

**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;

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

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

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

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

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

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

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

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

Furthermore, in populations where some degree of inbreeding is common, changes in the 'relationships' among possible mates resulting from polyandry may cause more complex changes in 'relatedness'. This is because shared ancestry between a focal pair's parents can increase the pair's relatedness above that expected given the same immediate 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.

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

We used comprehensive song sparrow pedigree data to quantify the consequences of extra-pair reproduction for sibship structures and distributions of relationships and relatedness between possible mates, and thereby quantify key processes that underlie the general 'indirect inbreeding avoidance hypothesis' for polyandry. First, we quantify the degree to which extra-pair reproduction changes the proportion of full-sib versus half-sib 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<sup>-1</sup>) 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

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

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

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

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*Social and genetic pedigrees*

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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. 2015a). 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, 2015a, 2015c; 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, 2015a). To minimize

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

### *Sibship structures*

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

extra-pair male across multiple broods. To explicitly quantify the combined effects of simultaneous and sequential polyandry on sibship structures, we further quantified the difference between  $\text{Prop}_{\text{Full-sibs}}$  given the genetic pedigree and the value of  $\text{Prop}_{\text{Full-sibs}}$  that would arise given strict lifelong monandry (i.e., 1.0, hence  $\text{Diff}_{\text{lifelong\_monandry-gen}} = 1.0 - \text{Prop}_{\text{Full-sibs[genetic]}}$ ). Finally, to quantify the degree to which observed sibship structures differed from those that would have arisen given the ‘distinct males assumption’ (i.e., no polygyny), we additionally considered a hypothetical pedigree in which extra-pair males could sire multiple offspring within a given brood but could not sire other within-pair or extra-pair offspring in the population (i.e., fig. 1A). We assigned a unique sire identity to all extra-pair offspring in each observed brood, maintaining the observed paternity distribution (i.e.,  $X_i$  extra-pair offspring sired by male  $i$ ), and then recalculated  $\text{Prop}_{\text{Full-sibs}}$  and  $\text{Prop}_{\text{Half-sibs}}$  for each female. To elucidate mechanisms underlying observed changes in sibship structures, we also calculated the total number of males that sired at least one of each female’s offspring given the social, genetic, and ‘distinct males’ pedigrees.

We fitted generalized linear mixed models (GLMMs) to test whether the sibship structures of females’ offspring (binomial error structures, weighted by  $N_{\text{sibs}}$ ), or the number of different sires (Poisson error structures), differed between the pedigrees. These models included fixed effects of pedigree (three levels) and random female identity effects. Goodness of fit ( $R^2$ ) for each model was assessed by the conditional coefficient of determination (Nakagawa and Schielzeth 2013). We used Tukey’s post-hoc tests to evaluate pairwise differences in  $\text{Prop}_{\text{Full-sibs}}$  and number of sires among the three pedigrees at  $\alpha = 0.05$ . We fitted generalized linear models (GLMs) to quantify how  $\text{Diff}_{\text{social-gen}}$  and  $\text{Diff}_{\text{lifelong\_monandry-gen}}$  varied with whether or not any of the female’s offspring were sired by an

extra-pair male (Supporting Information S1), or with the overall proportion of the female's lifetime offspring that were sired by an extra-pair male (i.e., were extra-pair offspring, EPO).

To examine the effects of pre-reproductive mortality on realized sibship structures among breeding individuals, all the above analyses were implemented across each female's offspring that survived to banding, and across offspring that survived to age one year (recruits). Females that were still alive in 2016, or that produced  $\leq 1$  banded or  $\leq 1$  recruited offspring (meaning that  $N_{\text{sibs}} = 0$ ), were excluded from the respective analyses. Analyses for banded offspring were also repeated across the subset of females that produced  $\geq 2$  recruited offspring, thereby allowing direct comparison across offspring stages within females (Supporting Information S2). While our primary analyses focused on sibship structures among females' offspring, further analyses demonstrated similar structures among males' offspring (Supporting Information S3).

#### *Distribution of relationships among possible mates*

To quantify how changes in sibship structures resulting from extra-pair reproduction translated into differences in relationships among possible mates, we used annual censuses of all adults alive in each year during 2008–2015 (annual means of  $26.9 \pm 8.8\text{SD}$  females [range 13–38] and  $35.1 \pm 10.5\text{SD}$  males [range 20–56]) to generate all possible female-male pairs that could possibly have mated in each year, assuming no mating constraints (hereafter 'all possible matings'). We analyzed relationships from the female perspective; due to extra-pair reproduction a female could possibly mate with any male in the population. We compared the frequencies of all possible matings for each female in each year that comprised key relationships given the social and genetic pedigrees. These relationships comprised: fathers, full-brothers, and sons (1<sup>st</sup> degree relatives); grandfathers,



uncles, half-brothers, double first cousins (i.e., both parents of each mating individual are full-sibs), nephews, and grandsons (2<sup>nd</sup> degree relatives); and great-grandfathers, single first cousins, and great-grandsons (3<sup>rd</sup> 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 (4<sup>th</sup> 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 3<sup>rd</sup> 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 1<sup>st</sup> 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 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> 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

2012; Sinnwell et al. 2014; Bates et al. 2015; Scholz and Zhu 2015). Raw means are reported  $\pm 1SD$ .

## Results

### *Sibship structure of banded offspring*

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

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

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

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

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

#### *Sibship structure of recruited offspring*

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

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

1C,E). Meanwhile, mean  $\text{Prop}_{\text{Full-sibs}}$  was slightly higher for recruited offspring than for banded offspring across all three pedigrees (table 1D,F), but mean  $\text{Prop}_{\text{Full-sibs}}$  among recruited offspring was again lower given the genetic versus social pedigrees (table 1F). At the individual level, 46% (17/37) of females had lower  $\text{Prop}_{\text{Full-sibs}}$  given the genetic pedigree, while 51% (19/37) had no change and one female had higher  $\text{Prop}_{\text{Full-sibs}}$  (fig. 2D).  $\text{Diff}_{\text{social-gen}}$  was again greater in females with intermediate proportions of extra-pair offspring (fig. 3C), and the effects of extra-pair reproduction on recruit sibship structure were smaller than would be observed given lifelong monandry (fig. 3D, Supporting Information S1). Finally, the difference in  $\text{Prop}_{\text{Full-sibs}}$  given the genetic versus 'distinct males' pedigrees was no longer significant across recruited offspring (Tukey test, table 1F; fig. 2D).

