic sires with >99% individual-level statistical confidence (Nietlisbach et al. 2015, 2017; Reid et al. 2015*a*). We then compiled a 'genetic pedigree' linking all banded offspring to their mother and true genetic father (Sardell et al. 2010; Reid et al. 2014, 2015*a*, 2015*c*; Nietlisbach et al. 2015). We thereby generated two parallel pedigrees spanning 1993–2015 that describe sibship structures and the distributions of relationships and relatedness among all population members as they would have been had all observed breeding pairs been monogamous within broods ('social pedigree'), and given the realized pattern of extra-pair reproduction and underlying polyandry ('genetic pedigree', Lebigre et al. 2012; Reid et al. 2014). Because there is no extra-pair maternity (Sardell et al. 2010), the two pedigrees differ only in the paternity of ~28% of individuals, and are identical in terms of individual longevity, female reproductive success, and offspring survival to recruitment. Differences in sibship structure, relationships and relatedness among possible mates between the two pedigrees therefore stem solely from extra-pair reproduction and hence underlying simultaneous polyandry (see Discussion).

To maximize use of all available pedigree data and relax the alternative assumption that all 1993 breeders are unrelated, we grafted each of the 1993–2015 social and genetic pedigrees onto the basal 1975–1992 social pedigree (Reid et al. 2014, 2015*a*). To minimize

301 error in estimates of relationships and relatedness stemming from inadequate pedigree
302 depth and/or remaining paternity error for some individuals hatched during 1975–1992, we
303 restricted analyses to adults alive during 2008–2015. All such individuals had genetically-
304 verified ancestors back to all great-great-grandparents, or were descendants of immigrants,
305 meaning that any error due to misassigned paternities before 1993 was trivial (Reid et al.
306 2015*a*). Immigrants are assumed to be unrelated to existing residents, and therefore to all
307 possible mates, in their arrival year (Keller et al. 2001; Reid et al. 2006, 2014, 2015*a*), but
308 could potentially inbreed with their own descendants in subsequent years.
309

310 *Sibship structures*

311 To quantify the degree to which extra-pair reproduction altered the proportions of full-sibs
312 versus half-sibs that each female produced over her lifetime, we compared sibship
313 structures between the social and genetic pedigrees. We first calculated each female's total
314 lifetime number of banded offspring (*j*) and calculated the total number of sibships (i.e., all
315 possible full-sib and half-sib relationships, hereafter N_{sibs}) among the *j* offspring as
316 $N_{Sibs} = \frac{j(j-1)}{2}$. We then calculated the numbers of full-sibships and maternal half-sibships
317 among each female's offspring given the social and genetic pedigrees, and divided these
318 numbers by N_{sibs} to obtain the lifetime proportions of full-sibships ($Prop_{Full\text{-}sibs}$) and half-
319 sibships ($Prop_{Half\text{-}sibs}$) produced by each female (where $Prop_{Half\text{-}sibs} = 1 - Prop_{Full\text{-}sibs}$) given each
320 pedigree. The absolute difference between each female's value of $Prop_{Full\text{-}sibs}$ given the
321 social and genetic pedigrees (i.e., $Diff_{social\text{-}gen} = |Prop_{Full\text{-}sibs[social]} - Prop_{Full\text{-}sibs[genetic]}|$) quantifies
322 the effect of extra-pair reproduction (i.e., simultaneous polyandry) on sibship structures
323 while fully accounting for natural patterns of variation in paternity stemming from female
324 re-pairing between broods (i.e., sequential polyandry) and repeat mating with the same

325 extra-pair male across multiple broods. To explicitly quantify the combined effects of
326 simultaneous and sequential polyandry on sibship structures, we further quantified the
327 difference between $Prop_{Full\text{-}sibs}$ given the genetic pedigree and the value of $Prop_{Full\text{-}sibs}$ that
328 would arise given strict lifelong monandry (i.e., 1.0, hence $Diff_{life_monandry\text{-}gen} = 1.0 - Prop_{Full\text{-}}$
329 $_{sibs[genetic]}$). Finally, to quantify the degree to which observed sibship structures differed from
330 those that would have arisen given the 'distinct males assumption'(i.e., no polygyny), we
331 additionally considered a hypothetical pedigree in which extra-pair males could sire multiple
332 offspring within a given brood but could not sire other within-pair or extra-pair offspring in
333 the population (i.e., fig. 1A). We assigned a unique sire identity to all extra-pair offspring in
334 each observed brood, maintaining the observed paternity distribution (i.e., X_i extra-pair
335 offspring sired by male *i*), and then recalculated $Prop_{Full\text{-}sibs}$ and $Prop_{Half\text{-}sibs}$ for each female.
336 To elucidate mechanisms underlying observed changes in sibship structures, we also
337 calculated the total number of males that sired at least one of each female's offspring given
338 the social, genetic, and 'distinct males' pedigrees.
339 We fitted generalized linear mixed models (GLMMs) to test whether the sibship
340 structures of females' offspring (binomial error structures, weighted by N_{sibs}), or the number
341 of different sires (Poisson error structures), differed between the pedigrees. These models
342 included fixed effects of pedigree (three levels) and random female identity effects.
343 Goodness of fit (R^2) for each model was assessed by the conditional coefficient of
344 determination (Nakagawa and Schielzeth 2013). We used Tukey's post-hoc tests to evaluate
345 pairwise differences in $Prop_{Full\text{-}sibs}$ and number of sires among the three pedigrees at α =
346 0.05. We fitted generalized linear models (GLMs) to quantify how $Diff_{social\text{-}gen}$ and
347 $Diff_{life_monandry\text{-}gen}$ varied with whether or not any of the female's offspring were sired by an

348 extra-pair male (Supporting Information S1), or with the overall proportion of the female's
349 lifetime offspring that were sired by an extra-pair male (i.e., were extra-pair offspring, EPO).
350 To examine the effects of pre-reproductive mortality on realized sibship structures
351 among breeding individuals, all the above analyses were implemented across each female's
352 offspring that survived to banding, and across offspring that survived to age one year
353 (recruits). Females that were still alive in 2016, or that produced ≤1 banded or ≤1 recruited
354 offspring (meaning that $N_{sibs} = 0$), were excluded from the respective analyses. Analyses for
355 banded offspring were also repeated across the subset of females that produced ≥2
356 recruited offspring, thereby allowing direct comparison across offspring stages within
357 females (Supporting Information S2). While our primary analyses focused on sibship
358 structures among females' offspring, further analyses demonstrated similar structures
359 among males' offspring (Supporting Information S3).
360
361 *Distribution of relationships among possible mates*
362 To quantify how changes in sibship structures resulting from extra-pair reproduction
363 translated into differences in relationships among possible mates, we used annual censuses
364 of all adults alive in each year during 2008–2015 (annual means of 26.9±8.8SD females
365 [range 13–38] and 35.1±10.5SD males [range 20–56]) to generate all possible female-male
366 pairs that could possibly have mated in each year, assuming no mating constraints
367 (hereafter 'all possible matings'). We analyzed relationships from the female perspective;
368 due to extra-pair reproduction a female could possibly mate with any male in the
369 population. We compared the frequencies of all possible matings for each female in each
370 year that comprised key relationships given the social and genetic pedigrees. These
371 relationships comprised: fathers, full-brothers, and sons (1st degree relatives); grandfathers,

uncles, half-brothers, double first cousins (i.e., both parents of each mating individual are full-sibs), nephews, and grandsons (2nd degree relatives); and great-grandfathers, single first cousins, and great-grandsons (3rd degree relatives). We also considered half-uncles, half-single first cousins (i.e., one parent of each mating individual is a half-sib), and half-nephews (4th degree relatives) and thereby quantified effects of extra-pair reproduction (and consequent production of half-sibs rather than full-sibs) on possible matings that would otherwise have involved 3rd degree relatives. Matings involving immigrants were defined as 'unrelated' except where immigrants could mate with their own descendants. All possible matings that did not fall into any of the above categories were considered 'more distantly related'. If a possible mating fell into multiple categories (e.g., one case where a possible mate was both a female's son and grandson [i.e., the progeny of a female mating with another son]) it was allocated to the closer relationship.

