

The evolution of sexual imprinting in socially monogamous populations

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Abstract Sexual imprinting is a common mechanism of mate preference learning. It is thought to influence how traits evolve and in some cases to promote speciation. Recently there has been increasing interest in how sexual imprinting itself evolves. Theoretical work on polygynous mating systems predicts that females will evolve paternal imprinting, which means they learn to prefer phenotypes expressed by their fathers. In nature however, females of some species learn to prefer phenotypes expressed by their mothers instead. We used a dynamical systems model and tools from adaptive dynamics to study how sexual imprinting evolves in species with socially monogamous mating systems. We considered cases in which the target trait for imprinting is under viability selection but is not a reliable signal of paternal investment. Thus, the target trait signals the genetic benefits rather than the parental care benefits of mate choice. When mating is socially monogamous and there is some extra-pair paternity, we show that maternal imprinting can be favored over paternal imprinting. Counterintuitively, females often become choosier when selecting social partners in systems where extra-pair mating is more frequent. That is, females may be more selective when choosing social partners that will sire a smaller percentage of their offspring. Our results offer new testable hypotheses, and advance our understanding of the mechanisms that drive the evolution of mate choice strategies in nature [*Current Zoology* 61 (6): 1043–1061, 2015].

Keywords Sexual imprinting, Mate preference learning, Monogamy, Extra-pair mating, Evolution, Model

Learned behaviors can have profound effects on evolution (Wade and Pruett-Jones, 1990; Danchin et al., 2004; Beltman and Metz, 2005; Servedio et al., 2009; Verzijden et al., 2012). One type of learned behavior that is drawing increasing interest for its potential to influence evolution is sexual imprinting (Laland, 1994; Aoki et al., 2001; Verzijden et al., 2005; Kozak et al., 2011; Yeh and Servedio, 2015). Sexual imprinting occurs when an individual learns a mate preference by observing the phenotype (i.e., the target trait) of some other individual (i.e., a model) in its population. Imprinted mate preferences are usually learned before sexual maturity, and are not learned from mating or courting experience (Immelmann, 1975).

Sexual imprinting in nature is both widespread and common. It is found in diverse groups of vertebrates including fish (Verzijden et al., 2008; Kozak and Boughman, 2009), birds (ten Cate and Vos, 1999), and mammals (Kendrick et al., 1998), and also in invertebrates (Hebets, 2003; Westerman et al., 2012). In birds, where it has been most frequently studied, sexual imprinting has been found in almost every species in which it has been sought (but see Saether et al., 2007):

about half of all avian orders include at least one species where sexual imprinting has been identified (ten Cate and Vos, 1999). Because it has not yet been studied in most species, sexual imprinting may be even more common than is currently believed.

Sexual imprinting can strongly influence evolution. Sexual selection caused by imprinting can either magnify or oppose natural selection, speeding up the fixation of advantageous traits or maintaining disadvantageous traits in populations (Kalmus and Maynard Smith, 1966; Laland, 1994; Aoki et al., 2001). Sexual imprinting can also facilitate speciation (Verzijden et al., 2005). Imprinting on parents promotes species-specific mating (e.g., in sheep and goats; Kendrick et al., 1998) and can maintain sexual isolation between sister species where no post-zygotic isolation is present (Verzijden and ten Cate, 2007; Kozak et al., 2011). Theoretical studies have investigated whether sexual imprinting alone can be responsible for speciation (O'Donald, 1960; Kalmus and Maynard Smith, 1966; Verzijden et al., 2005; Yeh and Servedio, 2015). Although other factors, such as a geographic isolation or post-zygotic barriers, are probably necessary to achieve full reproductive isolation,

Received July 9, 2015; accepted Sep. 26, 2015.

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imprinting can nevertheless push reproductive isolation to near completion (Laland, 1994).

Three distinct modes of sexual imprinting have been distinguished based on the identity of the imprinting model (Verzijden et al., 2005). In two of these, *maternal* and *paternal* imprinting, individuals imprint on their parents, while in so-called *oblique* imprinting individuals imprint on unrelated models. Theoretical studies have shown that different imprinting modes can lead to different evolutionary and speciation outcomes (Verzijden et al., 2005; Yeh and Servedio, 2015). Sexual imprinting is also characterized by its strength. Imprinting strength is a measure of how likely an individual is to reject a potential mate with a phenotype other than the one that it has learned to prefer. The imprinting strength that evolves in a system can depend on the imprinting mode (Chaffee et al., 2013).

Sexual imprinting evolves due to the role of the imprinting set (Tramm and Servedio, 2008). The imprinting set is the set of all models used for imprinting. For example, the paternal imprinting set is the set of fathers, and the maternal imprinting set is the set of mothers. If an imprinting set has greater heritable fitness than the population as a whole, then individuals that imprint on that set will select fitter mates and obtain fitter alleles for their offspring. Thus, imprinting will be favored by selection. Disequilibria between learned preferences and heritable traits under natural selection (i.e., phenogenotypic disequilibria) can also promote the evolution of sexual imprinting. This occurs when individuals that imprint on fit phenotypes are more likely to express fit phenotypes themselves (i.e., when phenogenotypic disequilibria are positive). In this case, natural selection increases the proportion of individuals imprinted on fitter phenotypes, and amplifies the positive effect of sexual imprinting. In maternal and paternal imprinting, positive phenogenotypic disequilibria arise because individuals can inherit the same phenotypes that they learn to prefer. If one imprinting mode generates a more positive phenogenotypic disequilibrium than another, then imprinting by that mode will offer a greater fitness advantage. The effect of phenogenotypic disequilibria on the evolution of imprinting is usually believed to be small, and in past models it has been noticed only when different imprinting modes have imprinting sets with identical fitnesses (Tramm and Servedio, 2008).

Target traits can be under natural selection, and in the chosen sex they are also under sexual selection. Thus, in systems with female choice, the target trait is under stronger selection in males than in females. As a result,

fathers carry fitter target trait alleles than mothers or unmated males, and theory predicts that paternal imprinting should be the most advantageous imprinting mode (Tramm and Servedio, 2008). Chaffee and colleagues (2013) predicted that the strength of paternal imprinting should evolve towards perfect imprinting, where a female always rejects a male that does not express her preferred phenotype, unless the evolution of imprinting strength is limited by costs or by sensory, neurological, ecological, or social constraints. These results suggest that strong paternal imprinting should be the rule in nature. Nonetheless, in some systems, females sexually imprint on their mothers rather than on their fathers (Grant and Grant, 1997; Witte et al., 2000; Burley, 2006; Verzijden et al., 2008).

Past models of the evolution of sexual imprinting assumed that mating is polygynous (i.e., females bear the offspring of only one male but males can father broods with multiple females) and that offspring can accurately identify both parents. Both of these assumptions may be violated in nature. For example, in many species, mated pairs form social bonds, and most mating occurs within bonded pairs (Reichard and Boesch, 2003). Such species often provide biparental care, which may facilitate paternal imprinting because it means that fathers are readily identifiable to act as models. However, in most species with pair bonds, some portion of the offspring is sired by extra-pair males (Griffith et al., 2002). This means that some offspring will recognize their mother's social partner as their father, but will be genetically descended from different males. In birds that form pair bonds (more than 90% of passerines), rates of extra-pair paternity range from 0% in some species (Griffith et al., 2002) to 72% in superb fairy wrens *Malurus cyaneus* (Mulder et al., 1994; Double and Cockburn, 2000). Thus, in some paternally imprinting species, a large proportion of offspring may imprint on unrelated males.

Extra-pair paternity may affect the evolution of sexual imprinting for two reasons. First, extra-pair paternity reduces the quality of the paternal imprinting set, because the paternal imprinting set is not identical to the set of successful fathers. Second, in species where both males and females express the target trait, extra-pair paternity weakens phenogenotypic disequilibria under paternal imprinting. This is because the daughters of extra-pair mates do not inherit the target trait alleles on which they have imprinted, and so are less likely to be imprinted on the same phenotype they express. For both of these reasons, paternal imprinting may be less likely

to evolve in systems with extra-pair paternity than in systems where offspring imprint on their biological fathers.

Here, we used a dynamical systems model to simulate different sexual imprinting strategies competing in a population with female mate choice, social monogamy, and extra-pair mating. We assumed that the target trait is expressed by both sexes (i.e., is sexually monomorphic) and does not signal the parental care offered by a male. In some birds, traits such as beak shape, beak color and plumage color meet these assumptions, and these can be target traits for imprinting (Grant and Grant, 1997; Witte and Sawka, 2003; ten Cate et al., 2006; Witte and Caspers, 2006). To study how imprinting evolves, we analyzed our model using tools borrowed from adaptive dynamics. We asked 1) how does the evolutionarily stable imprinting strength under different imprinting modes depend on the rate of extra-pair paternity and on the strength of viability selection acting on the target trait, and 2) which imprinting modes should we expect to see in socially monogamous systems in nature.

1 Materials and Methods

1.1 The Model

Genetic architecture

We modeled a haploid, sexually reproducing population. Each member of the population has a genome comprised of two independently assorting diallelic loci: a target trait locus and an imprinting strategy locus. We assumed that the population is large enough that stochasticity is unimportant, and we tracked genotype frequencies rather than individuals over time. We formalized the model in Appendix 1.