#### *Distribution of relationships among possible mates*

There was a total of 8028 possible matings between adult females and males alive in each year during 2008–2015, spanning 114 females and 144 males. On average, there were 0.6 fewer possible matings between individual focal females and their full-brothers given the genetic versus social pedigrees, but 1.6 more possible matings with half-brothers (table 2). However the distributions of the within-female differences in the numbers of full- and half-brothers between the two pedigrees spanned zero, showing that some females had more full-brothers and/or fewer half-brothers given the genetic pedigree (table 2; fig. 4). This illustrates that patterns of extra-pair reproduction enacted by some female's ancestors increased rather than decreased the number of possible matings between focal females and full-brothers versus half-brothers.

On average, there were also fewer possible matings between females and their full uncles, nephews, double first-cousins and single first-cousins given the genetic versus social

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

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

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

#### *Distribution of relatedness among possible mates*

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

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

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

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

## Discussion

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

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



mean inbreeding rate (Webster et al. 1995, 2007; Freeman-Gallant et al. 2005; Schlicht and Kempenaers 2013). Such effects are often small, including in song sparrows (Lebigre et al. 2012, see also Karl 2008). However, such results do not preclude the possibility that extra-pair reproduction could substantially affect individual-level inbreeding risk. This is because the same overall variance in male reproductive success, but very different sibship structures and distributions of relationships and relatedness, can arise if individual males sire several offspring of one polyandrous female (i.e., generating full-sibs) or sire one offspring of several polyandrous females (i.e., generating paternal half-sibs).

### *Sibship structures*

It may seem inevitable that extra-pair reproduction resulting from simultaneous polyandry will reduce full sibships, as assumed by the basic IAH, and by Cornell and Tregenza's (2007) initial theoretical model. However our analyses illustrate that such effects arising within a natural mating system are not so straightforward. Comparison of the social and genetic song sparrow pedigrees showed that extra-pair reproduction did indeed increase the mean number of different males that sired individual females' offspring and hence reduce the mean proportion of full-sibships ( $\text{Prop}_{\text{Full-sibs}}$ ) and increase the mean proportion of maternal half-sibships ( $\text{Prop}_{\text{Half-sibs}}$ ) among females' lifetime banded offspring. However, such means mask substantial among-female variation, including cases where extra-pair reproduction increased rather than reduced  $\text{Prop}_{\text{Full-sibs}}$  (fig. 2B). Such patterns can result from non-independent extra-pair paternity when females produce numerous extra-pair offspring with the same male across broods (as indicated by fig. 3A,C), and/or if a female's extra-pair male from one brood becomes her socially-paired male for another brood (or vice versa). Further, comparisons with the hypothetical occurrence of lifelong monogamy showed that the

occurrence of social re-pairing across breeding attempts (i.e., sequential polyandry) already reduced the effects of simultaneous polyandry on sibship structures by ~26%. Selection for simultaneous polyandry stemming from the IIAH process might consequently be weaker given iteroparity and associated repairing than given semelparity and/or strict lifelong monogamy. Comparison with the hypothetical 'distinct males' pedigree showed that 68% of females would have had lower  $\text{Prop}_{\text{Full-sibs}}$  among their banded offspring in the absence of polygyny than given the observed pattern of polygyny defined by the genetic pedigree (fig. 2B). This implies that Cornell and Tregenza's (2007) theoretical formulation of the IIAH might overestimate indirect selection on polyandry arising in polygynandrous systems.

While simultaneous polyandry can clearly affect the sibship structure of females' conceived offspring, its consequences for inbreeding risk and other kin interactions ultimately depend on its effects on the sibship structure of offspring that survive to life-history stages when key interactions occur. In song sparrows, further comparisons of the genetic and social pedigrees showed that the effects of extra-pair reproduction on sibship structures were qualitatively similar, but subtly different, across recruited versus banded offspring (fig. 2). Most notably,  $\text{Prop}_{\text{Full-sibs}}$  for recruits no longer differed between the genetic and 'distinct males' pedigrees (table 1B,D vs F). These patterns imply that theoretical predictions regarding indirect selection on polyandry might, in some instances, be relatively robust to an assumption of no polygyny. However, such inferences from observed genetic and social pedigrees require the additional, and commonly violated, assumption that offspring survival to recruitment does not depend on paternity. In song sparrows, female extra-pair offspring are less likely to recruit than female within-pair offspring reared in the same brood (i.e., maternal half-sisters, Sardell et al. 2011), and extra-pair offspring of both sexes have lower survival and/or reproductive success than within-

pair offspring in other passerine birds (e.g., house sparrows, *Passer domesticus*, Hsu et al. 2014; coal tit, *Periparus ater*, Schmoll et al. 2009). Any small reduction in inbreeding among polyandrous females' offspring might therefore be further reduced by stochastic and/or deterministic variation in survival of offspring sired by different males. The ultimate consequences of polyandry for the expected frequency of close inbreeding and consequent fitness among descendants of polyandrous females in natural populations may therefore be smaller than predicted by models that do not consider differential offspring survival (e.g., Cornell and Tregenza 2007), and estimated in laboratory populations where variation in survival may be minimized (e.g., Power and Holman 2014). Future theoretical and empirical studies considering the evolutionary causes and consequences of polyandry arising through its effects on sibship structures should therefore consider such effects within the context of the overall mating system, including natural variation in paternity arising through polygyny and iteroparity, as well as differential offspring survival.