We used Wilcoxon matched pair tests to evaluate whether the lifetime number of possible matings between individual females and male relatives in each category differed between the genetic versus social pedigrees. While changes in some relationships given the genetic pedigree may be counted in multiple years (if both the female and possible mate survive across years), these represent separate potential opportunities for inbreeding given random mating, and were thus retained. Although each female has exactly one father in each pedigree, changes in assigned father between the two pedigrees could change whether or not a female's assigned father is still alive in certain years and hence available as a possible mate. Since there is no extra-pair maternity, the number of possible female-son matings cannot change between the two pedigrees. However, such matings were counted to provide a complete summary of possible matings among 1st degree relatives.

Distribution of relatedness among possible mates

To quantify how observed changes in relationship frequencies translated into quantitative differences in relatedness among possible mates, we used standard pedigree algorithms (Lange 1997) to calculate the coefficient of kinship (k) between females and males for all possible matings under the social (k_{SOC}) and genetic (k_{GEN}) pedigrees. The coefficient k measures the probability that two homologous alleles sampled from two individuals will be identical by descent relative to the pedigree baseline, and equals the coefficient of inbreeding (f) of resulting offspring (Jacquard 1974; Lynch and Walsh 1998; Reid et al. 2016).

We quantified differences in k between each individual female and her lifetime set of possible mates given the genetic and social pedigrees in two ways. First, we quantified the differences in each female's mean k_{SOC} and k_{GEN} with all possible mates that were identified as 1st, 2nd, 3rd, and 4th degree relatives, or as more distantly related or unrelated, given the social pedigree. Second, we calculated the difference in k for each possible mating as $k_{DIFF} = k_{GEN} - k_{SOC}$, calculated mean k_{DIFF} for each individual female, and quantified the proportion of females for whom mean k_{DIFF} increased, decreased, or did not change given the genetic versus social pedigrees.

Finally, we quantified the degree to which extra-pair reproduction altered the overall potential for inbreeding across the whole population. We pooled all possible matings during 2008–2015 and used a two-sample Anderson-Darling test to test whether the shapes of the continuous distributions of k_{GEN} and k_{SOC} differed significantly (using 10,000 resampling permutations).

Analyses were run in R version 3.2.2 (R Development Core Team 2015) using packages *MasterBayes*, *nadiv*, *lme4*, *kinship2*, and *kSamples* (Hadfield et al. 2006; Wolak

419 2012; Sinnwell et al. 2014; Bates et al. 2015; Scholz and Zhu 2015). Raw means are reported
420 ±1SD.

421

422 **Results**

423 *Sibship structure of banded offspring*

424 A total of 98 female song sparrows alive during 2008–2015 produced at least two banded
425 offspring over their lifetime (mean 11.4±10.6; median 7–8, range 2–60), and hence at least
426 one sibship. Table 1A,B summarizes the number of sires and $Prop_{Full\text{-}sibs}$ among these
427 females' lifetime banded offspring given the social, genetic and 'distinct males' pedigrees.

428 Given the social pedigree, the mean number of sires per female was 1.9, and mean
429 $Prop_{Full\text{-}sibs}$ was 0.74 (table 1A,B; fig. 2A,B). Thus, even without considering extra-pair
430 reproduction (i.e., simultaneous polyandry), the occurrence of re-pairing between breeding
431 events (i.e., sequential polyandry), meant that the mean proportion of full-sibships among
432 females' banded offspring was on average ~26% less than expected under lifelong
433 monandry (i.e., 1.0).

434 Given the genetic pedigree, the mean number of sires per female was 2.9, equating
435 to a mean increase of 1.0 sire per female compared to the social pedigree (table 1A; fig. 2A).
436 Consequently, as might be expected, $Prop_{Full\text{-}sibs}$ among the banded offspring of most
437 females (60%; 59/98) was lower given the genetic pedigree than given the social pedigree
438 (table 1B; fig. 2B). However, for 38% (37/98) of females there was no change, and 2% (2/98)
439 of females actually had higher $Prop_{Full\text{-}sibs}$ given the genetic pedigree, illustrating that
440 polyandry can increase rather than decrease full sibships (fig. 2B). Indeed, mean $Diff_{social\text{-}gen}$
441 was greater in females where at least one offspring was sired by an extra-pair male, but

442 greatest in females with intermediate proportions of extra-pair offspring (fig. 3A; Supporting
443 Information S1). However, the effects of extra-pair reproduction on sibship structure (fig.
444 3A) were smaller than would be observed had all females been strictly monandrous
445 throughout their lifetimes rather than sequentially polyandrous (fig. 3B).

446 As expected, the number of sires per female was greatest given the 'distinct males'
447 pedigree (fig. 2A), but in fact did not differ significantly from the genetic pedigree (table 1A).
448 However, most females (69%, 68/98) had even lower $Prop_{Full\text{-}sibs}$ given the 'distinct males'
449 pedigree than given the genetic pedigree and no females had higher $Prop_{Full\text{-}sibs}$ (fig. 2B),
450 creating a mean reduction in $Prop_{Full\text{-}sibs}$ of ~8% relative to the genetic pedigree (table 1B).
451 Thus, while female song sparrows produced offspring with similar numbers of males in
452 reality (i.e., given the genetic pedigree) as given the 'distinct males assumption', the former
453 resulted in more full-sibships.

454

455 *Sibship structure of recruited offspring*

456 A total of 37 females produced at least two recruited offspring over their lifetime (mean
457 4.2±3.0; median 3, range 2–13). Across these females, the numbers of males that sired
458 banded offspring and $Prop_{Full\text{-}sibs}$ were consistently higher and lower, respectively, than
459 across the full set of 98 females (table 1A,B vs C,D). This is because females that produced
460 ≥2 recruits typically produced numerous banded offspring spanning multiple broods.
461 However, the patterns of differences between the pedigrees mirrored those estimated
462 across all 98 females (Tukey tests, table 1A,B vs C,D).

463 Comparisons within the 37 females showed that the mean number of sires
464 decreased between banded and recruited offspring, as might be expected given offspring
465 mortality, and hence no longer differed as substantially among the three pedigrees (table

466 1C,E). Meanwhile, mean $Prop_{Full\text{-}sibs}$ was slightly higher for recruited offspring than for
467 banded offspring across all three pedigrees (table 1D,F), but mean $Prop_{Full\text{-}sibs}$ among
468 recruited offspring was again lower given the genetic versus social pedigrees (table 1F). At
469 the individual level, 46% (17/37) of females had lower $Prop_{Full\text{-}sibs}$ given the genetic pedigree,
470 while 51% (19/37) had no change and one female had higher $Prop_{Full\text{-}sibs}$ (fig. 2D). $Diff_{social\text{-}gen}$
471 was again greater in females with intermediate proportions of extra-pair offspring (fig. 3C),
472 and the effects of extra-pair reproduction on recruit sibship structure were smaller than
473 would be observed given lifelong monandry (fig. 3D, Supporting Information S1). Finally, the
474 difference in $Prop_{Full\text{-}sibs}$ given the genetic versus 'distinct males' pedigrees was no longer
475 significant across recruited offspring (Tukey test, table 1F; fig. 2D).
476
477 *Distribution of relationships among possible mates*
478 There was a total of 8028 possible matings between adult females and males alive in each
479 year during 2008–2015, spanning 114 females and 144 males. On average, there were 0.6
480 fewer possible matings between individual focal females and their full-brothers given the
481 genetic versus social pedigrees, but 1.6 more possible matings with half-brothers (table 2).
482 However the distributions of the within-female differences in the numbers of full- and half-
483 brothers between the two pedigrees spanned zero, showing that some females had more
484 full-brothers and/or fewer half-brothers given the genetic pedigree (table 2; fig. 4). This
485 illustrates that patterns of extra-pair reproduction enacted by some female's ancestors
486 increased rather than decreased the number of possible matings between focal females and
487 full-brothers versus half-brothers.
488 On average, there were also fewer possible matings between females and their full
489 uncles, nephews, double first-cousins and single first-cousins given the genetic versus social

490 pedigree and correspondingly increased numbers of possible matings with half-uncles and
491 half-single first cousins (but little change in the number of possible matings with half-
492 nephews, table 2). However, the distributions of the within-female differences again
493 spanned zero, especially for half-single first cousins (fig. 4). There was consequently
494 substantial among-individual variation in the consequences of extra-pair reproduction for
495 the risk of inbreeding with 3rd versus 4th degree relatives.