The target trait locus houses allele T or t , which confer phenotypes T and t respectively. The target trait is expressed by both sexes, and is under sexually monomorphic viability selection. Choosy females use the target trait to assess potential mates. In Darwin's finches, females assess potential mates in part by their beak shape (Grant and Grant, 1997), and thus beak shape is an example of a target trait. Recent work suggests that much of the variation in beak shape in Darwin's finches may be controlled by a single locus (Lamichhaney et al., 2015).

The imprinting strategy locus houses allele S or s , which confer imprinting strategies S and s , respectively, to females. Because males are not choosy, they do not express imprinting strategies. A female's imprinting strategy determines 1) her imprinting mode, 2) her imprinting strength for social partners, and 3) her im-

printing strength during extra-pair mating. The imprinting mode determines whether a female learns to prefer the target phenotype expressed by her mother (maternal imprinting), her father (paternal imprinting) or a randomly selected male from her parents' generation (oblique imprinting). The imprinting strength for social partners (or extra-pair mates) determines the probability that a female rejects a potential social partner (or extra-pair mate) with a phenotype other than the one she prefers. Thus, imprinting strength is a measure of choosiness (Kopp and Hermisson, 2008). Imprinting strategies S and s differ in only one of these three attributes (i.e., mode, imprinting strength for social partners, or imprinting strength for extra-pair mates).

In nature, modes and strengths of imprinting may be controlled by different loci. We assumed that mutations at all loci affecting the imprinting strategy are rare relative to the strength of selection, so that each mutation is either fixed or eliminated before a new one arises anywhere in the genome. Thus, at any given time, only one locus affecting the imprinting strategy is polymorphic, and that locus is diallelic. Therefore, although there may be many potential imprinting strategy alleles, we only need to track one diallelic imprinting strategy locus in our model. We note that our model would be the same if we assumed that imprinting were controlled by a single locus with an infinite number of possible alleles that arise due to rare mutations. Our model assumes that the imprinting mode is a discrete phenotype that can be changed by a single mutation. This serves as a working assumption until empirical information on the genetics of mate preference learning becomes available.

Each male in the population is fully characterized by his genotype (ST , St , sT or st). However, in addition to her genotype, each female has a non-genetic phenotype that she learns by imprinting. Females with imprinted phenotype P prefer males with target phenotype T and females with phenotype p prefer males with target phenotype t . For example, a paternally imprinting female whose father has phenotype T will acquire imprinted phenotype P . Each female is fully characterized by her phenogonotype (STP , STp , StP , Stp , sTP , sTp , stp and stp). We tracked the frequencies of male genotypes and female phenogonotypes through generations.

Model dynamics

The population in our model experiences discrete generations that comprise viability selection and mating. Viability selection acts on the target trait. We defined phenotype t as the less viable phenotype. We assumed that all individuals with phenotype T survive to adult-

hood, and that individuals with phenotype t survive to adulthood with probability $(1 - c_t)$. Thus, c_t captures the fitness effect of the t allele due to viability selection alone (i.e., before sexual selection). We assumed that alleles S and s have no direct effect on viability. Thus, imprinting strategies do not carry fixed costs (*sensu* Otto et al., 2008). Previous work has shown that fixed costs prevent the evolution of sexual imprinting (Chaffee et al., 2013).

After viability selection, social pairs form. We assumed that there is a 1:1 sex ratio and social pair formation occurs in rounds. In each round, 10% of the unpaired females in the population meet unpaired males. Meetings are random with respect to male genotype and female phenogroup. Each female assesses the male she has met and either accepts or rejects him as a social partner. If the male expresses her preferred phenotype (i.e., target phenotype T for females with imprinted phenotype P , or target phenotype t for females with imprinted phenotype p), she accepts him. Otherwise, she accepts him with probability $\exp(-\alpha_{SP})$, where α_{SP} is her strength of imprinting for social partners. Females that accept males and males that are accepted are removed from the pool of available social partners. We modeled 50 rounds of social pair formation per generation. Thus, each female has the opportunity to assess an average of 5 males. Individuals that have not found social partners after 50 rounds do not form social pairs. We considered longer periods of social pair formation in Appendix 2.

We assumed that every female that forms a social pair has the same expected number of offspring, independent of her social partner's genotype and her phenogroup, and that unpaired females cannot successfully raise offspring. This is reasonable if males provide necessary direct benefits (e.g., parental care) to the offspring of their social partners, and if a male's target phenotype is not a signal of the direct benefits he provides. Failure to find a social partner carries heavy costs for both females and males. Females that do not accept social partners have no offspring, and males that are not accepted have offspring only if they achieve extra-pair matings. In our model, the cost of choosiness is realized only when females fail to find social partners. In nature choosiness may also be costly if choosier individuals find social partners later, and if individuals that find social partners later produce fewer offspring. This implementation of choosiness costs has been studied elsewhere (Chaffee et al., 2013).

If a female produces offspring, some of those offspr-

ing may be fathered by males other than her social partner through extra-pair mating. As with social partners, females search for extra-pair mates in rounds. In each round, each female encounters one male from the population at random. This male may be part of a social pair or he may be unpaired. If the male expresses her preferred phenotype, she mates with him. Otherwise, she mates with him with probability $\exp(-\alpha_{EP})$, where α_{EP} is her strength of imprinting for extra-pair mates. Females that choose extra-pair mates are removed from the pool of females seeking extra-pair mates. We modeled five rounds of extra-pair mate search per generation. Each female that chooses an extra-pair mate during these five rounds has a portion u of her offspring sired by that male. Each female that does not accept an extra-pair mate has all of her offspring sired by her social partner. Thus, failure to accept an extra-pair mate does not reduce the number of offspring a female produces. In nature, socially paired males may have less time than unpaired males to seek copulations with paired females. Alternatively, if females copy the mate choice of others, socially paired males might have greater extra-pair mating success than unpaired males (Dugatkin 1992). Our model studies a baseline case, in which each male's extra-pair mating success is independent of his social pairing.

After mating, females produce offspring. Offspring inherit one target trait allele and one imprinting strategy allele from their biological parents, with free recombination. Thus, an individual may inherit one allele from each parent or both alleles from the same parent. Each target trait allele in each offspring mutates to the opposite allele with probability $\mu = 10^{-4}$. Mutation ensures that selection does not eliminate the less fit t allele from the population. Each female offspring acquires an imprinted phenotype by observing her mother, her social father, or a randomly selected male from the parental generation according to her imprinting strategy. Thus, paternally imprinting daughters of social partner males imprint on their biological fathers, but paternally imprinting daughters of extra-pair mates imprint on unrelated males. Offspring form the population in the next generation.

1.2 Analysis

Our goal was to understand how the evolutionarily stable strategy (ESS) of sexual imprinting depends on 1) the rate of extra-pair paternity (u) and 2) the strength of viability selection acting on the target trait (c_t). An ESS is a strategy that, if played by all members of a population, cannot be invaded by any other strategy (Maynard-

Smith and Price, 1973). Thus, ESSs are the strategies we expect to see in nature. We asked two specific questions. First, if all females use a given imprinting mode, how strong should we expect imprinting to become (i.e., what are the evolutionarily stable values of α_{SP} and α_{EP})? Second, if females can evolve any imprinting mode, which mode should we expect to see? We used our model to answer these questions for all combinations of u in the set $\{0, 0.01, 0.02, \dots, 1\}$ and c_i in the set $\{0, 0.01, 0.02, \dots, 0.63\}$.

Finding evolutionarily stable imprinting strengths within modes

We considered three scenarios in which sexual imprinting might evolve. In the social partner (SP) scenario, females can be choosy when selecting social partners but select extra-pair mates at random. This might be the case if extra-pair mating is forced or is by sneak copulation (Jones et al., 2001). In the extra-pair (EP) scenario, females can be choosy when selecting extra-pair mates but select social partners at random. This might be the case if females choose social partners only for the direct benefits (e.g., parental care, high quality territory) they provide, and those benefits are independent of the male target phenotype (Forsgren et al., 1996; Moller and Jennions, 2001). In the both partner (BP) scenario, females can be choosy when selecting both social partners and extra-pair mates. In this case, we assumed that females use the same imprinting mode for both mates (i.e., they have only one imprinted phenotype), but that they may be choosier when selecting one type of mate than the other.

To find the evolutionarily stable imprinting strength for combinations of u and c_i within each mode, we borrowed tools from adaptive dynamics (Geritz et al., 1997; Dercole and Rinaldi, 2008). For the SP and EP scenarios, we initialized our model with a randomly mating population. That is, we set the frequency of the S allele to one and the imprinting strength conferred by the S allele to zero. We set the initial frequency of the T allele to 0.5, and we iterated generations until the T and t alleles reached mutation-selection balance. We called the population at mutation-selection balance the resident population. Into this population, we introduced a low frequency (10^{-4}) of s alleles that conferred imprinting slightly stronger than the resident S allele. In particular, if the S allele conferred imprinting strength α , then the s allele conferred imprinting strength $\alpha + 0.1$. Following convention, we called the introduced s allele the mutant (Geritz et al., 1997; Dercole and Rinaldi, 2008). We introduced the mutant in linkage equilibrium with the T

and t alleles. We iterated 1,000 generations, and we asked whether the frequency of the mutant increased over the last 500 generations (no mutants reached fixation). We called this an invasion trial. If the mutant increased in frequency, then we recorded that the mutant had invaded the resident, and we assumed that the mutant would replace the resident in the population (Dercole and Rinaldi, 2008). We then conducted another invasion trial in which the successfully invading mutant became the resident, and a new mutant had slightly stronger imprinting. We repeated this process until we found a resident strategy that could not be invaded and replaced by slightly stronger imprinting. If the resident imprinting strength reached $\alpha = 7$ (i.e., a female evaluating a male with a phenotype she does not prefer accepts him with a probability of 0.001) before reaching a stable state, then we conducted an invasion trial to ask whether perfect imprinting ($\alpha = \infty$) could invade and replace very strong imprinting ($\alpha = 7$). If so, then we recorded perfect imprinting as the evolutionarily stable imprinting strength. Because this approach starts with random mating and allows progressively stronger imprinting to evolve, we called this the bottom-up approach (Chaffee et al., 2013).