#### *Distributions of relationships and relatedness*

The effects of simultaneous polyandry on sibship structures among recruited offspring are likely to alter the frequencies of diverse types of half-relatives versus full-relatives spanning multiple (overlapping) generations, thereby altering any individual's overall potential for inbreeding or interacting with different types of relatives. The form and magnitude of indirect selection on polyandry stemming from the IIAH process might then differ from that predicted in restricted situations with within-brood mating and non-overlapping generations (e.g., Cornell and Tregenza 2007). Indeed, our comparisons of the social and genetic song sparrow pedigrees showed that extra-pair reproduction reduced the potential for inbreeding among different degrees of full-relatives and increased the potential for

inbreeding among more distant half-relatives, but this change was not consistent across all individual females and types of relationship (table 2, fig. 4, Supporting Information S4). Similarly, simultaneous polyandry reduced the mean kinship between females and their possible mates, most notably with mates that would otherwise have been 1<sup>st</sup> degree relatives (fig. 5). These overall conclusions remained unchanged when all possible matings among 1<sup>st</sup> degree relatives were excluded (Supporting Information S5), thereby considering a scenario where individuals actively avoid inbreeding with 1<sup>st</sup> degree relatives (as observed in other species, e.g., Stow and Sunnucks 2004; Gerlach and Lysiak 2006; Archie et al. 2007; Brouwer et al. 2011; Ihle and Forstmeier 2013). Overall, the individual-level differences in relatedness among possible mates stemming from simultaneous polyandry resulted in fewer possible matings at intermediate and higher  $k$  (i.e., among closely related pairs), and more possible matings at lower but non-zero  $k$  (fig. 6).

Such conclusions rely on the implicit assumptions of our study design that mating decisions and recruitment are unaffected by pedigree structure, and hence that there is no active inbreeding avoidance or differential survival by within-pair versus extra-pair offspring. Indeed, song sparrows do not actively avoid inbreeding through social pairing or extra-pair reproduction (Keller and Arcese 1998; Reid et al. 2015a). However, to further consider the implications of such assumptions, we conducted additional analyses to quantify effects of polyandry on relatedness within a single cohort (Supporting Information S6). Such analyses have the advantage that they do not require any assumptions regarding patterns of mating or survival in the absence of extra-pair reproduction, but the disadvantage that they eliminate effects of polyandry on relatedness generated across multiple (overlapping) generations. These analyses also showed reduced potential for close inbreeding ( $k \geq 0.25$ ) given the genetic versus social pedigrees, but no reduction in more distant inbreeding

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

### *Implications*

Our results imply that the magnitude and direction of indirect selection on simultaneous polyandry stemming from the intrinsic consequences of such polyandry for distributions of  $k$  among offspring, and hence grand-offspring  $f$ , will depend on the shape of the relationship between fitness and  $f$  (i.e., the form of inbreeding depression). Given multiplicative effects of deleterious recessive alleles, inbreeding depression is expected to be log-linear, such that the reduction in fitness decreases with increasing  $f$  (fig. 7, Morton et al. 1956; Charlesworth and Charlesworth 1987; Charlesworth and Willis 2009). Counter-intuitively, under these conditions, polyandry might in fact cause a net decrease in mean fitness, even though it slightly reduces mean grand-offspring  $f$ . Intrinsic indirect selection on polyandry stemming from ‘indirect inbreeding avoidance’ might then impede rather than facilitate polyandry evolution. However, given epistatic or threshold effects, inbreeding depression could be weak up to some value of  $f$  above which fitness decreases markedly (e.g., fig. 7, Charlesworth and Willis 2009). Given such threshold effects, the long-term relative frequency of alleles underlying polyandry could then increase due to the reduced frequency of matings among close relatives and the resulting net increase in mean offspring fitness that would arise despite an increased frequency of matings among more distant relatives.

The form of inbreeding depression is very difficult to quantify in natural populations, not least because close inbreeding often occurs infrequently and may be more likely in high-

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

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## 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 1<sup>st</sup> degree relatives
- Supporting Information S6:** Distribution of relatedness within cohorts

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

Response variable	Pedigree	Mean ( $\pm$ SD)	Median (Range)	df	R <sup>2</sup>	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 <sub>Full-sibs</sub>	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 <sub>Full-sibs</sub>	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 <sub>Full-sibs</sub>	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



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

Relationship		Social pedigree	Genetic pedigree	Mean Difference	Z (p)
1 <sup>st</sup> 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)	<b>-0.60 ±1.05</b> <b>(-6–1)</b>	<b>2.9</b> <b>(0.004)</b>
	Son	0.90 ±1.85 (0–11)	0.90 ±1.85 (0–11)	0.00 ±0.00 (0–0)	0.0 (1.00)
2 <sup>nd</sup> 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)	<b>-0.39 ±0.75</b> <b>(-4–1)</b>	<b>3.4</b> <b>(&lt;0.001)</b>
	Half-brother	0.96 ±1.71 (0–10)	2.54 ±2.87 (0–12)	<b>+1.59 ±2.17</b> <b>(-1–11)</b>	<b>5.7</b> <b>(&lt;0.001)</b>
	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)	<b>-0.75 ±2.12</b> <b>(-14–1)</b>	<b>2.2</b> <b>(0.03)</b>
	Grandson	0.37±1.20 (0–7)	0.39 ±1.48 (0–12)	+0.02 ±0.59 (-2–5)	0.4 (0.69)
3 <sup>rd</sup> 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)	<b>-1.57 ±2.44</b> <b>(-13–2)</b>	<b>5.5</b> <b>(&lt;0.001)</b>
	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 <sup>th</sup> Degree	Half-uncle	1.08 ±1.75 (0–8)	2.00 ±2.30 (0–10)	<b>+0.92 ±2.09</b> <b>(-6–6)</b>	<b>3.6</b> <b>(&lt;0.001)</b>
	Half-single first cousin	2.46 ±3.17 (0–17)	5.39 ±6.44 (0–35)	<b>+2.94 ±5.53</b> <b>(-13–28)</b>	<b>4.1</b> <b>(&lt;0.001)</b>
	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)

