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# SEXUAL CONFLICT OVER FLORAL RECEPTIVITY

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*Abstract.*—In flowering plants, the onset and duration of female receptivity vary among species. In several species the receptive structures wilt upon pollination. Here we explore the hypothesis that postpollination wilting may be influenced by pollen and serve as a general means to secure paternity of the pollen donor at the expense of female fitness. Taking a game-theoretical approach, we examine the potential for the evolution of a pollen-borne wilting substance, and for the coevolution of a defense strategy by the recipient plant. The model without defense predicts an evolutionarily stable strategy (ESS) for the production of wilting substance. The ESS value is highest when pollinator visiting rates are intermediate and when the probability that pollen from several donors arrives at the same time is low. This finding has general implications in that it shows that male traits to secure paternity also can evolve in species, such as plants, where mating is not strictly sequential. We further model coevolution of the wilting substance with the timing of stigma receptivity. We assume that pollen-receiving plants can reduce the costs induced by toxic pollen by delaying the onset of stigmatic receptivity. The model predicts a joint ESS, but no female counter-adaptation when the wilting substance is highly toxic. This indicates that toxicity affects the probability that a male manipulative trait stays beneficial (i.e., not countered by female defense) over evolutionary time. We discuss parallels to male induced changes in female receptivity known to occur in animals and the role of harm for the evolution of male manipulative adaptations.

*Key words.*—Arms race, floral longevity, pollen competition, pollination, protandry, receptivity.

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Over all reproductive modules, the female function of many plant species is often pollen limited (De Jong and Klinkhamer 2005). Nevertheless, in animal-pollinated plants, pollen deposited on single flowers often exceeds the number of fertilizable ovules (Levin 1990; Bernasconi et al. 2006a) and is derived from genetically different pollen donors (Ellstrand 1984; Marshall and Ellstrand 1985; Campbell 1998; S. Teixeira and G. Bernasconi, unpubl. ms.), providing opportunity for competition among different pollen donors for fathering the seeds (Delph and Havens 1988; Snow and Lewis 1993; Stanton 1994; Bernasconi 2003).

The length of time a flower is open and the duration of receptivity of female function beyond the first pollen deposition may influence the number of effective pollinator visits and thus reproductive success. Specifically, variation in floral longevity may affect the number and genetic diversity of competing pollen donors (Primack 1985; Galen et al. 1986; Bingham and Orthner 1998; Ashman 2004) and yield a range of benefits to the pollen recipient. These include ensuring sufficient pollen; optimizing genetic composition of the pollen load; increasing the probability of outcrossing; and increasing number, genetic diversity or quality of the offspring (Schemske and Pautler 1984; Schlichting et al. 1987, 1990; Niesenbaum 1999; Skogsmyr and Lankinen 2000; Armbruster 2002a; Paschke et al. 2002, 2005; Barrett 2003; Bernasconi et al. 2003, 2004, 2006b; Rathcke 2003). Although the causes and mechanisms leading to fitness benefits can be complex, our point here is that prolonged receptivity can increase female fitness at least under some circumstances.

From the perspective of a given pollen donor, however, prolonged female receptivity beyond pollen deposition is very likely to be disadvantageous, because it leads to pollen competition and possible loss of paternity. Pollen that can induce wilting of the recipient upon arrival on the stigma will avoid or reduce competition to its own advantage and to the advantage of the pollen parent. This is analogous to the ‘‘defense ability’’ described in animal sperm competition (Service and Vossbrinks 1996). Consequently, there is a potential conflict between pollen-donor and pollen-recipient plants over receptivity of female function beyond the first pollen deposition, similar to male-female conflict over remating in animals (Rice and Holland 1997; Arnqvist and Rowe 2005). Selection will favor pollen (or pollen donors) that are able to reduce the chances of fertilization of later-arriving pollen.