The bottom-up approach finds the stable imprinting strength that evolves from random mating by a series of small mutations under a particular combination of u and c_i . However, there may be additional stable imprinting strengths for the same values of u and c_i that cannot evolve from random mating. To find out whether such strengths exist, we initialized simulations with a resident S allele that conferred very strong imprinting ($\alpha = 7$). Then, we conducted invasion trials as in the bottom-up approach, except that each resident was tested against a mutant that conferred slightly weaker imprinting ($\alpha - 0.1$). If the mutant could invade the resident, we conducted a new invasion trial in which the resident had imprinting strength $\alpha - 0.1$ and a new mutant again had slightly weaker imprinting. We iterated this process until we found an imprinting strength that could not be invaded by a slightly weaker imprinting strategy.

In the BP imprinting scenario, we allowed both the imprinting strength for social partners and the imprinting strength for extra-pair mates to evolve. We let the two strengths evolve alternately, so that invasion trials against mutants to one strength were followed by invasion trials against mutants to the other. Whenever a mutant to one strength successfully invaded the population, we tested the new strategy first against a mutant with weaker imprinting and then against a mutant with

stronger imprinting for the other mate type. For example, if a mutant with $(\alpha_{SP}, \alpha_{EP}) = (\alpha, \beta)$ successfully invaded a resident with $(\alpha_{SP}, \alpha_{EP}) = (\alpha - 0.1, \beta)$, then we tested the new strategy for invasion first by a mutant with $(\alpha_{SP}, \alpha_{EP}) = (\alpha, \beta - 0.1)$ and then by a mutant with $(\alpha_{SP}, \alpha_{EP}) = (\alpha, \beta + 0.1)$. This allows for the possibility that, as the imprinting strength for one type of mate increases, the evolutionarily stable imprinting strength for the other type of mate might decrease. We never encountered a case in which both stronger and weaker mutants to the same imprinting strength could invade the same resident population (i.e., we did not detect evolutionary branching points). We iterated this process until we found a combination of imprinting strengths that could not be invaded by small mutations to either strength.

The bottom-up approach finds a stable pair of imprinting strengths that can evolve by a series of small mutations to an initially randomly mating population. To find out if there is another stable pair of imprinting strengths that cannot evolve from random mating, we analyzed the BP imprinting scenario using a top-down approach. We started with a resident population in which the imprinting strengths for both the social partner and extra-pair mates were strong (i.e., $\alpha_{SP} = \alpha_{EP} = 7$), and we asked whether progressively weaker imprinting strengths could invade and replace the resident. We iterated this process until we reached a combination of imprinting strengths that could not be invaded by a small mutation to either strength.

In the BP imprinting scenario, the stable imprinting strength for one type of mate may depend on the imprinting strength for the other type. This means that the evolutionary trajectory, and possibly the stable state that the trajectory reaches, depends on the relative rates at which the two strengths evolve. Thus, while our bottom-up approach always finds a stable pair of imprinting strengths, in principle this may not be the only stable pair of imprinting strengths than can evolve from random mating by a series of small mutations. In practice, we found that the imprinting strength for extra-pair mates always evolves to perfect imprinting, regardless of the imprinting strength for social partners. Moreover, as the imprinting strength for extra-pair mates increases, the stable imprinting strength for social partners also increases. This means that the stable states we find using our bottom-up approach are the only stable states that can evolve from random mating by a series of small mutations. Additionally, it means that if our bottom-up and top-down approaches converge to the same stable

state, then this stable state is unique.

The imprinting strengths we found using our bottom-up and top-down approaches are locally stable. That is, they cannot be invaded by strategies with the same imprinting mode and slightly different imprinting strengths. To confirm that these strategies are also globally stable (i.e., cannot be invaded by any strategy with the same mode and a different strength), we conducted invasion trials in which the locally stable imprinting strength was resident and mutants had strengths in the set $\{0, 0.1, 0.2, \dots, 7\}$.

To gain a more detailed picture of how imprinting strength evolves within modes in a subset of cases, we constructed pairwise invasibility plots (PIPs) (Christiansen and Loeschcke, 1980; Matsuda, 1985) for selected combinations of u , c_t , and imprinting mode. We initialized invasion trials with resident imprinting strengths in the set $\{0, 0.1, \dots, 7\}$ and we tested each resident for invasion by mutants with strengths in the same set. PIPs show where mutants of each imprinting strength can or cannot invade residents of each imprinting strength, and can be used to illustrate expected evolutionary trajectories (Dercole and Rinaldi, 2008).

Finding evolutionarily stable imprinting modes

To find the evolutionarily stable imprinting mode for each combination of u and c_t , we conducted invasion trials with each mode as resident against each other mode as mutant. We initialized our model with a population fixed for a S allele that conferred imprinting of the resident mode at its evolutionarily stable strength (or, in the BP scenario, its evolutionarily stable strengths, since imprinting for social partners and extra pair mates can have different strengths). We set the initial frequency of the T allele to 0.5, and we iterated generations until the population reached mutation-selection balance. Then, we introduced a mutant s allele that conferred imprinting of a different mode at the evolutionarily stable strength(s) of the resident mode, and we asked if the mutant could invade and replace the resident. If an imprinting mode at its evolutionarily stable strength could not be invaded by any other mode, then we said that mode was evolutionarily stable.

In general, invading modes do not have the same stable strengths as resident modes. If the invading mode has only one stable strength (or, in the BP scenario, one pair of stable strengths, because imprinting for social partners and extra pair mates can have different strengths), then it will evolve to that strength (or pair of strengths) after invasion. However, if the invading mode has more than one stable strength, then we do not know

a priori to which stable strength it will evolve. For example, one can envision a case in which maternal imprinting evolves to its stable strength, then paternal imprinting invades and replaces maternal imprinting, and after invading paternal imprinting evolves to a new stable strength that it could not have reached from random mating. Therefore, after each successful invasion, we conducted additional bottom-up and top-down analyses starting from the imprinting strength of the previous resident to determine the new stable imprinting strength for the invading mode after invasion.

In all of our analyses, we assumed that invasion implies replacement. We expect this to be true when mutations have small effects (e.g., small quantitative mutations to imprinting strength) (Dercole and Rinaldi, 2008). In models similar to ours, this has also been true for mutations that change imprinting modes (Tramm and Servodio, 2008; Chaffee et al., 2013). To test whether invasion implies replacement in our model, we generated 1000 resident populations with parameter values drawn independently from uniform distributions ($u \in [0, 1]$, $c_t \in [0, 0.63]$, $\alpha_{SP} \in [0, 7]$, $\alpha_{EP} \in [0, 7]$) and with the imprinting mode assigned with equal probability to be maternal, paternal, or oblique. We tested each of these resident populations for invasion by mutants with the same imprinting strength and each other imprinting mode, and with the same mode but with slightly stronger imprinting (i.e., $\alpha_{SP} + 0.01$, $\alpha_{EP} + 0.01$). We started each mutant allele at linkage equilibrium with the target trait alleles and with each frequency in the set (0.01, 0.02, ..., 0.99). Each mutant either increased when started at every frequency or decreased when started at every frequency. Thus, invasions always led to replacement of the resident allele.

2 Results

2.1 Evolutionary stable imprinting strengths within modes

The evolutionarily stable strength of sexual imprinting for the social partner depends on the rate of extra-pair paternity (u), the strength of viability selection on the target trait (c_t) and the imprinting mode (Fig. 1). In the SP scenario, the evolutionarily stable strength of imprinting increases with the strength of viability selection and decreases with the rate of extra-pair paternity (Fig. 1A, C, E). Imprinting in this scenario involves a trade-off. Under each imprinting mode, females are more likely to imprint on the more common and fitter target phenotype. Females that imprint more strongly are more likely to choose social partners with the fitter

phenotype, and so obtain fitter target trait alleles for their offspring. However, females that imprint more strongly are also more likely to reject all potential social partners they encounter, and females that do not accept social partners produce no offspring. As the strength of viability selection increases, the fitness cost of choosing a mate with the less fit allele increases. Moreover, the frequency of the less fit allele decreases, so the probability that a female imprinted on the fitter phenotype fails to find a social partner decreases. Because the benefit of imprinting goes up and the cost goes down, the evolutionarily stable strength of imprinting increases. As the rate of extra-pair paternity goes up, the proportion of offspring sired by the social partner goes down and it becomes less important for a female to choose a social partner that carries the fitter target trait allele. Thus, the evolutionarily stable strength of imprinting declines.

