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The influence of pleiotropy between viability and pollen fates on mating system evolution

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HIGHLIGHTS

- I model pleiotropy between viability and pollination.
- Such pleiotropy expands opportunities for the evolution of "mixed mating".
- Mixed mating evolves with high inbreeding depression, even lacking pollen limitation.

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ABSTRACT

Floral displays are functionally and genetically integrated structures, so modifications to display will likely affect multiple fitness components (pleiotropy), including pollen export and self-pollination, and therefore selfing rate. Consequently, the great diversities of floral displays and of mating systems found among angiosperms have likely co-evolved. I extend previous models of mating system evolution to determine how pleiotropy that links viability (e.g., probability of survival to reproduction) and the allocation of pollen for export and selfing affects the evolution of selfing, outcrossing, and in particular, mixed mating. I show that the outcome depends on how pollen shifts from being exported, unused, or used for selfing. Furthermore, pleiotropy that affects viability can explain observations not addressed by previous theory, including the evolution of mixed mating despite high inbreeding depression in the absence of pollen-limitation. Therefore, pleiotropy may play a key role in explaining selfing rates for such species that exhibit otherwise enigmatic mating systems.

1. Introduction

Floral displays are functionally integrated structures (Armbruster et al., 2004; Harder, 2009; Bissell and Diggle, 2010), so mutations that affect the morphology of a floral display will affect multiple functions. For example, the relative positions of floral parts determine both how a pollen vector (e.g., wind, insect) removes pollen from anthers and its deposition onto stigmas (e.g., *Pontederia cordata*, Harder and Barrett, 1993, Harder, 2000). In addition to this functional integration, floral displays are genetically integrated, as indicated by extensive genetic correlations among display traits (Armbruster et al., 2004; Ashman and Majetic, 2006; Bissell and Diggle, 2010). Integration at both functional and genetic levels likely imposes constraints that affect the evolutionary divergence of populations (Schluter, 1996), so that pleiotropy (*i.e.*, when a locus affects multiple traits) has important consequences for the diversity of floral displays.

Pleiotropy also holds important consequences for the evolution of selfing rates (Ritland, 1991; Kohn and Barrett, 1994; Galen, 1999; Fishman, 2000), which vary from complete outcrossing to almost complete selfing among plants (Goodwillie et al., 2005). For example, pleiotropy that affects pollen export can reduce the transmission bias for an allele that increases selfing (Johnston, 1998). A transmission bias arises because an allele that increases selfing can be passed to the next generation in three doses (two doses in a selfed seed and one in pollen exported to other plants) whereas an allele that causes strict outcrossing is transmitted in only two doses (one in the maternal seed and one in seeds sired on other plants; Fisher, 1941, Porcher and Lande, 2005). This transmission bias favours the evolution of increased selfing, but it can be reduced by either pollen discounting (the reduction in pollen export due to its use in self-pollination, Harder and Wilson, 1998) or inbreeding depression (δ; Charlesworth and Charlesworth, 1987). Classic models of mating system evolution based on the transmission bias tend to predict the evolution of either complete selfing

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or outcrossing when inbreeding depression is low ($\delta < \frac{1}{2}$) or high ($\delta > \frac{1}{2}$), respectively (reviewed in Johnston et al., 2009). However, mixed mating (the use of both self- and outcross-pollen for mating) can evolve when pleiotropy causes the rate of pollen discounting to increase with the selfing rate (e.g., Johnston, 1998). On a more general level, numerous models have shown that pleiotropy between aspects of pollination (e.g., attraction: Lloyd, 1979; modes of selfing: Schoen et al., 1996, Harder and Wilson, 1998; male and female function: Johnston et al., 2009) and selfing rate affect the conditions under which complete selfing, complete outcrossing, or mixed mating evolve.

Variation in floral and inflorescence characteristics can also be subject to viability selection (i.e., the probability of survival to reproduction, or differences in fertility that are not dependent on sex; reviewed by Strauss and Whittall, 2006), so that selection by non-pollinating agents can affect mating system evolution via pleiotropy (Galen, 1999). For example, unpredictable or stressful environments can favour faster development, which is often associated with production of smaller flowers (e.g., Guerrant, 1989, Runions and Geber, 2000, Elle, 2004, Mazer et al., 2004, Snell and Aarssen, 2005); in some cases, small-flowered genotypes experience very large viability benefits (e.g., *Mimulus guttatus*; Mojica and Kelly, 2010). In turn, opportunities for self pollination can change (reviewed by Elle, 2004), for example, because faster development affects within-flower temporal separation of sex functions (Mazer et al., 2004) or decreases in flower size affect anther–stigma distance (Armbruster et al. (2002), but see Fenster et al. (1995)). Hence, flower size variation may accompany both viability and mating system differences; (Jordan and Otto, 2012) provide further examples and discussion.