This idea of male tactics to secure paternity rests on empirical evidence that pollen deposition elicits changes of the receptive structures and induces floral wilting (Gori 1983; Primack 1985; Lloyd and Webb 1986; O’Neill 1997) in many flowering plant species (at least 60 genera, not including the orchids; van Doorn 1997). Senescent flowers become unattractive to pollinators and receive fewer or no visits (Gori 1983; Lloyd and Webb 1986), and success of later-arriving pollen is lowered for longer interpollination intervals in several species (Marshall and Ellstrand 1985; Cowan et al. 2000; Snow et al. 2000). Postpollination changes include wilting (Primack 1985; Preston 1991; Aizen 1993; O’Neill 1997; Bingham and Orthner 1998; Meagher and Delph 2001; Arathi et al. 2002; Young and Gravitz 2002), perianth senescence, changes in flower pigmentation, cessation of nectar and scent

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production, and development of the ovary (O'Neill 1997). Postpollination wilting can reduce longevity of pollinated flowers very rapidly, with a typical timing pattern (Gori 1983; Herrero and Arbeola 1989). Consistent with pollen-mediated effects, these changes are linked to pollen receipt rather than pollen export. For example, in *Mimulus guttatus*, reduced longevity is triggered by the successful deposition of pollen on the stigma but not by removal of pollen from the flower (Arathi et al. 2002; see also Proctor and Harder 1995; Clayton and Aizen 1996). It is unclear whether any of these postpollination changes evolved through sexual conflict, yet they are at least consistent with male-manipulation of female receptivity (Arnqvist and Rowe 2005; Bernasconi et al. 2006b), which we will explore here.

Possible mechanisms of pollination-induced wilting may be directly mediated by substances on the pollen coat (Zinkl and Preuss 2000; Fiebig et al. 2004), through alleles expressed in the gametophyte (da Costa-Nunes and Grossniklaus 2003; Bernasconi et al. 2004), or paternal alleles expressed in the developing embryo (e.g., Shaanker and Ganeshaiah 1989). Evidence supports a pollen-borne chemical, since pollination-regulated development precedes pollen germination or pollen tube growth and happens before embryo formation (O'Neill 1997). In most species, this primary pollination event is accompanied by an increase in ethylene evolution in the stigma and style shortly after pollination. Candidates for the primary pollen signal that induce ethylene biosynthesis have been identified in pollen, including pollen-borne 1-aminocyclopropane-1-carboxylic acid, auxin, pectic oligosaccharides, brassinosteroids, and methyl jasmonate (O'Neill 1997; Taylor and Hepler 1997; see also Jones 2002). Interestingly, substances on the pollen coat have been reported to be toxic to insects (Stanley and Linskens 1974, pp. 104–105; Pimentel de Carvalho and Message 2004).

Theoretical studies investigated the male and female points of view separately. This included male-male competition up to pollen deposition by investigating how plant characteristics (e.g., number of pollen grains produced, efficiency of pollen delivery) affect male mating success (Harder and Thomson 1989; Stanton 1994) and optimal floral longevity for recipient plants, assuming a trade-off in resource allocation between floral construction and maintenance (Ashman and Schoen 1994; Schoen and Ashman 1995). These models, however, did not consider that changes in recipient longevity can also accrue costs and benefits to pollen donors and influence male mating success at the expense of the interest of the recipient. In fact, floral longevities across taxa were shorter than predicted by these models (Ashman and Schoen 1994; Schoen and Ashman 1995). To account for this discrepancy, in the present study we focus on donor-mediated effects on the recipients and recipient responses.

Pollen-receiving plants (female function) may evolve resistance to manipulation of receptivity schedules, that is, counter pollen-induced wilting to again enhance pollen capture. Indeed, it has been proposed that delayed fertilization increases the time for mate choice to the benefit of the female function (Willson and Burley 1983; Galen et al. 1986; Herrero 2003). This is consistent with empirical evidence suggesting that several female traits play an active role in controlling pistil-pollen interactions (e.g., Herrero and Arbeola 1989; Higashiyama et al. 2001; Herrero 2003), and that the number of competing pollen tubes in the pistil can increase due to female influences on postpollination receptivity (Ganeshaiah and Shaanker 1988; Douglas and Cruden 1994; Hormaza and Herrero 1994; Dahl and Fredrikson 1996). In *Talinum mengesii* (Portulacaceae), pollen germination is delayed after pollination only in some populations. In this example, reciprocal pollinations between plants with and without the delay trait revealed that the recipient regulates the timing of pollen germination (Murdy and Carter 1987). It is also known that pollen capture can precede stigma receptivity, such as in *Collinsia* species (Armbruster et al. 2002b).