In the EP scenario (not shown in Fig. 1), the imprinting strength under each mode evolves toward perfect imprinting whenever there is viability selection on the target trait. This is because there is no cost of imprinting in the EP scenario. Very choosy females that reject all potential extra-pair mates have the same number of offspring as females that find extra-pair mates, but all of their offspring are sired by their social partners. Thus, a female should reject any potential mate that is not fitter than her social partner. Strong imprinting helps her to do this. When there is no viability selection on the target trait (i.e., when $c_t = 0$) and the T and t alleles are in mutation-selection balance (i.e., each has frequency 0.5), imprinting is selectively neutral. This is because the T and t phenotypes are equally fit, so no imprinting set is fitter than the population as a whole. However, if the frequency of the T allele strays from exactly 0.5, then more females will imprint on the more common target phenotype, and the more common phenotype will be favored by sexual selection. This creates selection for imprinting, and the imprinting strength then evolves to perfect imprinting.

In the BP scenario, imprinting for extra-pair mates evolves toward perfect imprinting (just as in the EP scenario) and the strength of imprinting for social partners increases with the strength of viability selection (just as in the SP scenario). However, for low to moderate strengths of viability selection, the strength of imprinting for social partners is highest when the rate of extra-pair paternity is intermediate (Fig. 1B, D, F). That is, up to a point, females are choosier when selecting social partners that will sire fewer of their offspring.

This counterintuitive result is due to the effect of sexual selection during extra-pair mating. When the rate of extra-pair paternity is low, most males have the same number of offspring. A female can increase the viability of her male and female offspring by selecting a social partner with the more viable target trait allele, but all of her sons that survive to adulthood will have similar mating success. So, the benefit of choosing a social partner with the fitter target trait allele justifies only a small risk of not finding a social partner at all. This limits the strength to which imprinting evolves. As the rate

of extra-pair paternity increases, variability in male reproductive success also increases, because some males are chosen as extra-pair mates more often than others. Now, finding mates with the fitter target trait allele makes a female's offspring more viable, but it also makes her sons more successful in the extra-pair mating pool. Choosing a social partner with the right target trait allele becomes more important, and justifies a higher risk of not finding a social partner at all. Thus, stronger imprinting evolves. As the rate of extra-pair paternity continues to increase, the stable strength of imprinting

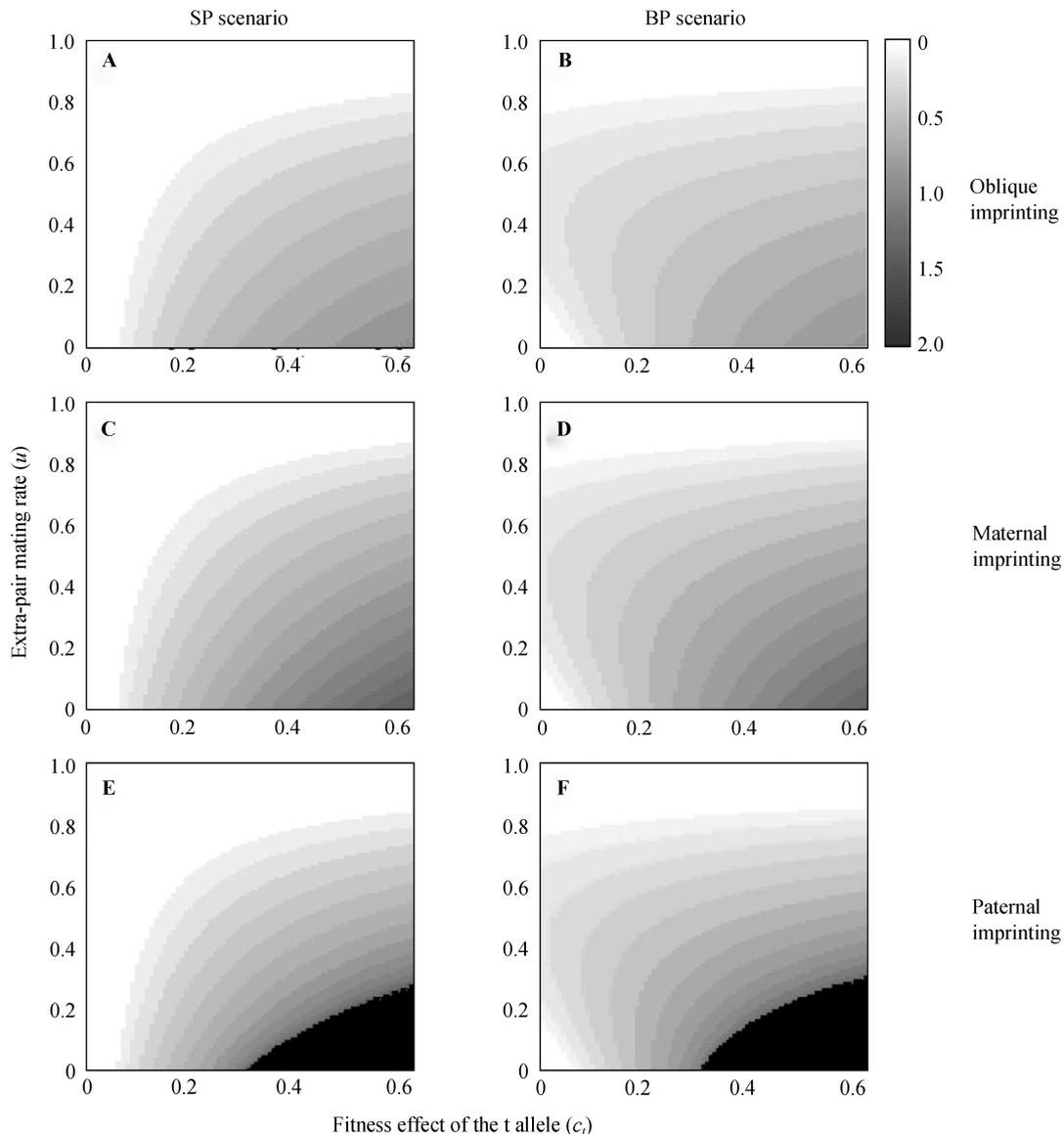


Fig. 1 Evolutionarily stable strengths of imprinting for the social partner, as a function of the extra-pair paternity rate and the fitness effect of the *t* allele

Panels show stable imprinting strengths under oblique (A, B), maternal (C, D), and paternal (E, F) imprinting in the SP (A, C, E) and BP (B, D, F) scenarios. In black areas, perfect imprinting evolves. When imprinting is paternal, perfect imprinting is always stable, but perfect imprinting cannot evolve from random mating outside of black areas. In the BP scenario, imprinting for the extra-pair partner (not shown) always evolves to perfect imprinting.

goes down again. This is because social partners sire a smaller proportion of offspring, and are less valuable for their genes than for the parental care they provide.

The previous analysis assumes that imprinting for extra-pair mates has the potential to become perfect, so that females never accept mates with phenotypes other than the ones they prefer. In nature, sensory or neurological constraints may prevent imprinting from becoming perfect. In Appendix 3, we study how imprinting for the social partner evolves when imprinting for extra-pair mates is constrained to be imperfect. Results are qualitatively similar to those shown in Fig. 1. However, when imprinting for extra-pair mates is weaker, sexual selection during extra-pair mating is weaker, and the tendency towards stronger imprinting for the social partner at intermediate rates of extra-pair paternity is less pronounced (Figure A 3.1).

In the maternal and oblique modes, imprinting for social partners reaches intermediate strengths (gray areas of Fig. 1A–D). In the paternal mode, when viability selection is strong and extra-pair paternity is low, the evolutionary trajectory is towards perfect imprinting (black areas of Fig. 1E, F). The difference is because of how sexual selection acts on the imprinting sets. In the paternal imprinting set (i.e., the set of males chosen by females as social partners), the target trait is under direct sexual selection. If imprinting is perfect, then the t allele is eliminated from the paternal imprinting set: all females imprint on the T phenotype, and all females choose T mates. A female that encounters only t males during the mating phase will fail to mate, but because t males are rare this almost never happens, so there is little cost for perfect imprinting. If a slightly weaker imprinting mutant arises, female mutants sometimes accept mates with the t phenotype. Those females' t sons never find mates, and their daughters (who are imprinted on their social fathers' t phenotype) rarely accept mates. Thus, there is strong selection against any weakening of imprinting, and perfect imprinting evolves. In contrast, in the maternal and oblique imprinting sets, the target trait is not under direct sexual selection. Even if imprinting were perfect, these sets would include individuals with the t phenotype, and some females would learn the p mate preference. Because the t phenotype is rare, most p females would fail to find mates, and thus p females would pay a high cost for strong imprinting. Intermediate-strength imprinting increases the probability that common P females will choose social partners with the T allele, but allows rare p females to sometimes accept T males despite their

imprinting.

Under maternal and oblique imprinting, the bottom-up and top-down approaches always converge. This means that, under each of these modes, there is only one evolutionarily stable imprinting strength for any combination of extra-pair paternity (u) and viability effect of the t allele (c_t). This is not true for paternal imprinting. Outside of the black areas in Fig. 1E, F, perfect paternal imprinting evolves in the top-down approach but intermediate imprinting or random mating evolves in the bottom-up approach. In these areas, perfect paternal imprinting is evolutionarily stable, but it cannot evolve from random mating by a series of small mutations. Thus, in these areas, there are alternative stable states for paternal imprinting. Each of these is globally stable within the paternal mode. That is, neither can be invaded by any other strength of paternal imprinting.