496 As expected there was no change in the number of possible female-son matings
497 given the genetic versus social pedigrees, and only small average changes in the numbers of
498 possible matings with fathers, grandfathers, grandsons, great-grandfathers and great-
499 grandsons (table 2) with little variation among individuals (fig. 4). Furthermore, there was
500 little or no change in the number of possible matings between females and more distant
501 relatives or completely unrelated males, respectively (table 2).

502 Overall, the individual-level differences in the distribution of relatives available as
503 possible mates translated into substantial population-level differences: extra-pair
504 reproduction meant that, across the population, females had 40% fewer possible matings
505 with full-brothers, 166% more possible matings with half-brothers, and 85% more possible
506 matings with 4th degree relatives than with analogous 2nd and 3rd degree relatives
507 (Supporting Information S4).

508

509 *Distribution of relatedness among possible mates*

510 Due to variation in inbreeding among females' ancestors, there was substantial among-
511 individual variation in the mean kinship (*k*) between females and their possible mates that
512 were identified as 1st, 2nd, 3rd or 4th degree relatives given the social pedigree (fig. 5A–D),
513 particularly for 1st and 2nd degree relatives. Of the females that had ≥1 possible mate that

514 was identified as a 1st, 2nd, 3rd or 4th degree relative given the social pedigree most, but not
515 all, had lower mean *k* with these same sets of possible mates given the genetic pedigree (fig.
516 5A–D). Across females, mean k_{GEN} was significantly lower than mean k_{SOC} for all four
517 categories of relative, but the magnitude of the difference was smallest for 4th degree
518 relatives (table 3). Conversely, mean k_{SOC} and mean k_{GEN} did not differ across females'
519 possible mates that were identified as more distant relatives given the social pedigree (table
520 3; fig. 5E). Because newly arrived immigrants were the only individuals that were completely
521 unrelated to their possible mates, mean k_{SOC} and mean k_{GEN} were identical across individuals
522 that were identified as non-relatives in the social pedigree (table 3; fig. 5F).

523 Of the 114 females, 71% (81) had negative values of mean k_{DIFF} across all possible
524 matings given the genetic pedigree versus the social pedigree, while 25% (29) had positive
525 values of mean k_{DIFF}, and 4% (4) had no change in mean k_{DIFF} (three female immigrants that
526 were alive in only one year, and one female immigrant whose only possible matings with
527 relatives were with sons or grandsons). Grand mean k_{DIFF} across all possible matings for
528 individual females was -0.007 ±0.01 (median -0.008, range -0.035–0.017), showing that, on
529 average, females were slightly less related to all possible mates given the genetic pedigree
530 than given the social pedigree.

531 However, across all pooled possible matings for all females, the distributions of k_{GEN}
532 and k_{SOC} were significantly different (two-sample Anderson-Darling test, $AD = 28.27$, $T =$
533 35.79, $p < 0.001$). This difference arose because the distribution of k_{GEN} included fewer
534 possible matings at higher *k* (fig. 6, black bars), but more possible matings at lower but non-
535 zero *k* (fig. 6, white bars), than the distribution of k_{SOC}. There was again no difference in the
536 number of possible matings among unrelated individuals (i.e., $k = 0$, fig. 6).

537

538 **Discussion**

539 Simultaneous polyandry is widely hypothesized to have evolved to facilitate inbreeding
540 avoidance in populations where relatives interact and inbreeding depression is strong (e.g.,
541 Stockley et al. 1993; Tregenza and Wedell 2000; Michalczyk et al. 2011). Consequently,
542 numerous empirical studies on diverse systems have tested whether polyandrous females
543 avoid inbreeding by expressing pre-copulatory and/or post-copulatory choice for less closely
544 related mates (Tregenza and Wedell 2002; Firman and Simmons 2008; Brouwer et al. 2011;
545 Reid et al. 2015*a*). However, no studies have quantified the degree to which intrinsic effects
546 of polyandry on sibship structures might indirectly reduce inbreeding risk (i.e., the 'indirect
547 inbreeding avoidance hypothesis', IIAH) in systems experiencing natural variation in
548 polyandry, polygyny and paternity within and across overlapping generations. Accordingly,
549 we compared long-term social and genetic pedigree data from free-living song sparrows to
550 examine the consequences of extra-pair paternity, and hence underlying simultaneous
551 polyandry, for sibship structures and distributions of relationships and relatedness. Further,
552 by comparing observed patterns to those that would have arisen given lifelong monandry
553 (i.e., no simultaneous or sequential polyandry) or given simultaneous polyandry but no
554 resulting polygyny (i.e., the 'distinct males assumption'), we isolated effects of major
555 components of the complex overall natural mating system on sibship structures. As one
556 node of a large meta-population, our study system provides an insightful model for systems
557 where reproductive interactions among relatives commonly arise and might consequently
558 drive mating system evolution (e.g., Sharp et al. 2008; Hatchwell 2010; While et al. 2011).

559 Analogous comparisons between social and genetic pedigrees have previously been
560 widely used to quantify effects of extra-pair reproduction on the variance in male
561 reproductive success and hence on effective population size and the consequent population

562 mean inbreeding rate (Webster et al. 1995, 2007; Freeman-Gallant et al. 2005; Schlicht and
563 Kempenaers 2013). Such effects are often small, including in song sparrows (Lebigre et al.
564 2012, see also Karl 2008). However, such results do not preclude the possibility that extra-
565 pair reproduction could substantially affect individual-level inbreeding risk. This is because
566 the same overall variance in male reproductive success, but very different sibship structures
567 and distributions of relationships and relatedness, can arise if individual males sire several
568 offspring of one polyandrous female (i.e., generating full-sibs) or sire one offspring of
569 several polyandrous females (i.e., generating paternal half-sibs).
570
571 *Sibship structures*
572 It may seem inevitable that extra-pair reproduction resulting from simultaneous polyandry
573 will reduce full sibships, as assumed by the basic IIAH, and by Cornell and Tregenza's (2007)
574 initial theoretical model. However our analyses illustrate that such effects arising within a
575 natural mating system are not so straightforward. Comparison of the social and genetic song
576 sparrow pedigrees showed that extra-pair reproduction did indeed increase the mean
577 number of different males that sired individual females' offspring and hence reduce the
578 mean proportion of full-sibships ($Prop_{Full\text{-}sibs}$) and increase the mean proportion of maternal
579 half-sibships ($Prop_{Half\text{-}sibs}$) among females' lifetime banded offspring. However, such means
580 mask substantial among-female variation, including cases where extra-pair reproduction
581 increased rather than reduced $Prop_{Full\text{-}sibs}$ (fig. 2B). Such patterns can result from non-
582 independent extra-pair paternity when females produce numerous extra-pair offspring with
583 the same male across broods (as indicated by fig. 3A,C), and/or if a female's extra-pair male
584 from one brood becomes her socially-paired male for another brood (or vice versa). Further,
585 comparisons with the hypothetical occurrence of lifelong monogamy showed that the

586 occurrence of social re-pairing across breeding attempts (i.e., sequential polyandry) already
587 reduced the effects of simultaneous polyandry on sibship structures by ~26%. Selection for
588 simultaneous polyandry stemming from the IIAH process might consequently be weaker
589 given iteroparity and associated repairing than given semelparity and/or strict lifelong
590 monogamy. Comparison with the hypothetical 'distinct males' pedigree showed that 68% of
591 females would have had lower $Prop_{Full\text{-}sibs}$ among their banded offspring in the absence of
592 polygyny than given the observed pattern of polygyny defined by the genetic pedigree (fig.
593 2B). This implies that Cornell and Tregenza's (2007) theoretical formulation of the IIAH
594 might overestimate indirect selection on polyandry arising in polygynandrous systems.
595 While simultaneous polyandry can clearly affect the sibship structure of females'
596 conceived offspring, its consequences for inbreeding risk and other kin interactions
597 ultimately depend on its effects on the sibship structure of offspring that survive to life-
598 history stages when key interactions occur. In song sparrows, further comparisons of the
599 genetic and social pedigrees showed that the effects of extra-pair reproduction on sibship
600 structures were qualitatively similar, but subtly different, across recruited versus banded
601 offspring (fig. 2). Most notably, $Prop_{Full\text{-}sibs}$ for recruits no longer differed between the
602 genetic and 'distinct males' pedigrees (table 1B,D vs F). These patterns imply that
603 theoretical predictions regarding indirect selection on polyandry might, in some instances,
604 be relatively robust to an assumption of no polygyny. However, such inferences from
605 observed genetic and social pedigrees require the additional, and commonly violated,
606 assumption that offspring survival to recruitment does not depend on paternity. In song
607 sparrows, female extra-pair offspring are less likely to recruit than female within-pair
608 offspring reared in the same brood (i.e., maternal half-sisters, Sardell et al. 2011), and extra-
609 pair offspring of both sexes have lower survival and/or reproductive success than within-