Here, we develop a game-theoretical model that examines the potential for the evolution of pollen capable of inducing floral wilting in the recipient plant. In our model, pollen (or pollen donors) can influence female receptivity after pollen deposition in an animal-pollinated plant. Our rationale (using the example of a pollen-transmitted chemical) is that pollen-induced stigmatic wilting manipulates the recipient plant's reproduction and thus serves to secure paternity against later-arriving pollen. We assume that pollen that can chemically induce wilting in the recipient gains advantage during pollen competition. We consider events affecting stigmatic receptivity after pollen deposition but before fertilization, and thus events that are independent of gene expression in developing embryos or parent-offspring conflict (De Jong et al. 2005). We explore two scenarios: the recipient either can or cannot defend itself. Thus, we also study coevolution between the pollen-borne wilting substance and delayed onset of receptivity as a defense strategy by the pollen recipient. We examine the influence of various parameters including costs to pollen donors of producing a pollen-borne wilting substance, and benefits and costs to pollen recipients of delaying floral receptivity. In the coevolutionary scenario we include costs for the recipient associated with variable levels of toxicity of the wilting substance. When evaluating a conflict over female receptivity in plants, it is necessary to consider the process of pollination, thus extending models assuming biological aspects of animal mating (e.g., Parker 1979; Johnstone and Keller 2000; Lessels 2005). Our model explicitly takes into account aspects of the pollination process, such as that animal-pollinated plants will often receive pollen from several donors simultaneously (pollen carryover). We then discuss the simplifying assumptions of the model and alternative hypotheses. Indeed, scenarios of reproductive harmony (i.e., that both donor and recipient benefit from rapid wilting) are also possible, yet our focus here is to show that sexual conflict over female receptivity, a well-documented phenomenon in animals (e.g., *Acp* proteins in *Drosophila*), may more generally apply to all sexually reproducing species, including plants (Chapman et al. 2003; Bernasconi et al. 2004; Arnqvist and Rowe 2005).

## MODEL

For simplicity we assume that each plant in a given population generates a single flower with only one ovule and pollen that produces an amount $s$ of wilting substance (continuous trait $\geq 0$) at a cost $c_s$ per pollen grain (Table 1). Plants are insect pollinated and self-incompatible. Individual

TABLE 1. Definition of variables and parameters in the ESS model of sexual conflict over floral receptivity.

| Notation | Definition |
|---|---|
| $s$ | amount of wilting substance produced per pollen grain, a continuous trait ($s \geq 0$) |
| $y$ | timing of stigma (female function) receptivity, a continuous trait ($0 \geq y \geq 1$); flowers can become receptive between the onset of flower opening ($y = 0$) and the end of the lifetime of the flower ($y = 1$) |
| $r$ | visitation rate by pollinators per time unit ($r > 1$); during a visit, pollinators both deposit pollen from previously visited flowers and collect pollen that will be deposited on the next visited flowers (Fig. 1) |
| $x$ | number of pollen donors that pollinators carry pollen from; we assume either $x = 1$ (all pollen deposited on a stigma derives from the last visited flower, i.e., no pollen carryover) or $x = 2$ (pollinators carry a mixture of pollen from the two last visited flowers, Fig. 1) |
| $n$ | number of pollen grains deposited per visit ($n \geq 1$) |
| $t$ | time period a flower is open before wilting; the maximum flower opening time occurs in the absence of wilting substance and is $t = 1$ |
| $a$ | rate of accumulation of wilting substance during the lifetime of a flower as a function of wilting substance per pollen grain |
| $V$ | absolute number of pollinator visits to a plant's unique flower, as a function of the amount of wilting substance per pollen grain or both wilting substance per pollen grain and timing of stigma receptivity, respectively |
| $k$ | a constant ($0 < k < 1$) |
| $S$ | total amount of wilting substance that accumulates on one pollen recipient flower during its lifetime |
| $M$ | number of pollen recipients a pollen donor will spread its pollen to |
| $F$ | pollen donor benefit obtained per flower when fertilizing a seed in competition with other pollen |
| $B$ | pollen donor benefit obtained when a pollen grain actually fertilizes the only seed |
| $c_s$ | pollen donor cost of producing the wilting substance per every produced pollen grain |
| $\beta$ | pollen recipient benefit obtained when more pollen compete on the stigma; we assume that arrival by additional pollen increases the genetic quality of the resulting progeny |
| $b$ | maximum pollen recipient benefit for higher number of pollen on the stigma, that is, after a given number of competing pollen the genetic quality of the resulting progeny will no longer improve |
| $l$ | a constant |
| $P$ | toxic effect of the wilting substance on the pollen recipient as a function of wilting substance per pollen grain; we assume that toxicity decreases fitness of the pollen recipient, for example, by lowering the quality of the resulting progeny |
| $p$ | toxic effect of the wilting substance measured per pollen grain |
| $c_y$ | female cost of delaying stigmatic receptivity |