The stable imprinting strengths we identified can also be understood by examining pairwise invasibility plots (PIPs) (Fig. 2). Fig. 2B shows a typical PIP for the evolution of maternal or oblique imprinting strength in the SP scenario. Weakly imprinting residents can be replaced by more strongly imprinting mutants, and strongly imprinting residents can be replaced by more weakly imprinting mutants, until an intermediate stable state is reached. Under paternal imprinting, three different patterns of evolution are possible. In 2D, a stronger imprinting mutant can always invade a weaker imprinting resident, and perfect imprinting evolves. In 2E, stronger imprinting mutants invade weaker imprinting residents until an intermediate stable state is reached, and in 2F an imprinting mutant can never invade a randomly mating population. However, in both 2E and 2F, if sufficiently strong imprinting is already resident in the population, then evolution is toward perfect imprinting. Thus, 2E and 2F represent systems with alternative stable states.

2.2 Evolutionary stable imprinting modes

The evolutionarily stable mode of sexual imprinting depends on the rate of extra-pair paternity (u) and the strength of viability selection acting on the target trait (c_t) (Fig. 3). In the SP and BP scenarios, paternal imprinting is stable when extra-pair paternity is low and the viability effect of the target trait is large. Otherwise, maternal imprinting is stable. This is due to the combined effects of the imprinting set and phenogenotypic disequilibrium.

In our model, both males and females must survive viability selection to reach adulthood. However, males must also be selected as mates by females in order to

enter the paternal imprinting set. Because most females imprint on, and thus prefer mates with, the fitter T allele, sexual selection ensures that the paternal imprinting set will have a higher frequency of fitter alleles than the maternal imprinting set. Thus, the imprinting set favors paternal imprinting. In contrast, the phenotypic

disequilibrium favors maternal imprinting. This is because all maternally imprinting offspring imprint on their biological mothers, but some paternally imprinting offspring imprint on social fathers that are not their biological fathers. As a result, maternal imprinters are more likely to inherit the same alleles they imprint on,

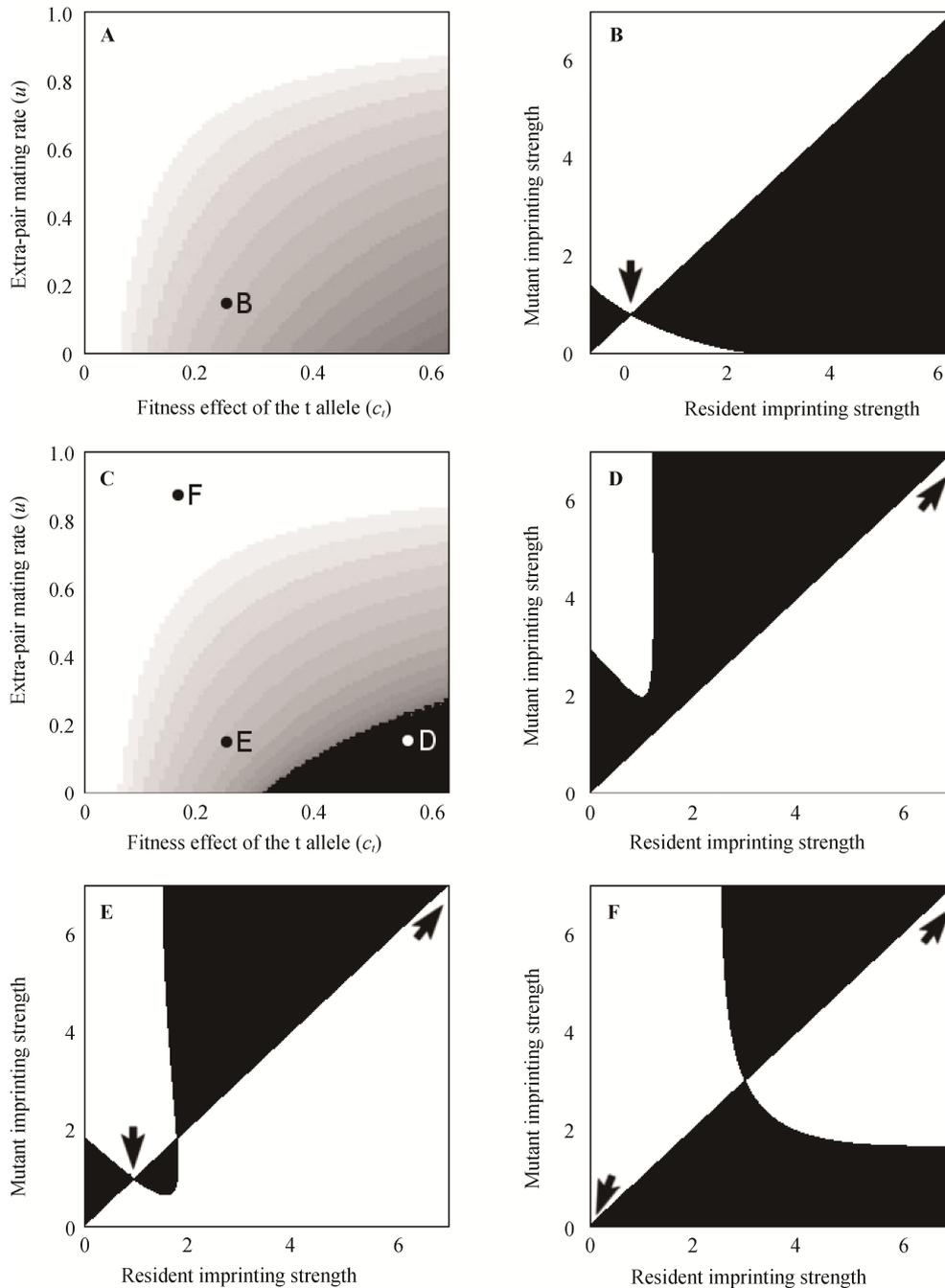


Fig. 2 Representative pairwise invasibility plots for imprinting strength for the social partner

Panels A and C show the stable imprinting strengths that evolve from random mating in the SP scenario under maternal (A) and paternal (C) imprinting at different strengths of viability selection (x -axis) and rates of extra-pair paternity (y -axis). PIPs correspond to the labelled points in A and C. Black indicates that the mutant imprinting strength can invade and replace the resident, and white indicates that it cannot. Arrows in PIPs indicate the stable imprinting strengths. In B (maternal imprinting), an intermediate imprinting strength is stable, and in D (paternal imprinting) perfect imprinting is stable. Panels E and F (paternal imprinting) illustrate systems with alternative stable states. In E, both intermediate and perfect imprinting are stable. In F, random mating and perfect imprinting are stable.

and fitter maternal imprinters are more likely to be imprinted on fitter alleles. Natural selection, acting through the phenogenotypic disequilibrium, increases the proportion of females that are imprinted on the fitter allele, and this increase is greater among maternal imprinters (which have stronger phenogenotypic disequilibria) than among paternal imprinters (which have weaker phenogenotypic disequilibria). As a result, natural selection improves the quality of maternal imprinting more than it improves the quality of paternal imprinting. When extra-pair paternity is rare, the difference in phenogenotypic disequilibria between maternal and paternal imprinters is small. Thus, the effect of the imprinting set outweighs the effect of phenogenotypic disequilibrium, and paternal imprinting is favored. When extra-pair paternity is common, the difference in phenogenotypic disequilibria between maternal and paternal imprinters is large. The effect of phenogenotypic disequilibrium outweighs that of the imprinting set, and maternal imprinting is favored.

In the EP scenario (not shown in Fig. 3), maternal imprinting is always stable. The EP scenario assumes that females are choosy when selecting extra-pair partners, but choose their social partners at random. Thus, the maternal and paternal imprinting sets have the same fitness, because they each undergo viability selection but not sexual selection. As in the BP and SP cases, the phenogenotypic disequilibrium favors maternal imprinters, so maternal imprinting is favored to evolve.

3 Discussion

Models of polygynous mating systems predict that females should sexually imprint on their fathers rather than their mothers (Tramm and Servedio, 2008; Chaffee et al., 2013). In nature however, females of some species imprint on their mothers instead (Grant and Grant, 1997; Witte et al., 2000; Burley, 2006; Verzijden et al., 2008). Here we show that maternal imprinting is favored to evolve in systems with social pair bonds and moderate to high levels of extra-pair paternity. Counterrintuitively, females may be choosier when selecting social partners in systems where extra-pair mating is more frequent.