610 pair offspring in other passerine birds (e.g., house sparrows, *Passer domesticus*, Hsu et al.
611 2014; coal tit, *Periparus ater*, Schmoll et al. 2009). Any small reduction in inbreeding among
612 polyandrous females' offspring might therefore be further reduced by stochastic and/or
613 deterministic variation in survival of offspring sired by different males. The ultimate
614 consequences of polyandry for the expected frequency of close inbreeding and consequent
615 fitness among descendants of polyandrous females in natural populations may therefore be
616 smaller than predicted by models that do not consider differential offspring survival (e.g.,
617 Cornell and Tregenza 2007), and estimated in laboratory populations where variation in
618 survival may be minimized (e.g., Power and Holman 2014). Future theoretical and empirical
619 studies considering the evolutionary causes and consequences of polyandry arising through
620 its effects on sibship structures should therefore consider such effects within the context of
621 the overall mating system, including natural variation in paternity arising through polygyny
622 and iteroparity, as well as differential offspring survival.
623
624 *Distributions of relationships and relatedness*
625 The effects of simultaneous polyandry on sibship structures among recruited offspring are
626 likely to alter the frequencies of diverse types of half-relatives versus full-relatives spanning
627 multiple (overlapping) generations, thereby altering any individual's overall potential for
628 inbreeding or interacting with different types of relatives. The form and magnitude of
629 indirect selection on polyandry stemming from the IIAH process might then differ from that
630 predicted in restricted situations with within-brood mating and non-overlapping
631 generations (e.g., Cornell and Tregenza 2007). Indeed, our comparisons of the social and
632 genetic song sparrow pedigrees showed that extra-pair reproduction reduced the potential
633 for inbreeding among different degrees of full-relatives and increased the potential for

634 inbreeding among more distant half-relatives, but this change was not consistent across all
635 individual females and types of relationship (table 2, fig. 4, Supporting Information S4).
636 Similarly, simultaneous polyandry reduced the mean kinship between females and their
637 possible mates, most notably with mates that would otherwise have been 1st degree
638 relatives (fig. 5). These overall conclusions remained unchanged when all possible matings
639 among 1st degree relatives were excluded (Supporting Information S5), thereby considering
640 a scenario where individuals actively avoid inbreeding with 1st degree relatives (as observed
641 in other species, e.g., Stow and Sunnucks 2004; Gerlach and Lysiak 2006; Archie et al. 2007;
642 Brouwer et al. 2011; Ihle and Forstmeier 2013). Overall, the individual-level differences in
643 relatedness among possible mates stemming from simultaneous polyandry resulted in
644 fewer possible matings at intermediate and higher *k* (i.e., among closely related pairs), and
645 more possible matings at lower but non-zero *k* (fig. 6).
646 Such conclusions rely on the implicit assumptions of our study design that mating
647 decisions and recruitment are unaffected by pedigree structure, and hence that there is no
648 active inbreeding avoidance or differential survival by within-pair versus extra-pair offspring.
649 Indeed, song sparrows do not actively avoid inbreeding through social pairing or extra-pair
650 reproduction (Keller and Arcese 1998; Reid et al. 2015*a*). However, to further consider the
651 implications of such assumptions, we conducted additional analyses to quantify effects of
652 polyandry on relatedness within a single cohort (Supporting Information S6). Such analyses
653 have the advantage that they do not require any assumptions regarding patterns of mating
654 or survival in the absence of extra-pair reproduction, but the disadvantage that they
655 eliminate effects of polyandry on relatedness generated across multiple (overlapping)
656 generations. These analyses also showed reduced potential for close inbreeding ($k \geq 0.25$)
657 given the genetic versus social pedigrees, but no reduction in more distant inbreeding

658 (0.03125 ≤ k < 0.25, Supporting Information S6). These supporting results illustrate that
659 overall effects of polyandry in reducing the potential for inbreeding at intermediate k
660 accumulate across generations, meaning that exact quantitative outcomes could be
661 influenced by patterns of differential survival of within-pair versus extra-pair offspring.
662

663 *Implications*

664 Our results imply that the magnitude and direction of indirect selection on simultaneous
665 polyandry stemming from the intrinsic consequences of such polyandry for distributions of k
666 among offspring, and hence grand-offspring f, will depend on the shape of the relationship
667 between fitness and f (i.e., the form of inbreeding depression). Given multiplicative effects
668 of deleterious recessive alleles, inbreeding depression is expected to be log-linear, such that
669 the reduction in fitness decreases with increasing f (fig. 7, Morton et al. 1956; Charlesworth
670 and Charlesworth 1987; Charlesworth and Willis 2009). Counter-intuitively, under these
671 conditions, polyandry might in fact cause a net decrease in mean fitness, even though it
672 slightly reduces mean grand-offspring f. Intrinsic indirect selection on polyandry stemming
673 from 'indirect inbreeding avoidance' might then impede rather than facilitate polyandry
674 evolution. However, given epistatic or threshold effects, inbreeding depression could be
675 weak up to some value of f above which fitness decreases markedly (e.g., fig. 7,
676 Charlesworth and Willis 2009). Given such threshold effects, the long-term relative
677 frequency of alleles underlying polyandry could then increase due to the reduced frequency
678 of matings among close relatives and the resulting net increase in mean offspring fitness
679 that would arise despite an increased frequency of matings among more distant relatives.
680 The form of inbreeding depression is very difficult to quantify in natural populations,
681 not least because close inbreeding often occurs infrequently and may be more likely in high-

682 fitness lineages where more relatives are available for mating, meaning that phenotypic
683 effects of inbreeding could be confounded with environmental and/or additive genetic
684 effects (Reid et al. 2008). Experimental assessments of the shape of inbreeding depression
685 across ranges of *f* relevant to animal mating systems are also scarce, because most
686 experimental studies consider inbred groups generated through one or multiple generations
687 of sib-sib mating (Charlesworth and Charlesworth 1987; Keller and Waller 2002;
688 Charlesworth and Willis 2009). Full quantitative, mechanistic evaluation of the 'indirect
689 inbreeding avoidance' process in driving or impeding polyandry evolution will therefore
690 require information on distributions of sibships, relationships and relatedness arising within
691 complex natural mating systems to be coupled with detailed experimental assessments of
692 the form of inbreeding depression arising across appropriate ranges of *f*.
693
694
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705

Supplementary Material

Supporting Information S1: Quantifying the combined effects of simultaneous and sequential polyandry on sibship structures

Supporting Information S2: Sibship structure among banded offspring of females that produced recruits

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

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

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

Supporting Information S6: Distribution of relatedness within cohorts

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953 **Table 1:** Summary statistics (left panel) and generalized linear mixed models (right panel)
954 estimating differences in the number of males that sired a female's offspring, and the
955 proportion of full-sibships ($Prop_{Full\text{-}sibs}$) among females' offspring given the social, genetic
956 and 'distinct males' pedigrees. Focal females and offspring comprise (A and B) banded
957 offspring of all females that produced ≥2 banded offspring (i.e., ≥1 sibship, *n* =98 females),
958 and (C and D) banded offspring and (E and F) recruited offspring of females that produced
959 ≥2 recruited offspring (*n* =37 females). Raw means are presented ± 1 standard deviation
960 (SD). Models assumed (A,C,E) Poisson or (B,D,F) binomial error structures. Estimated
961 pedigree effects (on latent scales) are presented ±1 standard error (SE), *df* is the residual
962 degrees of freedom, R^2 is the conditional coefficient of determination, and *Z* and *p* values
963 are presented for each fixed effect level where the social pedigree represents the intercept.
964 'Tukey' summarizes a Tukey post-hoc test assessing differences among pedigrees, where
965 different lower case letters (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) $Prop_{Full\text{-}sibs}$	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) $Prop_{Full\text{-}sibs}$	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) $Prop_{Full\text{-}sibs}$	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

Table 2: Mean ±SD (and range) of the number of lifetime possible matings for individual female song sparrows at 15 specified relationships, and with more distant relatives and unrelated individuals, given the social and genetic pedigrees. The mean difference shows the mean decrease (negative values) or increase (positive values) in the number of possible matings at each relationship level given the genetic versus social pedigrees across 114 individual females. Full distributions of the differences are shown in fig. 4. *Z* and *p* denote the Wilcoxon rank sum test statistic value and associated *p* value. Relationships where numbers of possible matings decreased or increased significantly given 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)

976

977 **Table 3:** Mean ±SD (and range) pairwise coefficient of kinship (*k*) between individual female
978 song sparrows and all possible mates that were classified as 1st, 2nd, 3rd or 4th degree
979 relatives, or as more distant relatives or as unrelated given the social pedigree, with *k*
980 calculated from the social pedigree (k_{SOC}) or genetic pedigree (k_{GEN}). *n* and ♀ respectively
981 represent the numbers of possible matings and individual females in each category. Mean
982 difference denotes the mean decrease (negative values) or increase (positive values) in
983 mean *k* for individual females given the genetic versus social pedigrees (i.e., k_{GEN} - k_{SOC}). *Z*
984 and *p* denote the Wilcoxon rank sum test statistic value and associated *p* value. Degrees of
985 relationship where mean *k* decreased significantly are highlighted in bold.