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

Relationship given social pedigree	$k_{SOC}$	$k_{GEN}$	Mean difference	$Z$ ( $p$ )
1 <sup>st</sup> degree ( $n = 378$ , ♀ = 104)	0.314 $\pm$ 0.034 (0.261–0.472)	0.263 $\pm$ 0.067 (0.031–0.368)	<b>-0.051<math>\pm</math>0.07</b> <b>(-0.301–0.062)</b>	<b>5.7</b> <b>(&lt;0.001)</b>
2 <sup>nd</sup> degree ( $n = 453$ , ♀ = 99)	0.197 $\pm$ 0.032 (0.147–0.361)	0.157 $\pm$ 0.042 (0.03–0.338)	<b>-0.041<math>\pm</math>0.045</b> <b>(-0.165–0.128)</b>	<b>7.2</b> <b>(&lt;0.001)</b>
3 <sup>rd</sup> degree ( $n = 297$ , ♀ = 78)	0.141 $\pm$ 0.026 (0.094–0.255)	0.112 $\pm$ 0.029 (0.057–0.198)	<b>-0.033<math>\pm</math>0.031</b> <b>(-0.14–0.063)</b>	<b>6.7</b> <b>(&lt;0.001)</b>
4 <sup>th</sup> degree ( $n = 629$ , ♀ = 97)	0.125 $\pm$ 0.022 (0.084–0.174)	0.108 $\pm$ 0.032 (0.031–0.179)	<b>-0.017<math>\pm</math>0.026</b> <b>(-0.099–0.06)</b>	<b>4.3</b> <b>(&lt;0.001)</b>
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)

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

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

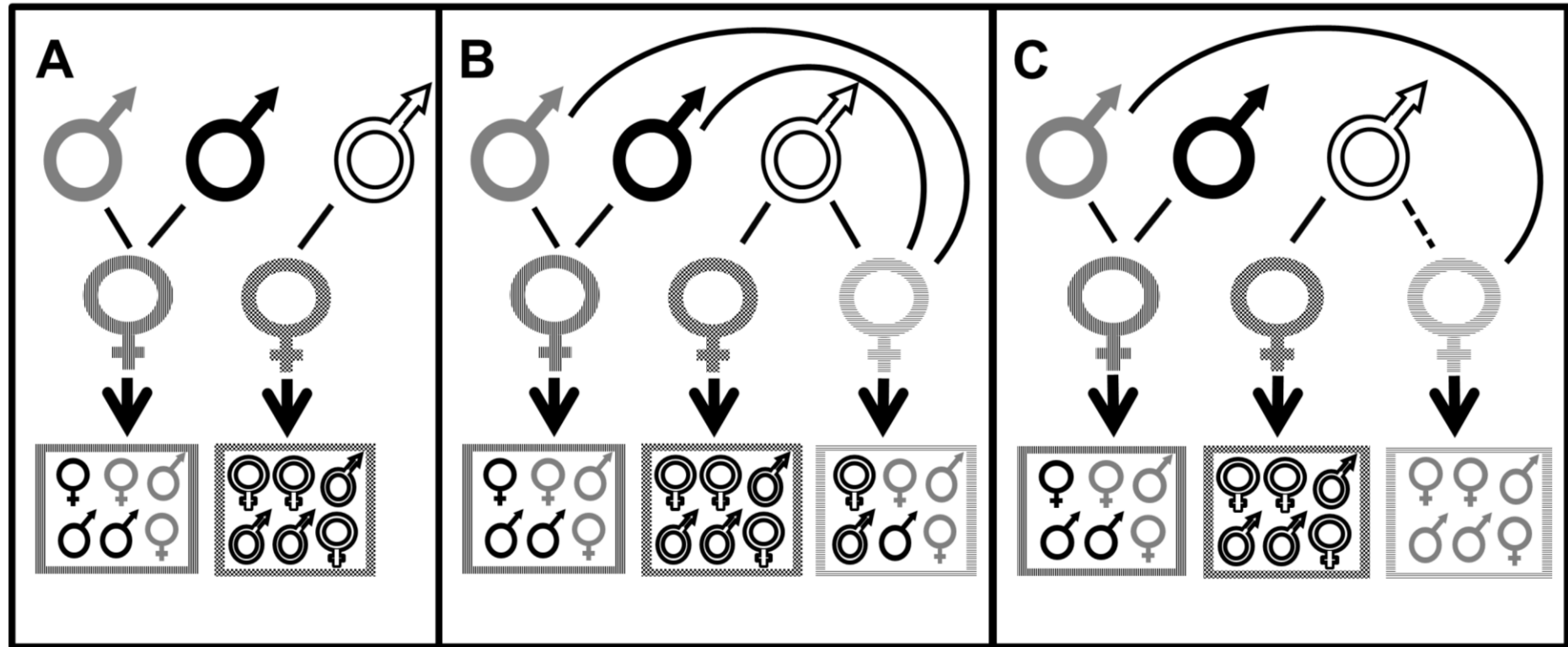
**Figure 4:** Distributions of the difference in the number of possible matings at each focal relationship level (listed in table 2) across 114 females given the genetic versus social pedigrees. Negative and positive values respectively indicate decreases and increases in the number of possible matings 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).

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

**Figure 6:** Overall distributions of pairwise coefficients of kinship across all possible song sparrow matings, calculated from the social pedigree (black bars) or genetic pedigree (white bars), with grey bars denoting overlap between the two distributions. Dotted, dashed, and dot-dashed lines depict kinship values equivalent to first cousin (0.0625), half-sib (0.125), and full-sib (0.25) matings, respectively. Box plots further visualize the distribution of  $k$  given each pedigree, where box lines represent the median, upper and lower quartiles, whiskers demarcate 1.5 $\times$  the interquartile range, and '+' represents the mean. Mean  $k_{SOC}$  was  $0.101 \pm 0.069$  (median 0.0914, range 0.000–0.472) and mean  $k_{GEN}$  was  $0.094 \pm 0.065$  (median 0.087, range 0.00–0.421), corresponding to a small but statistically significant mean decrease of  $-0.006 \pm 0.040$  (median -0.003, range -0.301–0.251, Wilcoxon signed rank test:  $Z = 18.95$ ,  $p < 0.001$ ).