Our results are consistent with some examples of maternal imprinting in nature. For example, maternal imprinting has been observed in Darwin’s finches (*Geospiza fortis*; Grant and Grant, 1997), zebra finches (*Taeniopygia guttata*; Vos, 1995a; Burley, 2006), and Javanese mannikins (*Lonchura leucogastroides*; Witte et al., 2000). All three species are socially monogamous. In *G. fortis*, extra-pair paternity has been estimated at 20% (Keller et al., 2001), which is high enough to promote maternal imprinting in our model. In *T. guttata*, extra-pair paternity is lower (2.4%; Birkhead et al., 1990) but may be enough to promote maternal imprinting if viability selection on the target trait (plumage color in Vos, 1995a; crest type in Burley, 2006) is weak. To our knowledge, extra-pair paternity in *L. leucoga-*

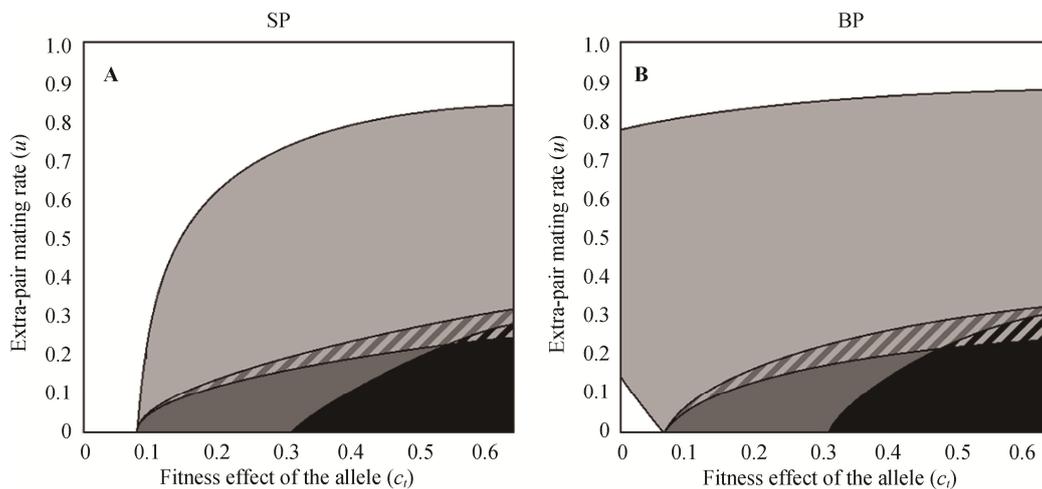


Fig. 3 Evolutionarily stable sexual imprinting strategies when females imprint for (A) social partners or (B) both social partners and extra-pair mates

The stable imprinting strategy for social partner choice can be no imprinting (white), intermediate (i.e., $0 < \alpha_{sp} < \infty$) maternal imprinting (light grey), intermediate paternal imprinting (dark grey) or perfect paternal imprinting (black). In hatched areas, maternal and paternal imprinting are both stable. Whichever evolves first persists. In B, imprinting for extra-pair mate choice always goes to perfect imprinting and has the same mode as imprinting for social partner choice. Where no imprinting for social partner choice evolves in B, imprinting for the extra-pair partner is maternal. Perfect paternal imprinting for social partner choice is stable in all areas of both panels, but cannot evolve from random mating outside of black or black-hatched areas.

stroides has not been measured. Maternal imprinting has also been observed in mallard ducks (*Anas platyrhynchos*; Klint, 1978) and in cichlid fish of the genus *Pundamilia* (Verzijden and ten Cate, 2007). In both of these species parental care is exclusively by mothers, and maternal imprinting may have evolved because fathers are not available to act as models.

Our results advance the theoretical understanding of the evolutionary mechanisms that can promote sexual imprinting. Tramm and Servedio (2008) explained that imprinting sets and phenogenotypic disequilibrium influence how sexual imprinting evolves. In their model, phenogenotypic disequilibrium made maternal imprinting a better strategy than oblique imprinting, but only because the maternal and oblique imprinting sets had identical fitnesses. Chaffee and colleagues (2013) showed that in polygynous systems like the one modeled by Tramm and Servedio (2008), paternal imprinting should exclude maternal and oblique imprinting whenever fathers are available to act as models. Together, these results might suggest that phenogenotypic disequilibrium is a triviality that rarely influences the evolution of sexual imprinting in nature. However, our results show that, for a large and biologically plausible part of parameter space, phenogenotypic disequilibrium may be an important factor in determining which sexual imprinting strategies evolve. Thus, the role of phenogenotypic disequilibrium in the evolution of sexual imprinting may be greater than previously appreciated.

Our model can be seen as a “good genes” model (Neff and Pitcher, 2005). Sexual imprinting evolves, at least initially, because it helps females to select mates with fit target trait alleles, and the same alleles are fit in all individuals. This may be appropriate for many target traits (e.g., traits under stabilizing or directional selection). In nature however, sexual imprinting might sometimes evolve for other reasons. For example, in some systems sexual imprinting might help individuals to select mates with compatible genes rather than simply good genes. An extreme example is when imprinting helps individuals to select conspecific mates, because hybrid offspring have reduced fitness. The ability to identify conspecifics has long been assumed to be an important outcome of sexual imprinting, and to be a possible cause of its evolution (Grant and Grant, 1997). Empirical studies of offspring cross-fostered among species have shown that imprinting aids in species recognition (Grant and Grant, 1997; ten Cate and Vos, 1999; Slagsvold et al., 2002) and may be the main mechanism of reproductive isolation between some species

(Verzijden and ten Cate, 2007; Kozak et al., 2011), but which imprinting modes should evolve in such cases is not known. Sexual imprinting may also help individuals in dimorphic species to select partners of the correct sex (Vos, 1995b; Banerjee and Adkins-Regan, 2014). In this case, we might expect imprinting to be on the opposite-sex parent.

In nature, sexual imprinting may also help females to select mates that offer greater direct (i.e., nongenetic) benefits (Moller and Jennions, 2001). For example, males may provide parental care or control territories with different qualities, and females may need to select social partners that provide the best care or the best territories for their young. Due to energetic or time constraints, males that invest more in parental care may have lower viability or mating success (Schradin et al., 2009) and may pass less viable alleles to their offspring (although the generality of this result has been questioned; Stiver and Alonzo, 2009). In such cases, females might have different preferences, and so use different imprinting models, when selecting social partners or extra-pair mates. Indeed, there is evidence that human females place more value on signals associated with direct benefits when choosing long-term than short-term partners (Li and Kenrick, 2006), and that differences in long- and short-term partner preferences are at least in part learned (Little et al., 2008), but this has been less well-studied in other species. Theoretical and empirical work that considers the possible role of direct benefits in shaping sexual imprinting strategies may reward effort.

In our model, we studied extra-pair mating, but we did not consider conspecific brood parasitism. In birds, conspecific brood parasitism occurs when females lay eggs in the nests of conspecific hosts, and these hosts raise the offspring as their own. In some species, conspecific brood parasitism is as common or more common than extra-pair paternity. For example, in zebra finches, conspecific brood parasitism in captive populations is as high as 5.4% (Schielzeth and Bolund, 2010), compared to 2.4% extra-pair paternity (Birkhead et al., 1990). Conspecific brood parasitism reduces the accuracy and weakens the phenogenotypic disequilibria created by parental imprinting. In systems that also have some extra-pair paternity, the weakening effect will be greater on maternal than on paternal imprinting. Thus, conspecific brood parasitism is likely to restrict the range of conditions under which sexual imprinting evolves, and when imprinting does evolve it is likely to favor paternal over maternal imprinting.

In our model, sexual imprinting is advantageous because it helps females to avoid mates that will provide less fit alleles to their offspring. If less fit alleles are rare, then selection for stronger imprinting, or for one imprinting mode over another, may be weak. Indeed, Chaffee and colleagues (2013) showed that even a small fixed cost prevents sexual imprinting from evolving when less fit target phenotypes are rare. If this is true, then imprinting strategies in nature may be shaped by genetic drift as much as by selection. In nature however, less fit phenotypes may be more common than in our model. Less fit alleles can be maintained at high frequency if there is migration from another population that experiences different selection (Lenormand, 2002) or if selective optima vary over time (Hairston and Dillon, 1990). Indeed, in natural populations, most individuals are believed to have many deleterious alleles (Sunyaev et al., 2001; Henn et al., 2015). Selection for sexual imprinting in such systems may be stronger than in models where less fit alleles are maintained by mutation alone.

Our results offer two testable hypotheses. First, if sexual imprinting evolves as a mechanism for helping individuals select mates with good genes, then in systems with social pair bonds we should expect to see more maternal imprinting when extra-pair paternity is higher. Second, in systems where females exercise mate choice for both social partners and extra-pair mates, we should expect sexual imprinting to be strongest when there are intermediate levels of extra-pair paternity. Previous studies have assessed imprinting modes by manipulating maternal and paternal phenotypes and monitoring offspring mate preferences (e.g., Vos, 1995a; Witte et al., 2000; Burley, 2006; Witte and Caspers, 2006), or have inferred imprinting modes from correlations between parental and mate phenotypes (e.g., Grant and Grant, 1997). Similar studies in species with a range of extra-pair paternity rates would allow testing of our first hypothesis. To test the second hypothesis, researchers will need to assess not only the mode but also the strength of imprinting in a range of systems. Most studies of sexual imprinting have not reported imprinting strength, but in some cases this might be estimated from the data or from reconstructed data (e.g., Rodriguez et al., 2013).

Previous theoretical work has suggested that choosy females should sexually imprint on their fathers' phenotypes whenever possible, but this does not agree with observations from nature. Our study explains how mating systems with pair bonds and some extra-pair mating

can promote imprinting on maternal phenotypes, and offers new insight into how sexual imprinting may evolve. On-going and future empirical work will test the predictions of our model, and help researchers to understand the ultimate causes of sexual imprinting in nature.

Acknowledgments The authors are grateful to Maria Servedio and two anonymous reviewers for advice, and thank the University of Manchester School of Engineering and Physical Sciences for the use of its HTCondor system. EI was partially funded by a BBSRC Research Experience Placement.