986

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)

987

988 **Figure 1:** Conceptualized mating systems with simultaneous polyandry and (A) distinct
989 males across females ('distinct males assumption'); (B) common males across females (i.e.,
990 polygyny) with independent paternity; and (C) common males across females and non-
991 independent (i.e., skewed) paternity. Top female and male symbols depict breeding females
992 and their mate(s) (connected by black lines). Boxed females and males depict resulting
993 offspring from each mating, where box edge patterns match offspring to their mother, and
994 individual shading match offspring to their father. In (A), a polyandrous female's (vertical
995 stripes) offspring have the same mother (i.e., enclosed within vertical striped box), but only
996 some have the same father (i.e., are full-sibs rather than maternal half-sibs; matching grey
997 or black shading). A monandrous female's (checkered box) offspring all have the same
998 mother and father. In (B), the same males can mate with multiple polyandrous and/or
999 monandrous females, creating more offspring that have the same father (i.e., paternal half-
1000 sibs), and fewer unrelated offspring that share neither parent. In (C), a polyandrous female
1001 (horizontal stripes) mates with an initial male (connected by dashed line) but all of her
1002 offspring are sired by the same additional male, resulting in full-sib offspring (as for A).

1003

1004 **Figure 2**: The numbers of different males that sired female song sparrows' (A) banded and
1005 (C) recruited offspring, and the sibship structures of females' (B) banded and (D) recruited
1006 offspring given the social pedigree ('Social'), genetic pedigree ('Genetic'), and 'distinct
1007 males' pedigree ('Distinct males'). In (A) and (C), box lines represent the median, upper and
1008 lower quartiles, whiskers demarcate 1.5× the interquartile range, and '+' shows the mean. In
1009 (B) and (D), the left and right axes respectively show the proportions of sibships among each
1010 female's offspring that are full-sibships ($Prop_{Full\text{-}sibs}$) and half-sibships ($Prop_{Half\text{-}sibs}$), where

points denote individual females (jittered for clarity), and lines join observations for individual females given the three pedigrees.

Figure 3: Relationships between the proportion of a female's lifetime offspring that were extra-pair offspring (Proportion EPO) and the absolute difference in $Prop_{Full\text{-}sibs}$ given (A and C) the genetic versus social pedigrees ($Diff_{social\text{-}gen}$), and (B and D) the genetic pedigree versus strict lifelong monandry ($Diff_{life_monandry\text{-}gen}$) for (A and B) banded and (C and D) recruited offspring. Predictions (black lines) and confidence intervals (grey bands) are from generalized linear models (Supporting Information S1).

Figure 4: Distributions of the difference in the number of possible matings at each focal relationship level (listed in table 2) across 114 females given the genetic versus social pedigrees. Negative and positive values respectively indicate decreases and increases in the number of possible matings at each relationship level. White bars denote lineal relatives (where little difference in the number of possible matings is expected), black bars denote relationship levels where the mean increase or decrease in the number of possible matings differed significantly from zero (table 2), and grey bars denote all other non-lineal relationship levels. Two relationship levels ('son' and 'unrelated') are not depicted because the difference in the number of matings between the social and genetic pedigrees was uniformly zero (table 2).

1032 **Figure 5:** Mean coefficient of kinship (*k*) between individual female song sparrows and all
1033 possible mates that were identified in the social pedigree as (A) 1st degree, (B) 2nd degree,
1034 (C) 3rd degree, (D) 4th degree and (E) more distant relatives, and (F) unrelated, where *k* is
1035 calculated given the social pedigree ('Social') or genetic pedigree ('Genetic'). Note that y-
1036 axis scales differ among rows of panels. Points denote individual females (jittered for
1037 clarity), and lines join observations for individual females given the two pedigrees. Of the
1038 females that had ≥1 possible mate that was identified as a 1st, 2nd, 3rd or 4th degree relative
1039 given the social pedigree most, but not all, had lower mean *k* with these same sets of
1040 possible mates given the genetic pedigree (80% [83/104], 84% [83/99], 87% [68/78] and
1041 73% [71/97] of females respectively).

1042

1043 **Figure 6:** Overall distributions of pairwise coefficients of kinship across all possible song
1044 sparrow matings, calculated from the social pedigree (black bars) or genetic pedigree (white
1045 bars), with grey bars denoting overlap between the two distributions. Dotted, dashed, and
1046 dot-dashed lines depict kinship values equivalent to first cousin (0.0625), half-sib (0.125),
1047 and full-sib (0.25) matings, respectively. Box plots further visualize the distribution of *k* given
1048 each pedigree, where box lines represent the median, upper and lower quartiles, whiskers
1049 demarcate 1.5× the interquartile range, and '+' represents the mean. Mean k_{SOC} was
1050 0.101±0.069 (median 0.914, range 0.000–0.472) and mean k_{GEN} was 0.094±0.065 (median
1051 0.087, range 0.00–0.421), corresponding to a small but statistically significant mean
1052 decrease of -0.006±0.040 (median -0.003, range -0.301–0.251, Wilcoxon signed rank test: Z
1053 = 18.95, $p < 0.001$).

1054

1055 **Figure 7:** Conceptualization of potential relationships between mean fitness (scaled relative
1056 to an outbred individual) and individual coefficient of inbreeding (*f*). Such relationships
1057 could be linear (white circles), concave (i.e., log-linear, given multiplicative allelic effects,
1058 grey circles), convex (given epistasis, black circles), or follow a threshold pattern (diamonds).
1059 Points denote x-axis intervals of 0.01 to depict the effects of different shapes of inbreeding
1060 depression on equal scales. Note that concave and convex forms of inbreeding depression
1061 are often depicted on a log scale (i.e., log-fitness) such that log-linear effects appear linear
1062 (e.g., Charlesworth and Willis 2009). Each series of points is meant to convey qualitative
1063 patterns of inbreeding depression and not quantitative values, and so are jittered for clarity.