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

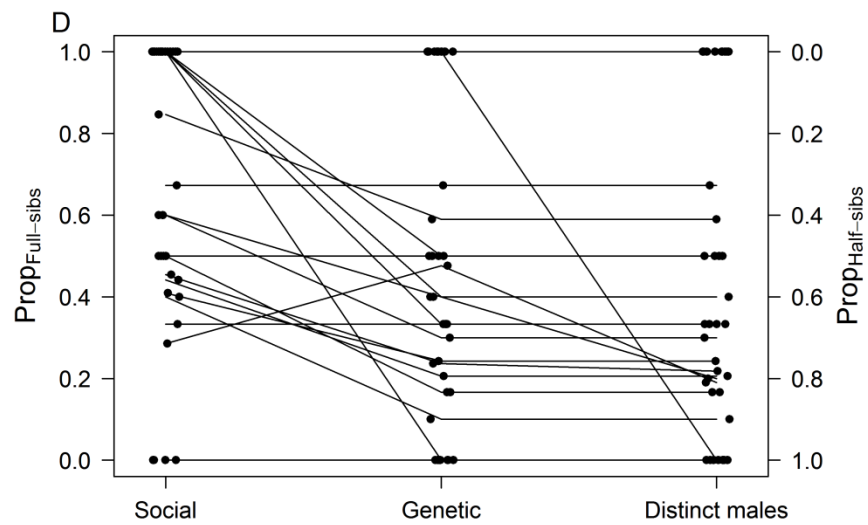
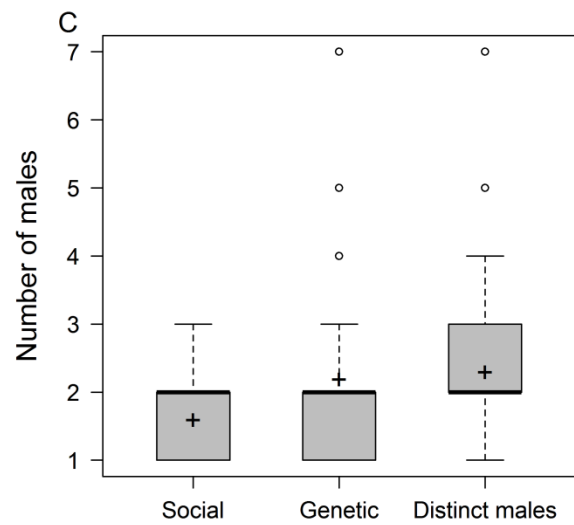
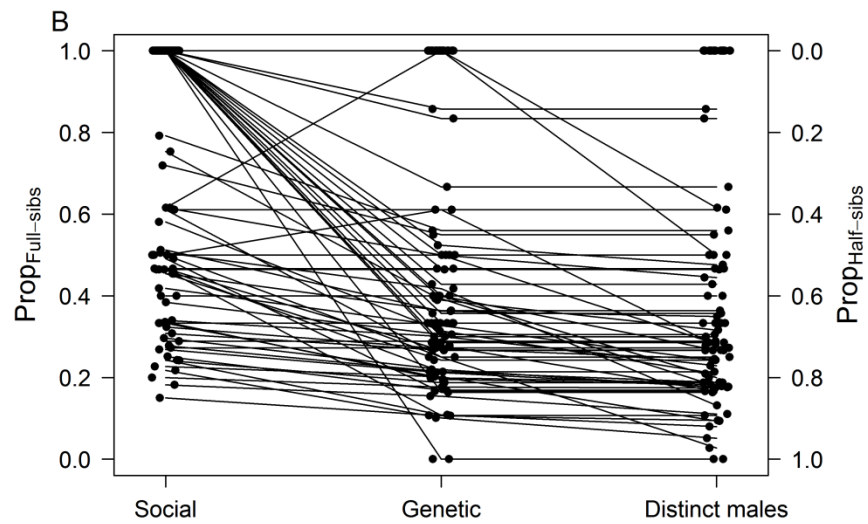
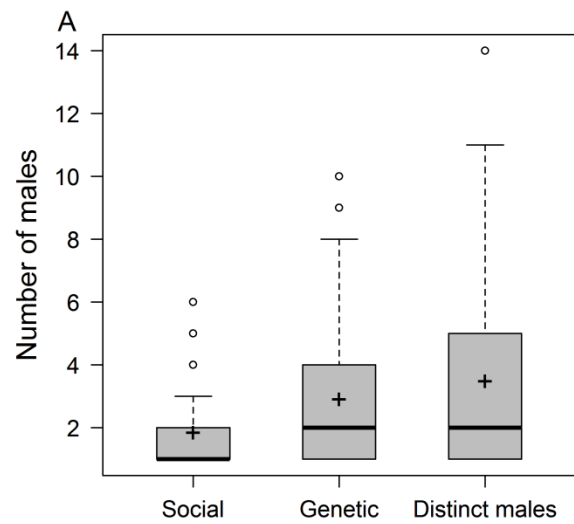
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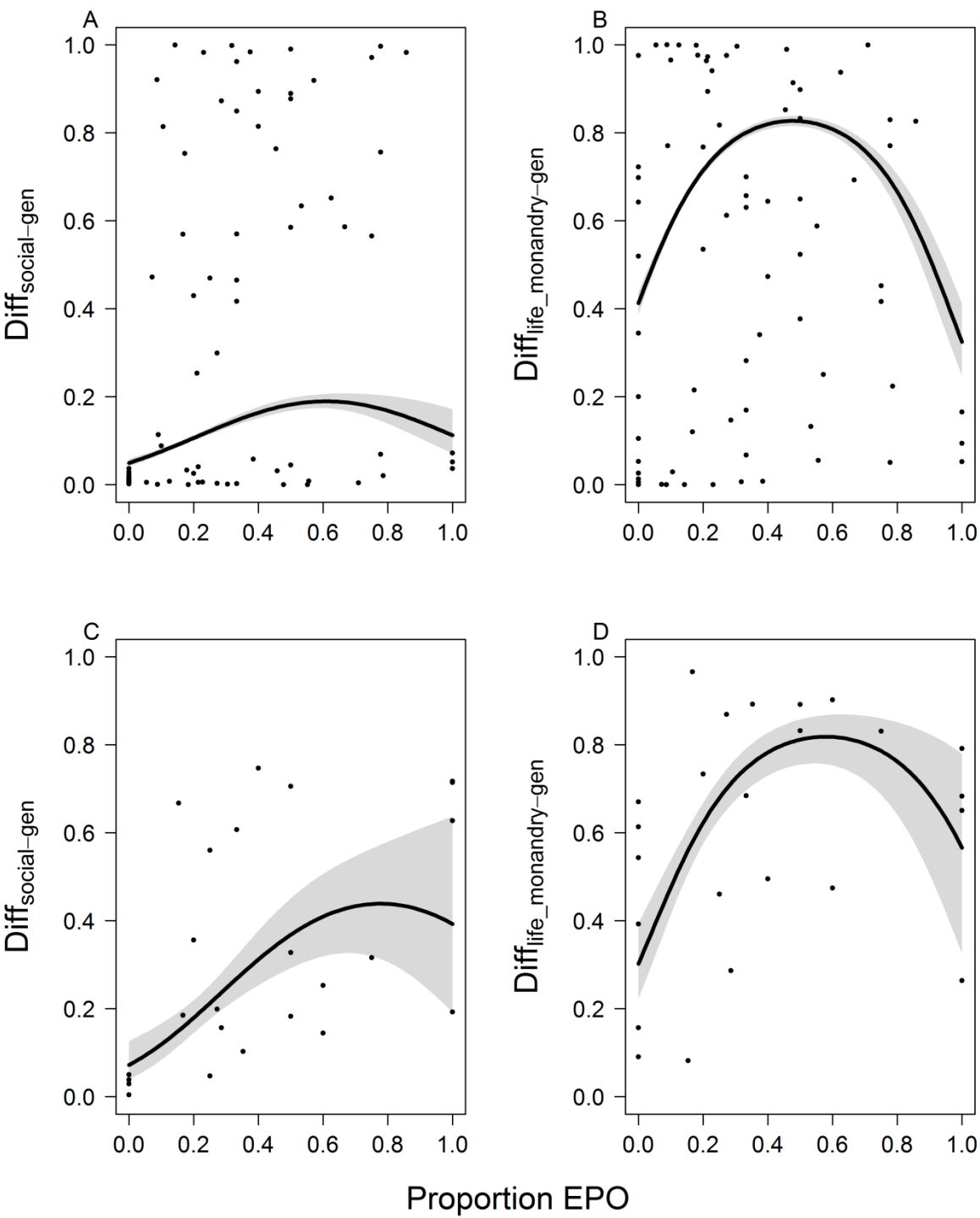
1066 **Figure 1**