Pleiotropy between selfing rate and viability may be critical for explaining mating systems in some species, particularly those with both mixed mating and high inbreeding depression (for examples, see Husband and Schemske, 1996). Although many models can explain mixed mating in species with low inbreeding depression (e.g., Uyenoyama, 1986, Holsinger, 1991, Yahara, 1992, Ronfort and Couvet, 1995, Johnston, 1998, Rausher and Chang, 1999; reviewed by Goodwillie et al., 2005), explanations for mixed mating in species with high inbreeding depression typically require that self-pollen provides reproductive assurance (e.g., Lloyd, 1979, Iwasa, 1990, Schoen and Brown, 1991, Lloyd, 1992, Sakai, 1995, Morgan and Wilson, 2005, Johnston et al., 2009, but see Harder et al., 2008), which does not apply to all species (e.g., Eckert and Herlihy, 2004). With pleiotropy between viability and selfing, viability benefits could allow selfing to invade outcrossing populations with high inbreeding depression and resource-limited reproduction; however, it is not obvious whether, following initial invasion, such viability benefits will be so strong as to cause the evolution of complete selfing, or whether stable mixed mating can evolve. The effects of pleiotropic interactions with viability on mating system evolution remain largely unexplored.

Here, I model the effect of viability selection on mating system evolution through pleiotropy, when selfing rates are functions of the relative amounts of self- and outcross-pollen received; Holsinger (1991) termed this formulation a "mass-action" model. Under mass-action, a genotype's selfing rate depends on both the amount of self-pollen it deposits and the amount of outcross pollen received from the other genotypes in the population. Therefore, selfing rates depend on the composition of the population if genotypes export different quantities of pollen (mating is frequency-dependent; Ross, 1990). The mass-action models considered here can describe the evolution of "competing selfing" (autonomous selfing that occurs at the same time as outcross pollen may arrive; Lloyd and Schoen, 1992), "facilitated selfing" (within-flower self-pollination due to a pollinator's actions; Lloyd and Schoen, 1992), or selfing due to geitonogamy (between-flower self-pollination). These modes of selfing all involve the simultaneous deposition of self- and outcross-pollen, so that they can be modelled similarly (but see Lloyd, 1992 for different treatments of these selfing modes). Compared to prior-selfing (anthers dehisce, stigmas become receptive and self-pollination occurs before flowers open; Lloyd and Schoen, 1992) or delayed-selfing (selfing occurs after the receipt of outcross pollen; Lloyd and Schoen, 1992), facilitated selfing and geitonogamy do not require special mechanisms for selfing (Holsinger, 1991; Lloyd and Schoen, 1992) and so may be more common. In a companion analysis, Jordan and Otto (2012) considered the joint effects of pleiotropy between pollen discounting and viability selection on mating system evolution when the population composition does not affect selfing rates (i.e., mating is frequency-independent); that is, their work characterized the evolution of "prior selfing". The biological and mathematical differences between frequency-dependent and frequency-independent mating warrants separate analyses of the effects of pleiotropy on mating system evolution. Results with prior selfing revealed diverse effects of viability selection for mating system evolution, including the unique result that mixed mating can evolve despite extremely high inbreeding depression, in the absence of pollen-limitation. Together, the current analysis and that of Jordan and Otto (2012) assess the impacts of pleiotropy between viability and selfing rate for most modes of selfing described by Lloyd and Schoen (1992).

Under mass-action models, female selfing rates can rise due to reductions in outcross-pollen receipt, increases in the amount of self-pollen deposited, or both. Hence, I consider all of these scenarios for a complete analysis of mating system evolution. Due to current interest in factors that cause mixed mating (Goodwillie et al., 2005; Igic and Busch, 2013), my analysis focuses on the influence of viability selection on the evolution of stable mixed mating (i.e., convergence stable, where neighbouring states evolve towards this state; Eshel, 1996). This analysis reveals that consideration of pleiotropic effects on viability greatly affects predictions for mating system evolution.

2. Model description

2.1. Characterizing pollen use and pleiotropy

The model considers a single, diallelic (A, a) locus that affects both viability and pollen use, where ij denotes the unordered genotypes AA, Aa, and aa; Table 1 summarizes the model's parameters. I assume pollen can be divided into three fractions (S_{ij}, X_{ij}, N_{ij}) that each experiences one of three fates and can differ among genotypes (ij) (cf. Harder and Wilson, 1998, Harder et al., 2008): deposition on stigmas as self-pollen, S_{ij}, removal by pollinators with the opportunity to be exported to other plants, X_{ij}, or remaining in anthers or otherwise not used in the pollination process (e.g., removed from the flower by a non-pollinating agent), N_{ij}, such that $S_{ij} + X_{ij} + N_{ij} = 1$. Note that not all pollen in the pools S_{ij} and X_{ij} successfully fertilizes ovules, and N_{ij} does not include these unsuccessful pollen grains. In the following analyses, I consider shifts in pollen use among all three possible combinations of these fates.

For illustration, imagine that evolution occurs through selection on an underlying floral (or plant) trait (e.g., flower size or colour, resistance to a virus) that simultaneously affects viability and the fraction of pollen used for self-pollination (S_{ij}) and/or export (X_{ij}). When a mutant allele, a, invades a population fixed for the A allele, it alters the underlying trait by an amount, ϕ, which can change both viability and pollen use.

Fitness is measured relative to that of the resident genotype, AA. With respect to viability (or non-sex-specific fertility), the homozygous mutant genotype has a relative viability of $W_{aa} = 1 + \upsilon\phi$. Here υ represents the sensitivity (i.e., rate of change)