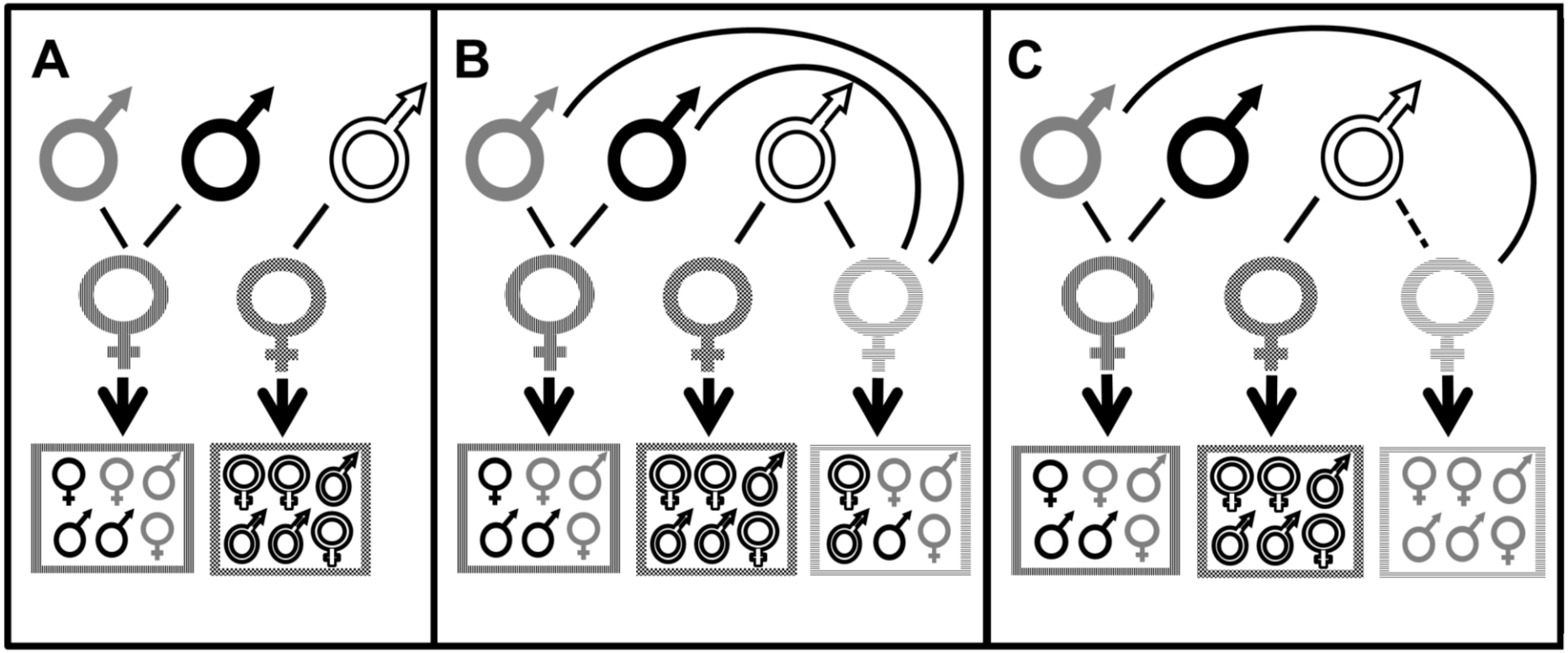


Figure 1

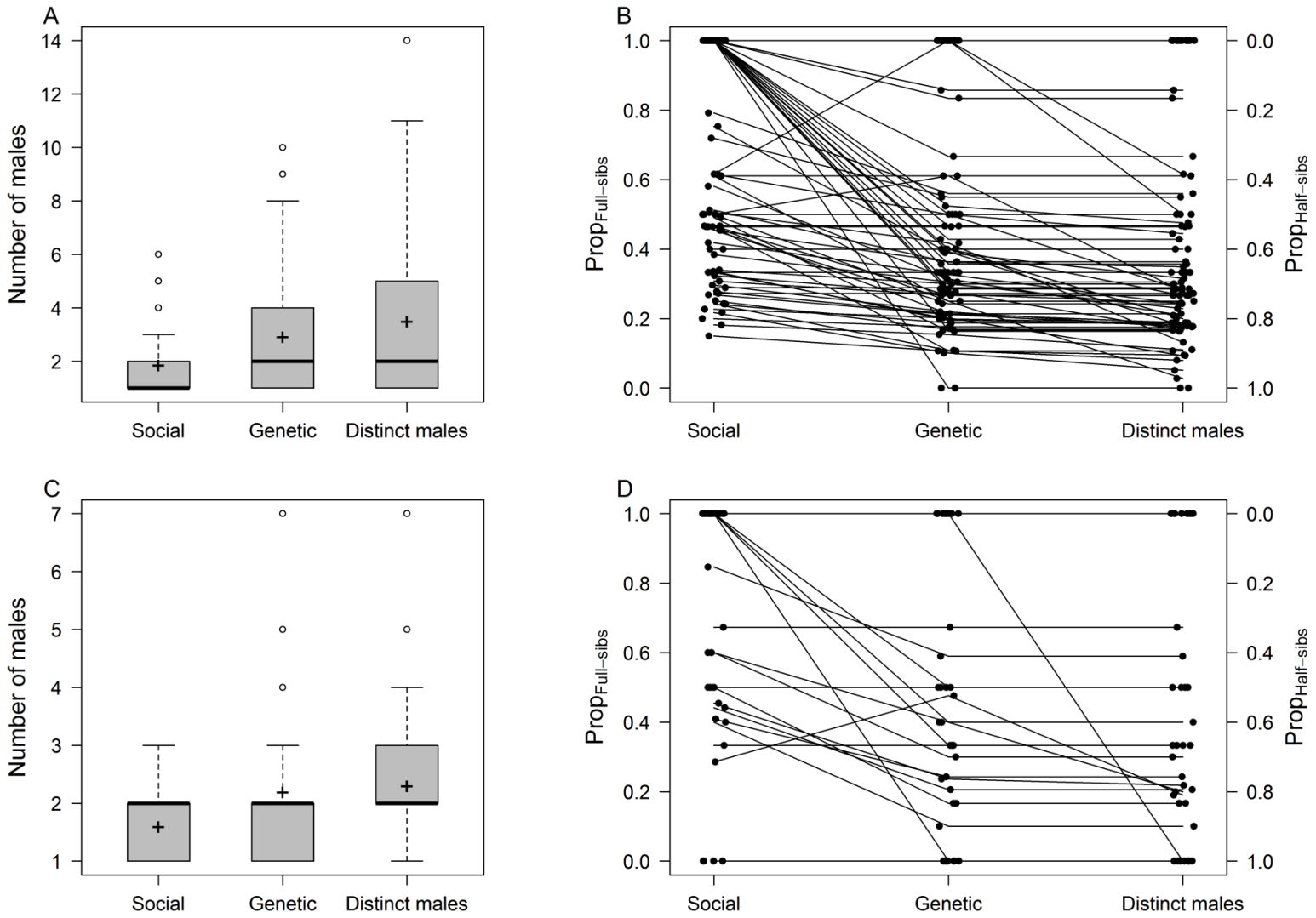
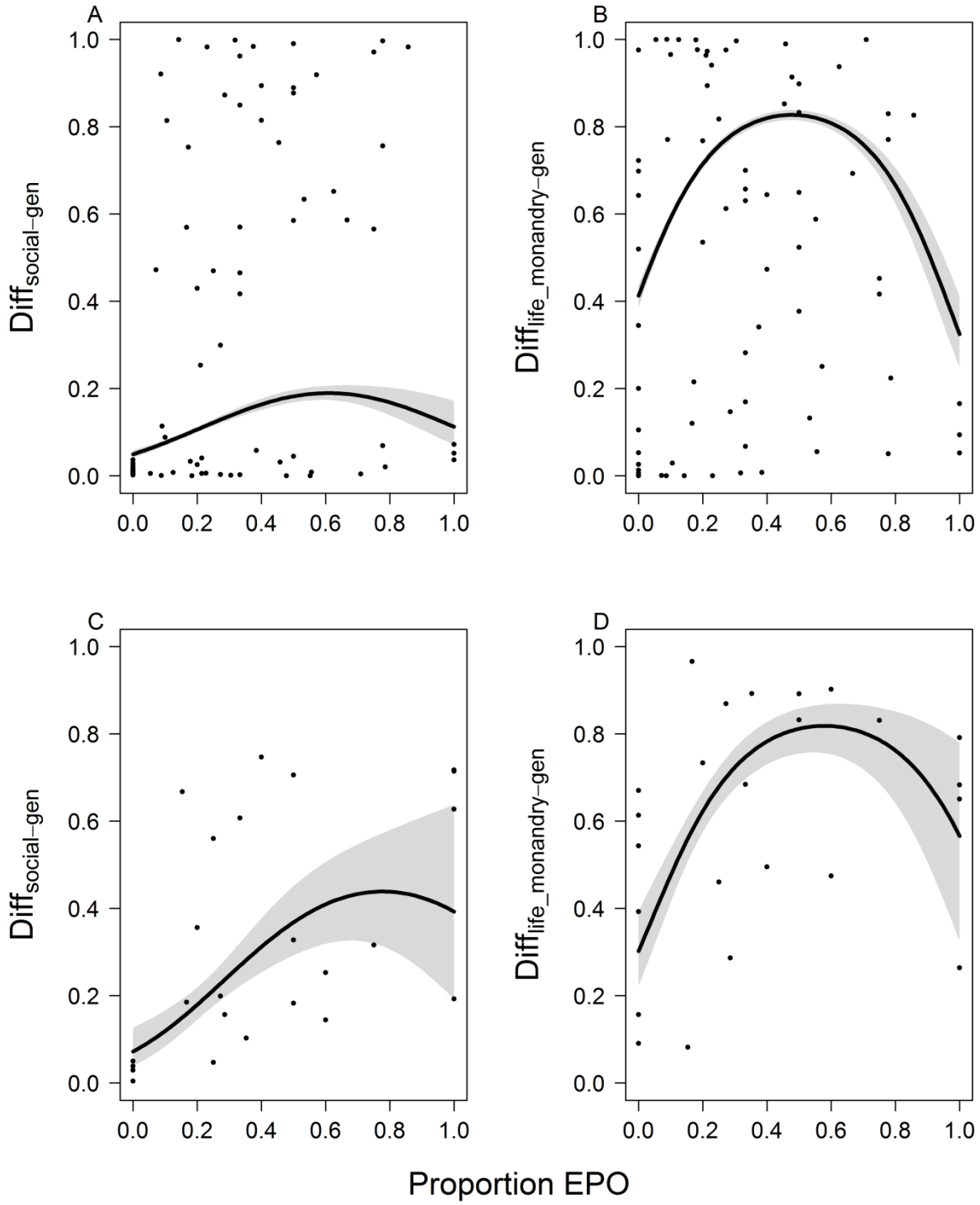