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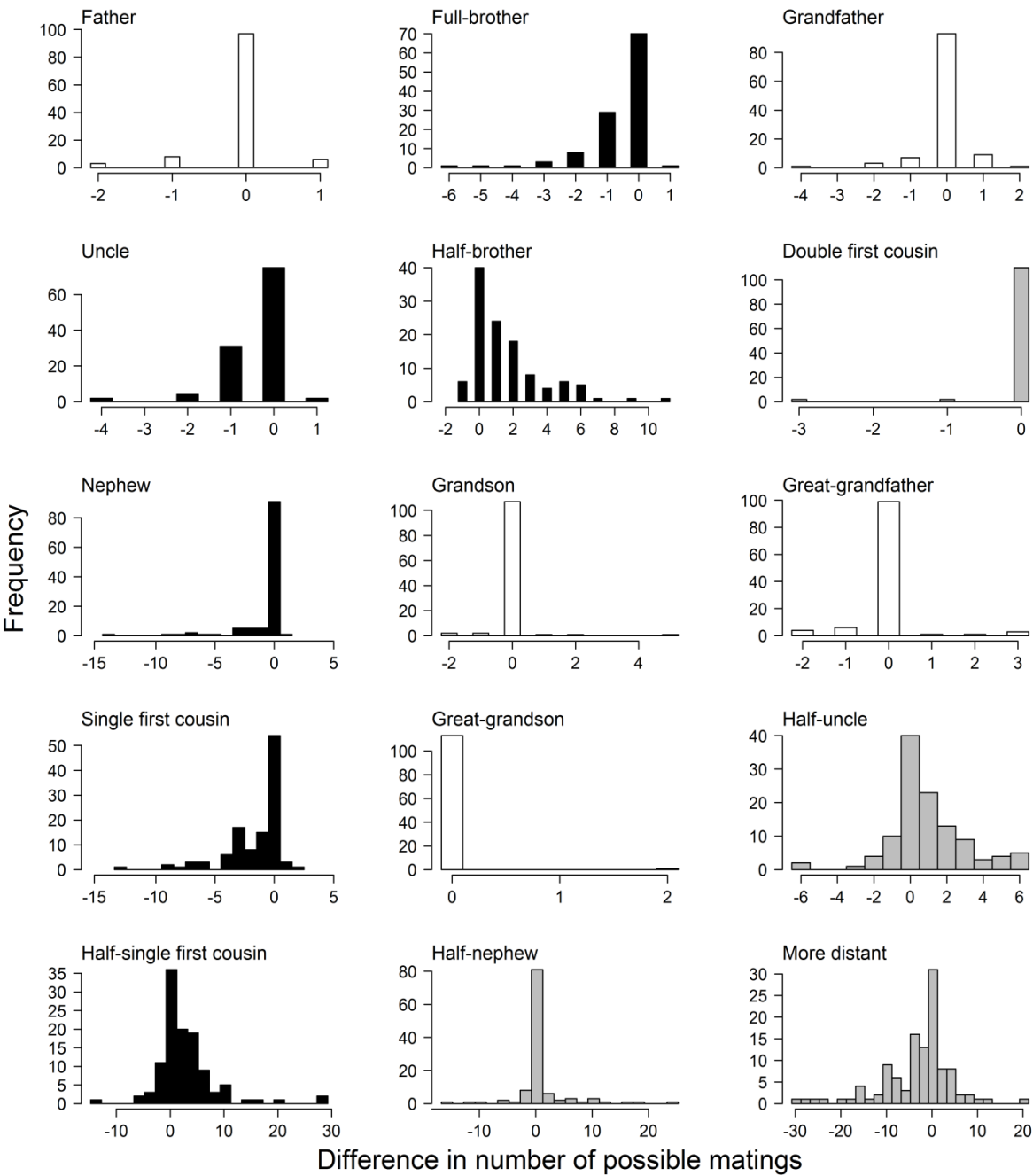
1068 **Figure 2**