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Supplementary Information

Appendix 1 Equations describing model dynamics

We studied a population comprising four male genotypes and eight female phenogenotypes. Let M_{ij} be the frequency at birth of males with imprinting strategy allele $i \in \{S, s\}$ and target trait allele $j \in \{T, t\}$ (*i.e.*, with genotype ij). Let F_{ijk} be the frequency at birth of females with imprinting strategy allele $i \in \{S, s\}$ target trait allele $j \in \{T, t\}$, and imprinted mate preference phenotype $k \in \{P, p\}$ (*i.e.*, with phenogenotype ijk). We scaled both male and female frequencies to unity and tracked them separately. Thus, $\sum_{ij} M_{ij} = \sum_{ijk} F_{ijk} = 1$.

After birth, both sexes undergo viability selection on the target trait. Let $v_T = 1$ be the viability of phenotype T conferred by allele T , and let $v_t = 1 - c_t$ be the viability of phenotype t conferred by allele t . The frequencies of males and females after viability selection are

$$M'_{ij} = \frac{v_j M_{ij}}{\sum_{xy} v_y M_{xy}} \quad (1)$$

and

$$F'_{ijk} = \frac{v_j F_{ijk}}{\sum_{xyz} v_y F_{xyz}} \quad (2)$$

The numerators on the right-hand side (RHS) of eqs. 1 and 2 capture viability selection, and the denominators scale the populations after selection to unity.

Males and females that survive viability selection enter the mating phase. The mating phase begins with social pair formation, which occurs in 50 rounds. In each round, 10% of the unpaired females in the population encounter unpaired males. Each female that encounters a male accepts him as a social partner with a probability that depends on her preferred mate phenotype, his target phenotype, and her strength of imprinting for social partners. In particular, the probability that a female with phenogenotype ijk accepts a potential social partner with genotype ab is A_{ikb} , where $A_{ikb} = 1$ if $(k, b) = (P, T)$ or $(k, b) = (p, t)$ and $A_{ikb} = \exp(-\alpha_{spi})$ otherwise. Thus, α_{spi} measures the strength of imprinting (*i.e.*, choosiness) for social partners conferred by imprinting strategy allele i .

Let $m_{ab}(r)$ and $f_{ijk}(r)$ be the frequencies of males with genotype ab and females with phenogenotype ijk , respectively, seeking social partners at the beginning of round r of social pair formation. Because all individuals that survive viability selection enter the mating phase, $m_{ij}(1) = M'_{ij}$ and $f_{ijk}(1) = F'_{ijk}$. The frequency of females with phenogenotype ijk that accepts males of genotype ab in round r is

$$d_{ijk}^{ab}(r) = 0.1 f_{ijk}(r) \frac{m_{ab}(r)}{\sum_{xy} m_{xy}(r)} A_{ikb} \quad (3)$$

Females that accept social partners and males that are accepted are removed from the pool of individuals seeking social partners. Thus

$$m_{ab}(r+1) = m_{ab}(r) - \sum_{ijk} q_{ijk}^{ab}(r) \quad (4)$$

and

$$f_{ijk}(r+1) = f_{ijk}(r) - \sum_{ab} q_{ijk}^{ab}(r) \quad (5)$$

After social pair formation, the frequency of females with phenogenotype ijk that are socially paired with males of genotype ab is

$$Q_{ijk}^{ab} = \frac{\sum_{r=1}^{50} q_{ijk}^{ab}(r)}{\sum_{ab} \sum_{ijk} \sum_{r=1}^{50} q_{ijk}^{ab}(r)} \quad (6)$$

We assumed that females without social partners cannot successfully raise offspring, and we tracked only the paired females in the population. Thus, the denominator on the RHS of eq. 6 scales the number of socially paired females to unity.

Each socially paired female seeks an extra-pair mate to sire a portion u of her offspring. We assumed that extra-pair mating occurs in 5 rounds. In each round, each female seeking an extra pair mate encounters one male. We assumed that all males, paired or unpaired, are available for extra-pair mating, and mating in one round does not affect whether a male mates in other rounds. Thus, the frequency of males with genotype ab encountered in each round of extra-pair mating is M'_{ab} . The probability that a female with phenogenotype ijk accepts a potential extra-pair mate with genotype ab is B_{ikb} , where $B_{ikb} = 1$ if $(k, b) = (P, T)$ or $(k, b) = (p, t)$ and $B_{ikb} = \exp(-\alpha_{EPi})$ otherwise. Thus, α_{EPi} measures the strength of imprinting for extra-pair partners conferred by imprinting strategy allele i . If a female accepts an extra-pair mate, she is removed from the pool of females seeking extra-pair mates. Thus, each female accepts at most one extra-pair mate, and that mate sires all of her extra-pair offspring. If a female does not accept an extra-pair mate, then her social partner sires all of her offspring. Thus, failure to accept an extra-pair mate does not affect the number of offspring that a female produces.

The probability that a female with phenogenotype ijk accepts an extra-pair mate in any given round of extra-pair mating is $\sum_{ab} M'_{ab} B_{ikb}$. Thus, the probability that she fails to accept a mate in any given round is

$$n_{ik} = 1 - \sum_{ab} M'_{ab} B_{ikb} \quad (7)$$

and the probability that she accepts an extra-pair mate before the end of extra-pair mating is $1 - n_{ik}^5$. If a female with phenogenotype ijk accepts an extra-pair mate, the probability that mate has genotype ab is

$$D_{ijk}^{ab} = \frac{M_{ab} B_{ikb}}{\sum_{xy} M'_{xy} B_{iky}} \quad (8)$$

Combining eqs. 6 and 8, the frequency of offspring with mothers of phenogenotype ijk , biological fathers of genotype gh , and social fathers of genotype ab is

$$W_{ijk}^{abgh} = \left((1-u) + un_{ik}^5 \right) + u \left(1 - n_{ik}^5 \right) D_{ijk}^{ab} Q_{ijk}^{ab} \quad (9)$$

if $gh = ab$, and is otherwise

$$W_{ijk}^{abgh} = u \left(1 - n_{ik}^5 \right) D_{ijk}^{gh} Q_{ijk}^{ab} \quad (10)$$

Each offspring described in eqs. 9 or 10 inherits one allele at the imprinting strategy locus and one allele at the target trait locus from its biological parents, with free recombination. Thus, each offspring described by W_{ijk}^{abgh} inherits, with equal probability, allele I or g and allele j or h . In addition, each female offspring acquires an imprinted phenotype according to the imprinting strategy she has inherited. If the strategy coded by her imprinting strategy allele (*i.e.*, allele i or g) is maternal, she acquires imprinted phenotype P if $j = T$ and imprinted phenotype p otherwise. If the strategy coded by her imprinting strategy allele is paternal, she acquires imprinted phenotype P if $b = T$ and imprinted phenotype p otherwise. If the strategy coded by her imprinting strategy allele is oblique, she acquires imprinted phenotype P with probability $(M'_{ST+} M'_{sT})$ and imprinted phenotype p otherwise. Finally, each T or t allele in each offspring mutates to the opposite allele with probability 10^{-4} . The offspring of all parental combinations are pooled to form the population at the start of the next generation.

Appendix 2 Evolutionarily stable imprinting strategies when the number of mating rounds is large.

In the main text, we assumed that the social pair formation phase comprises 50 rounds, with 10% of females meeting potential partners in each round. Thus, every female can expect to encounter 5 potential social partners.

The percentage of females that meets potential partners in each round determines how males are removed from the pool of available partners between pairing opportunities. If every female meets a male in every round, then a female that rejects a potential partner will not see another male until every other female has also had a pairing opportunity. This means that many high-quality males will be removed from the pool of available partners between pairing opportunities, which limits the benefit of choosiness. If a smaller percentage of females meets potential partners in each round, then a smaller number of high quality males are removed in each round, and a female that rejects a potential partner in one round may meet a high-quality male in the next. This makes rejecting potential partners less risky and favors the evolution of choosiness. In nature, females are unlikely to encounter potential partners in a strictly maintained order, as high meeting rates imply. Thus, we modelled a 10% meeting rate in the social pair formation phase because it is biologically plausible. During the extra-pair mating phase, males are not removed from the mating pool between encounters, so the percentage of females that meets males in each round of extra-pair mating does not affect the pool of available mates. Therefore, we set the meeting rate during extra-pair mating to 100% to increase computational speed.

Increasing the number of rounds of social pair formation increases the number of pairing opportunities for each female, and reduces the probability that choosy females fail to find partners. This favors the evolution of choosiness. At the same time, changing the number of rounds changes the pool of available males that choosy females encounter. In later mating rounds, most of the high-quality T males have been chosen, and many of the remaining males have the lower quality t phenotype. Many of the remaining females are p females (*i.e.*, they are imprinted on the t phenotype) that failed to find mates when T males were common. In later rounds of social pair formation, p females are likely to encounter t males, and so are likely to mate. Thus, adding rounds of social pair formation reduces the cost of imprinting for p females and increases the mating probability for t males more than it does for P females and T males.

By modelling a small number of social pairing rounds in the main text, we captured systems in which high-quality males are common in all rounds of social pair formation. This may be true in systems where many males are left unpaired, or if generations overlap or males reach sexual maturity at different times, so there is a constant influx of high-quality unpaired males into the pool of available social partners. However, in some systems in nature, high-quality males may become scarce over the course of the pairing season. In this appendix, we studied this case by modelling a system with 500 rounds of social pair formation. As in the main text, we assumed that 10% of females meet potential partners in each round. To keep the expected number of social pairing and extra-pair mating opportunities equal, we increased the number of extra-pair rounds to 50. Otherwise, the model is identical to that presented in the main text.