A
Number of males
Social
Genetic
Distinct males
B
Prop Full–sibs
Prop Half–sibs
Social
Genetic
Distinct males
C
Number of males
Social
Genetic
Distinct males
D
Prop Full–sibs
Prop Half–sibs
Social
Genetic
Distinct males

Figure 2

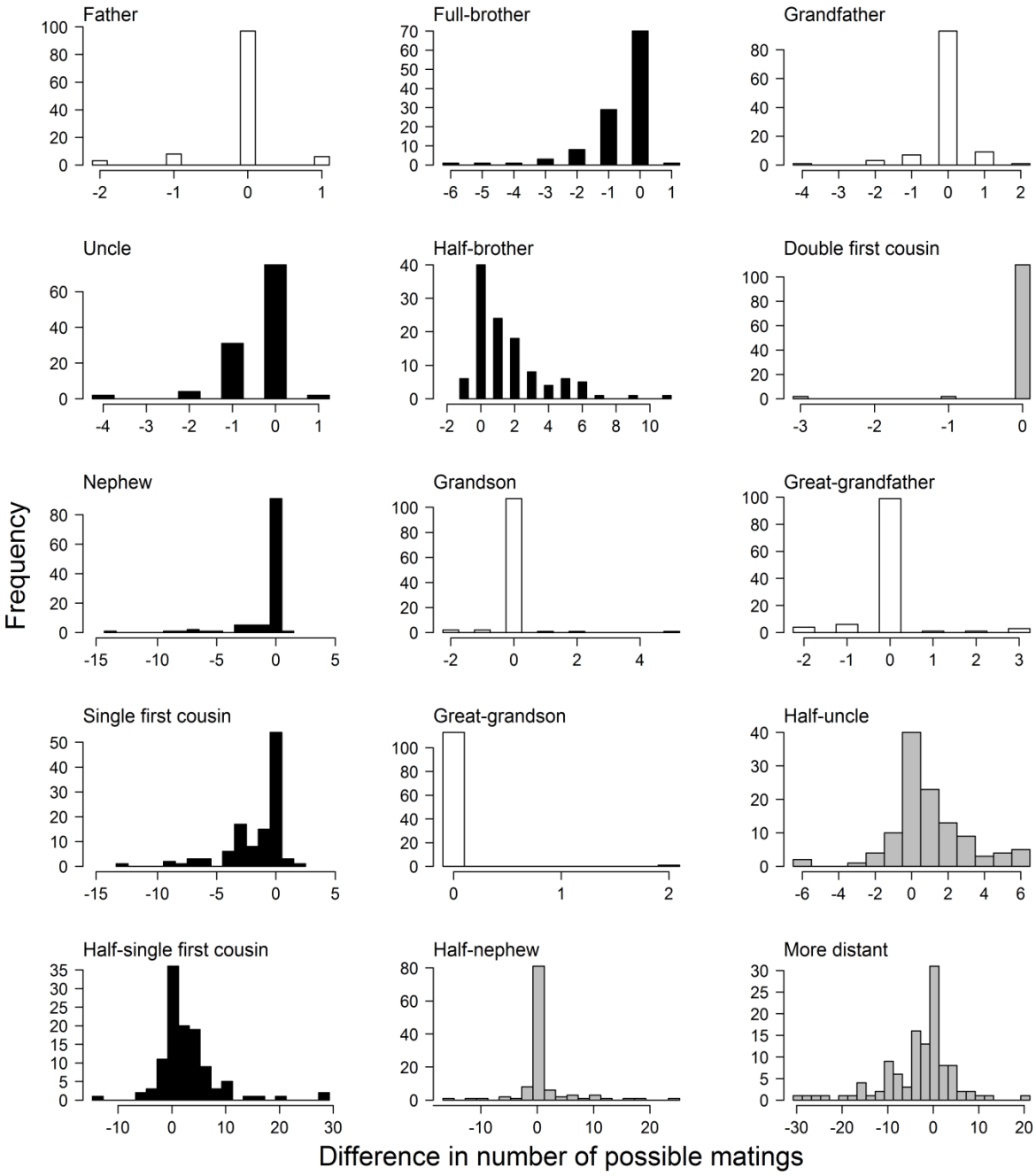