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1071 **Figure 3**

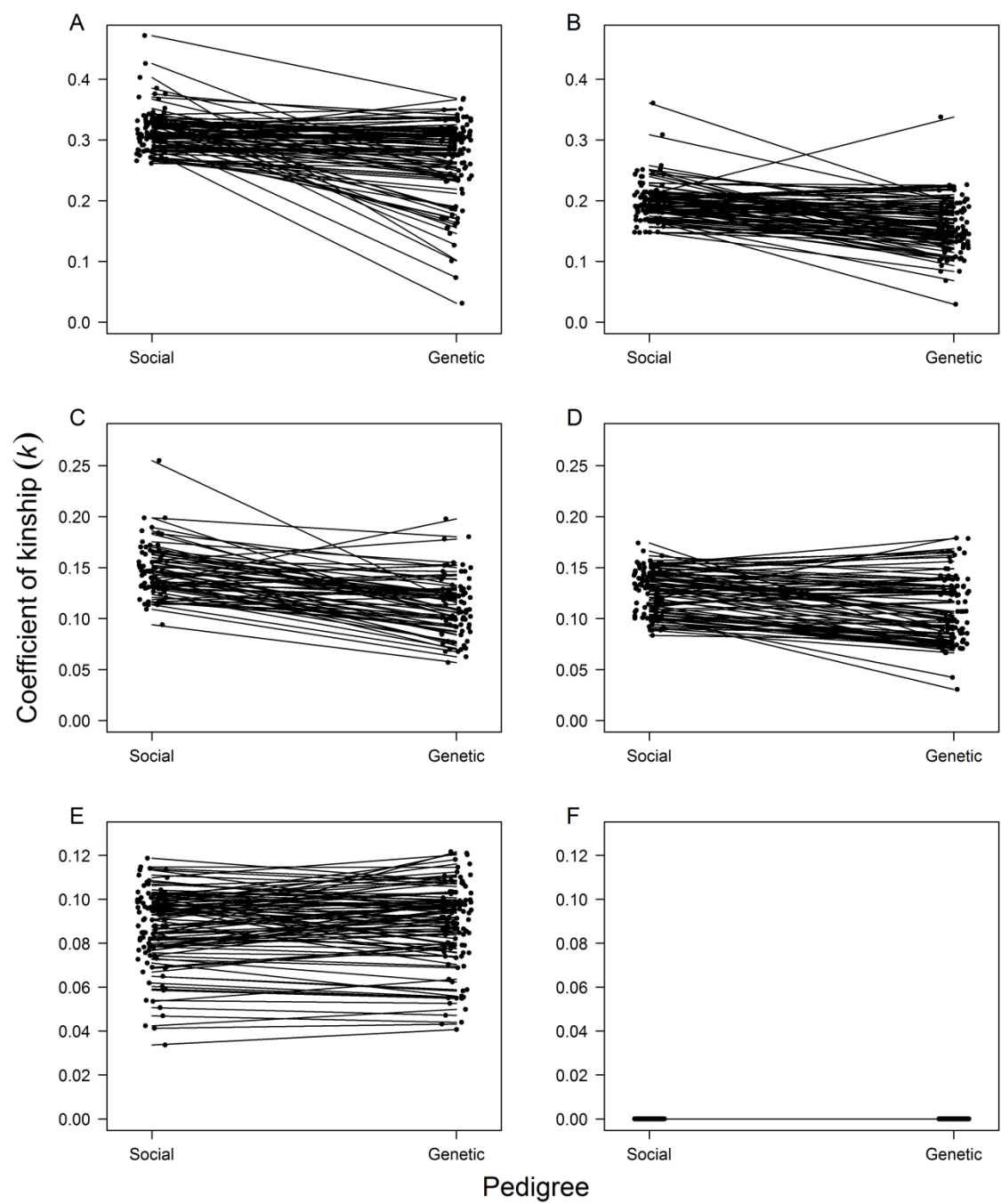
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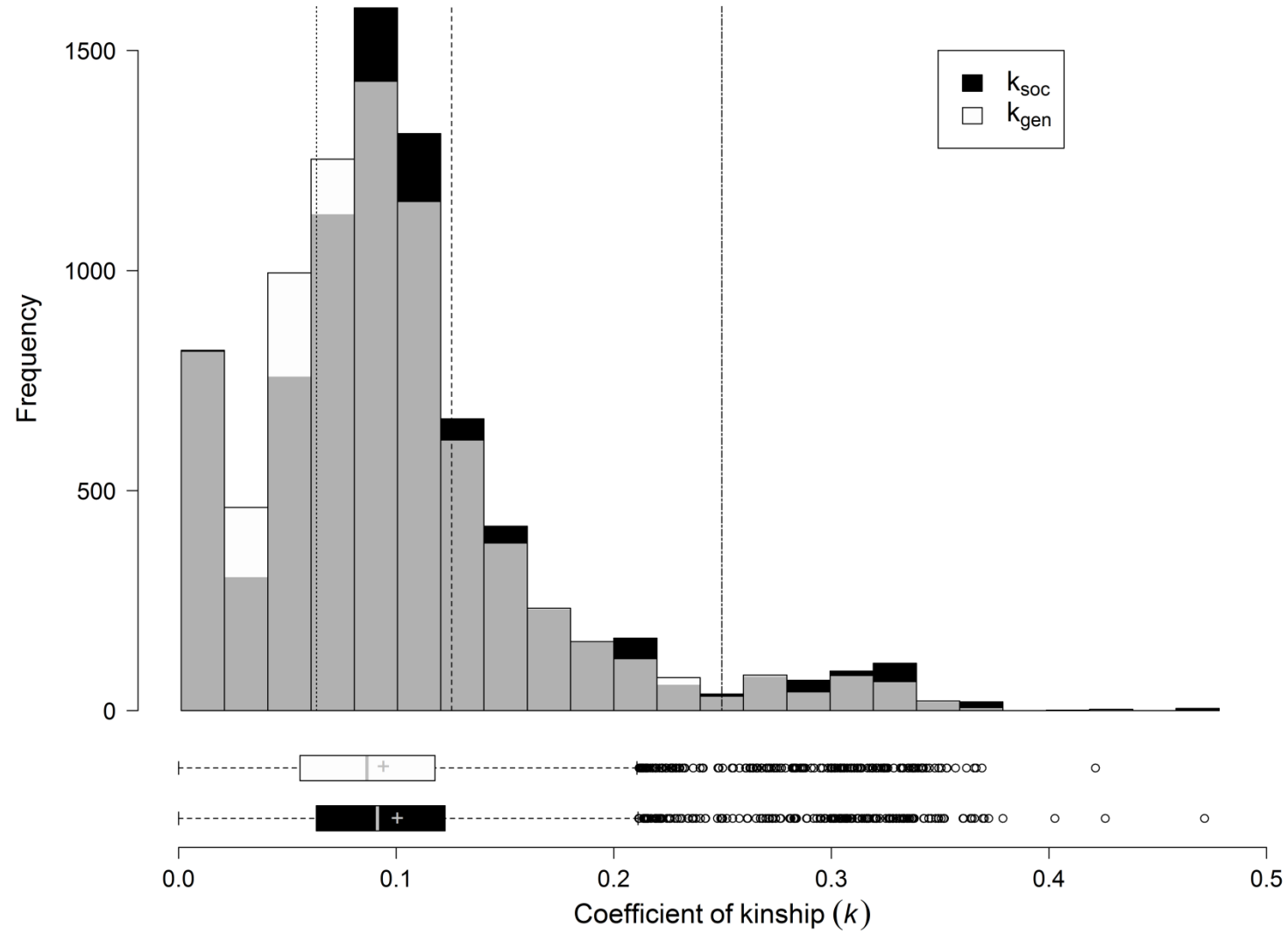
1074 **Figure 4**