Figure A2.1 shows the evolutionarily stable imprinting strengths for the maternal, paternal, and oblique modes in the BP scenario (*i.e.*, when imprinting for both social partners and extra-pair mates can evolve) when there are 500 rounds of social pair formation. Figure A2.2 shows the evolutionarily stable imprinting modes in the same scenario. The qualitative results from the main text hold: i) when selection on the target trait is weak, choosiness for the social partner becomes strongest at intermediate levels of extra-pair paternity (Fig. A2.1 C, E), and ii) in systems with high extra-pair paternity, maternal imprinting is more advantageous than paternal imprinting (Fig. A2.2). The imprinting strengths that evolve differ from those in systems with fewer mating rounds. Imprinting for the social partner becomes stronger when there are more rounds of social pair formation. This is because choosy females have a greater chance of finding mates, and therefore the cost of choosiness is lower. Under oblique imprinting, the frequency of female mate preferences exactly matches the frequency of available male phenotypes, so even under very strong oblique imprinting all females eventually find acceptable social partners. Under maternal and paternal imprinting, the frequency of female preferences does not exactly match the frequency of available males, and some choosy females do not find social partners. Thus, the cost of imprinting is higher and the stable imprinting strength for social partner choice is lower under parental imprinting. In contrast, the stable imprinting strength for extra-pair mate choice is weaker when there are more rounds of mating. Perfect imprinting ensures that common P females do not accept rare t males as extra-pair mates, but also ensures that p females will either accept t males or fail to find extra-pair mates. If imprinting is imperfect and there are many rounds of extra-pair mating, then many p females will accept T males before they encounter t males. Thus, imperfect imprinting maximises the proportion of T males chosen, and is favored by selection.

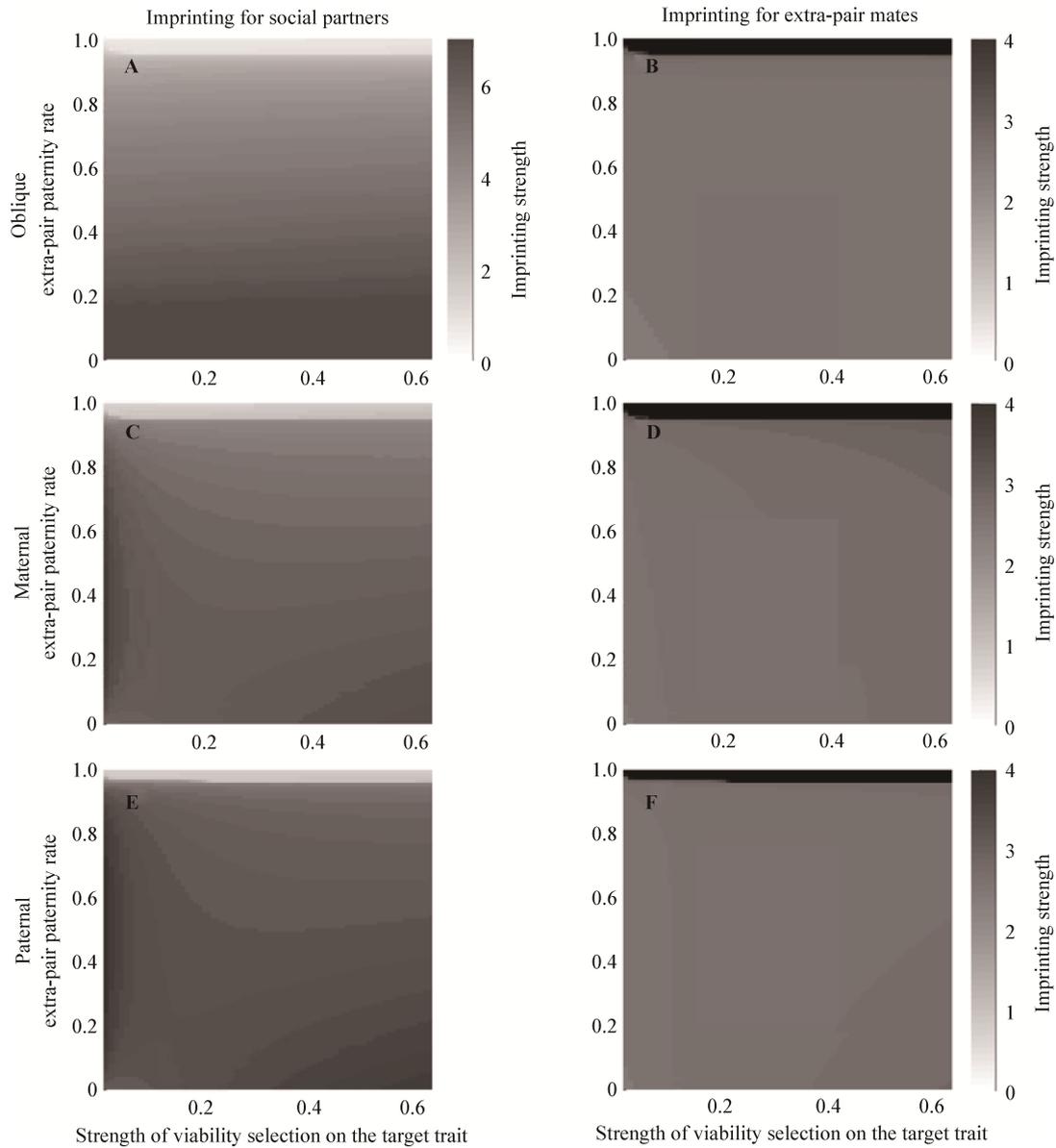


Figure A2.1 Evolutionarily stable imprinting strengths for (A, C, E) social partners and (B, D, F) extra-pair mates in the oblique (A, B), maternal (C, D) and paternal (E, F) imprinting modes in the BP scenario when there are 500 rounds of social pair formation. Black areas indicate perfect imprinting. The color scaling of panel A differs from that of the other panels.

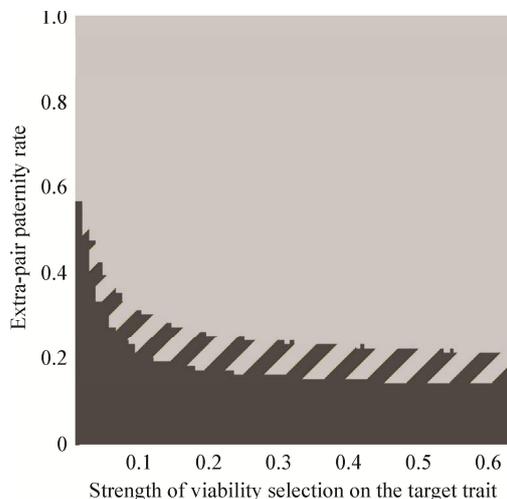


Figure A 2.2 Evolutionarily stable imprinting modes in the BP scenario when there are 500 rounds of social pair formation. Paternal (maternal) imprinting is stable in dark (light) gray areas. In the striped area, there are alternative stable states. Corresponding imprinting strengths are shown in figure A2.1.

Appendix 3 The evolutionarily stable imprinting strength for social partners depends on the imprinting strength for extra-pair partners.

In the main text, we showed that imprinted preferences for social partner phenotypes evolved to be stronger when females also use imprinted preferences to evaluate extra-pair mates. There, we assumed that there was no limit to how strong imprinting for extra-pair mates could become. In nature, imprinting strength may be subject to sensory, neurological, physiological, or behavioral constraints. Here, we show how the evolutionarily stable imprinting strength for social partners depends on the imprinting strength for extra-pair mates (α_{EP}). We placed limits on how strong imprinting for extra-pair mates could become, and then allowed imprinting to evolve as in the BP scenario. The stable imprinting strength for social partners was always less than 0.4. Therefore, to increase the resolution of our results, we reduced the evolutionary step size for imprinting strength to 0.002 (rather than 0.1 as in the main text).

Figure A3.1 shows the evolutionarily stable imprinting strength for social partner choice as a function of the extra-pair paternity rate for values of α_{EP} in the set $\{0, 0.5, 1, 2, 4\}$ when the fitness effect of the target trait allele is $c_t = -0.1$. Stronger imprinting for extra-pair mates leads to stronger imprinting for social partners. When extra-pair mates are chosen at random, imprinting strength for social partners declines monotonically as the extra-pair paternity rate increases. When females use imprinted phenotypes to evaluate extra-pair mates, imprinting strength for social partners is highest when extra-pair paternity rates are intermediate. This pattern is more pronounced when imprinting for extra-pair partners is stronger. The mechanism is explained in the main text.

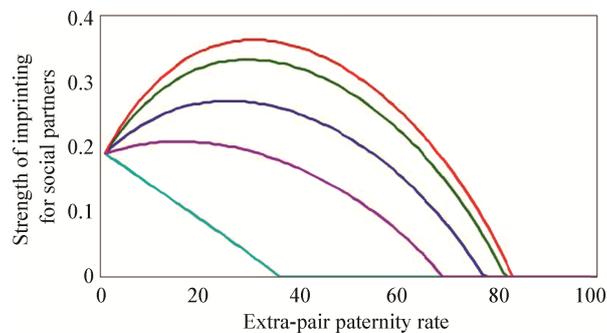


Figure A 3.1 Imprinting strength for social partners as a function of the extra-pair paternity rate (u) when the imprinting strength for extra-pair mates is 0 (light blue), 0.5 (purple), 1.0 (dark blue), 2.0 (green), or 4.0 (red).