1069



1070

1071 **Figure 3**

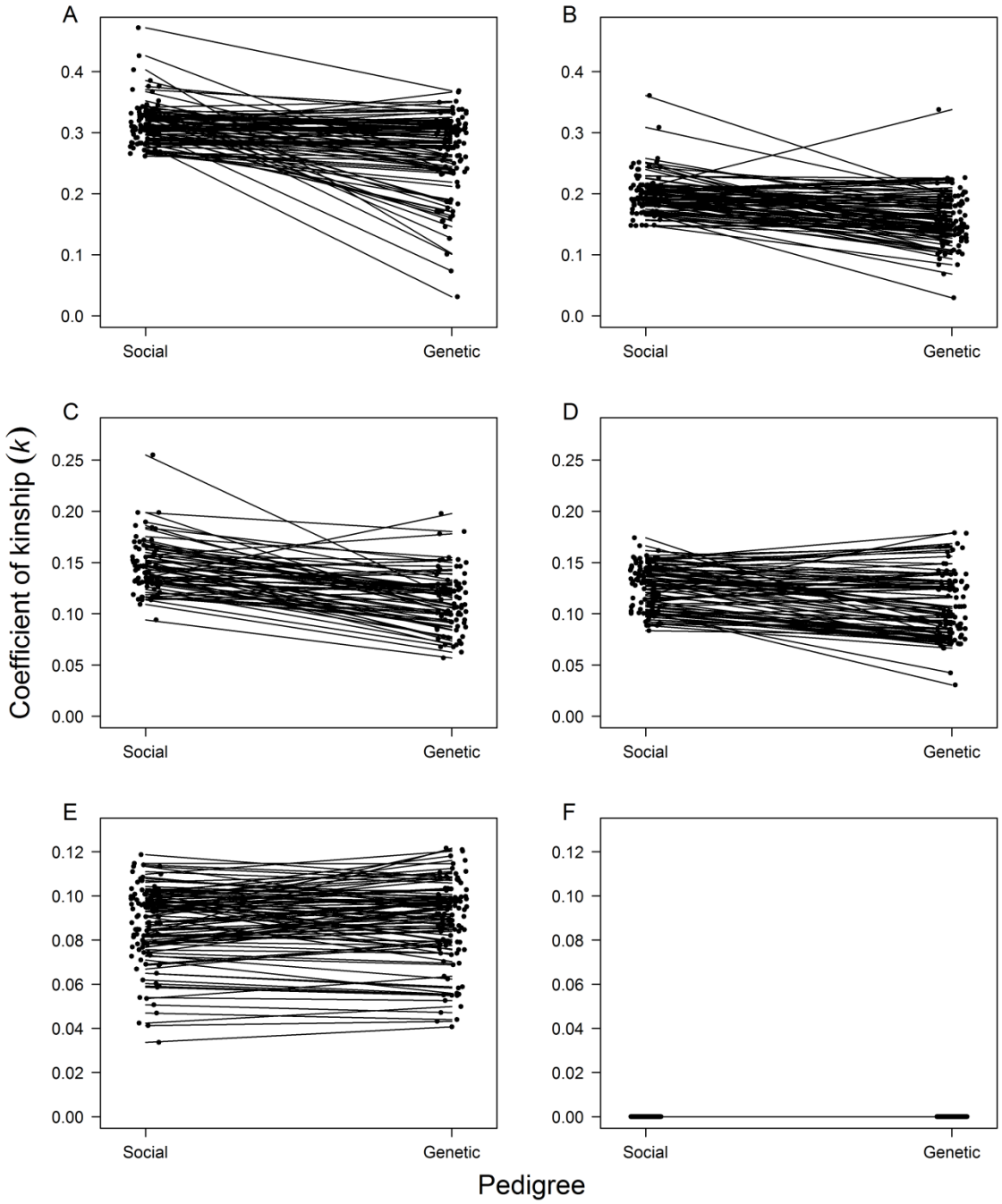
1072



1073

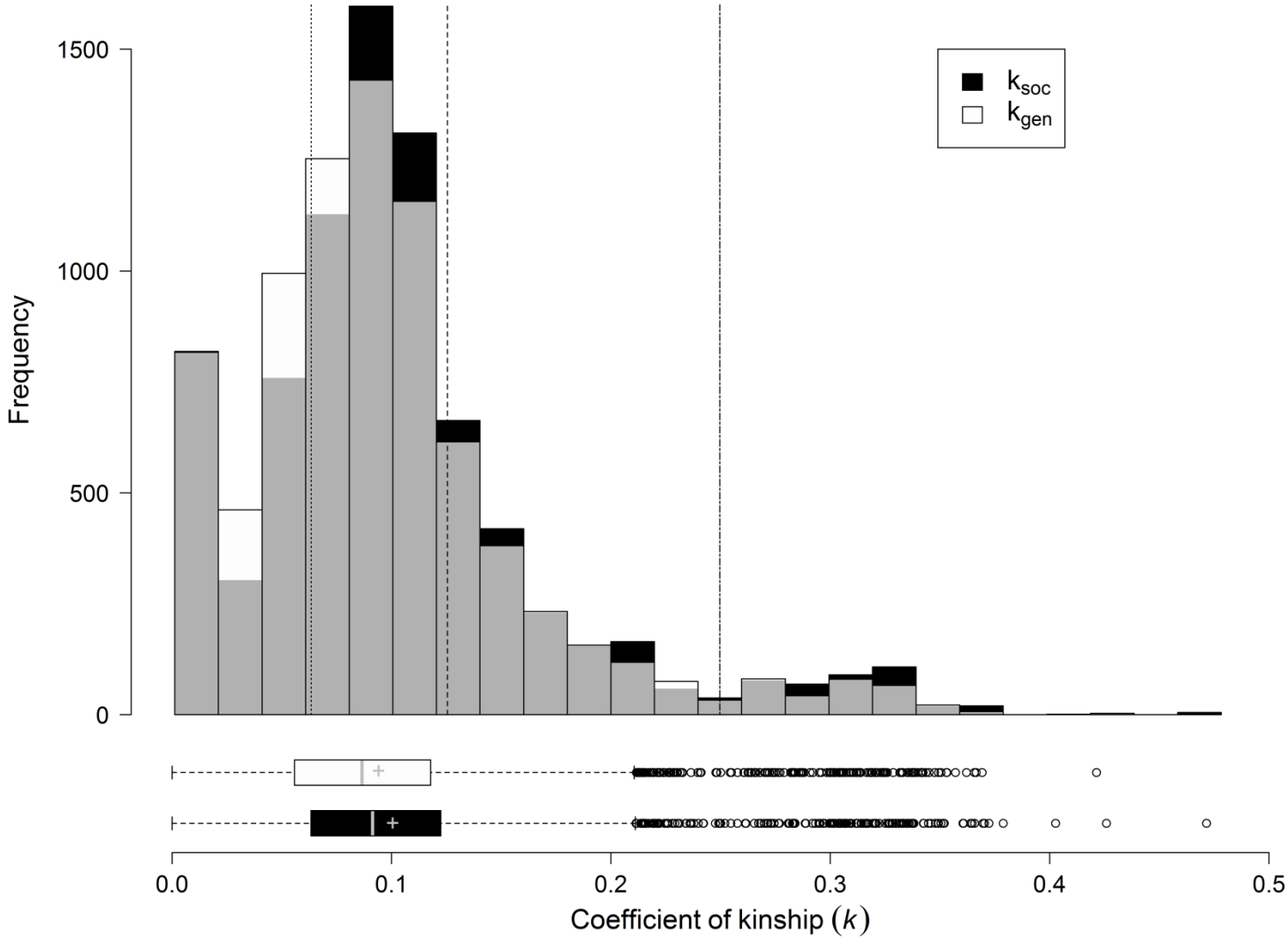
1074 **Figure 4**

1075



1076

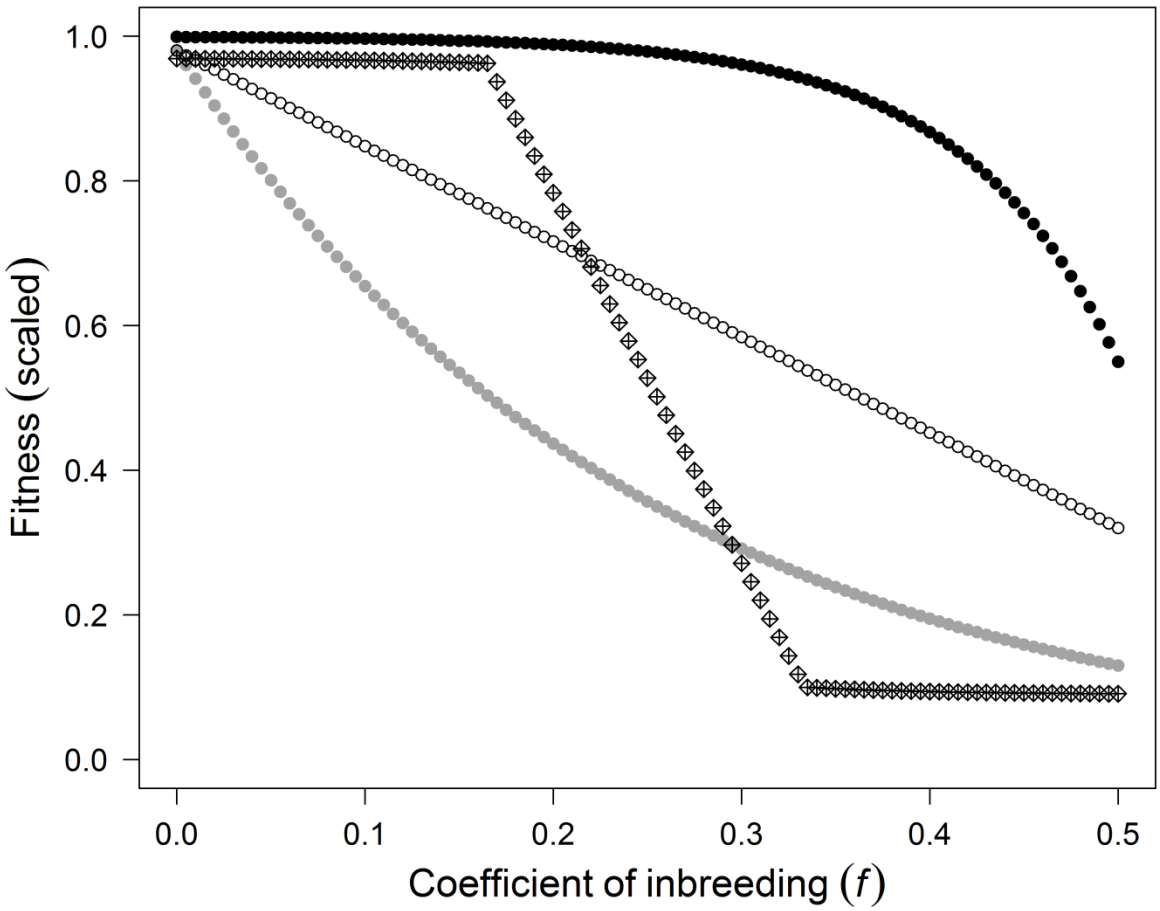
1077 **Figure 5**



1078

1079 **Figure 6**

1080



1081

1082 **Figure 7**