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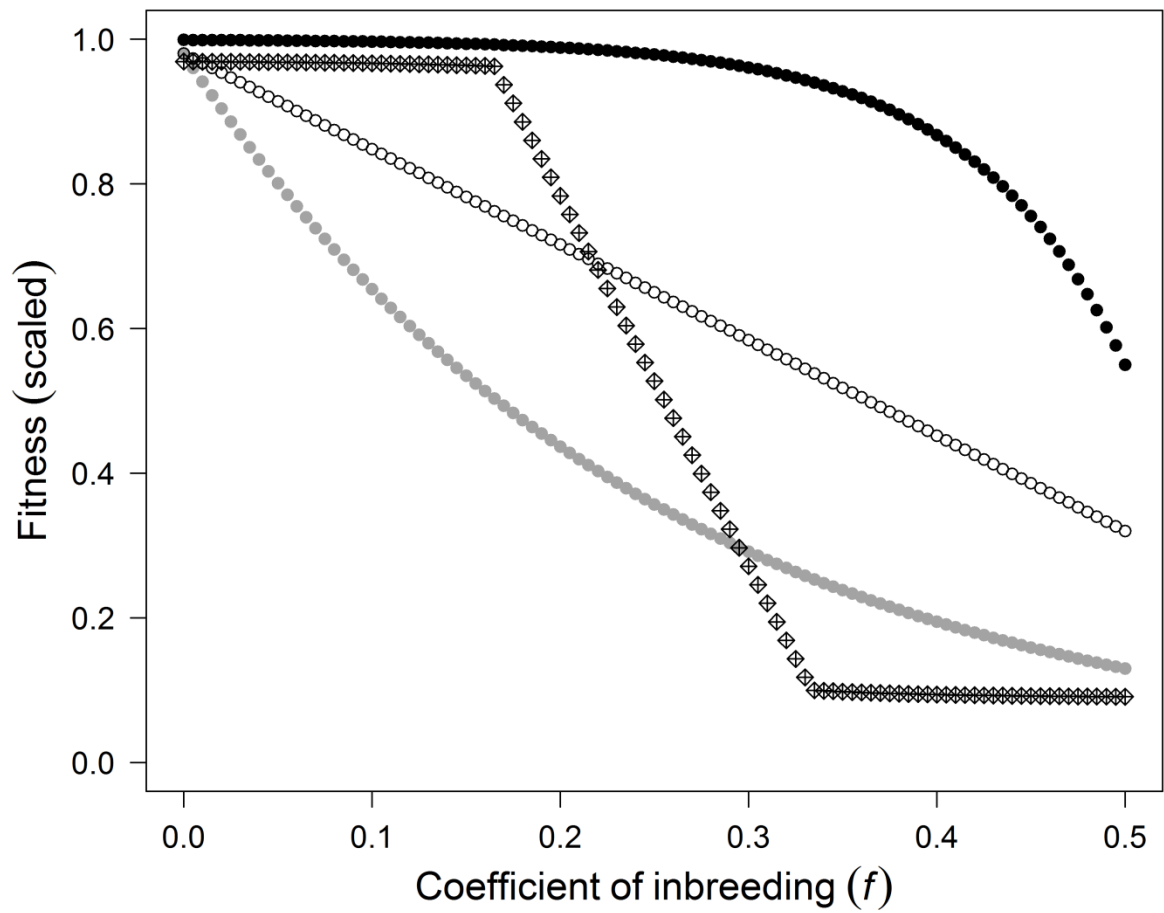
1077 **Figure 5**



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1079 **Figure 6**

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1082 **Figure 7**