pollinators carry a constant pollen load containing a mixture of $n(x + 1)/x$ pollen grains from the last $x$ plants they have visited ($x \geq 1$; Fig. 1). We consider either one ($x = 1$) or two ($x = 2$) pollen donors. We refer to pollen carryover only in the latter case, when insects deliver to the recipient flower pollen from the last two plants they visited. Thus, at each flower visit pollinators deliver $n$ pollen grains either from a single donor ($x = 1$) or from a mixture of pollen from two donors ($x = 2$) to the stigma and pick up $n$ new grains from the anthers of the currently visited plant (Fig. 1). We further

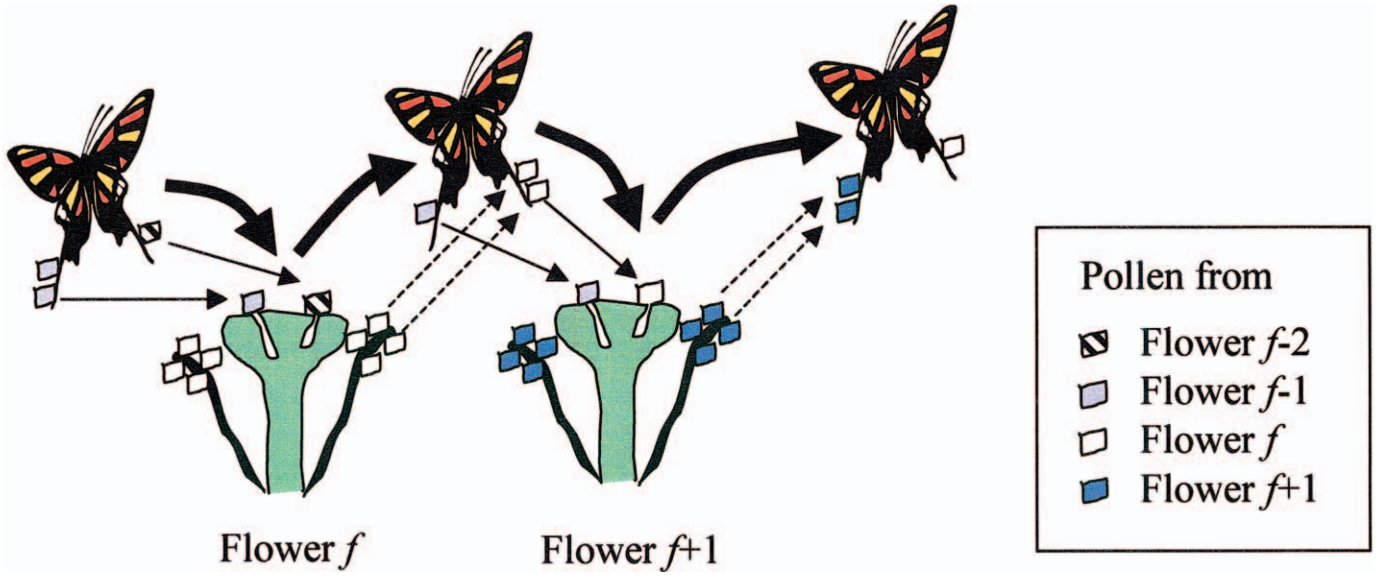

FIG. 1. Pollen deposition patterns assumed in the ESS model of sexual conflict over floral receptivity. Pollinators carry a constant pollen load containing a mixture of $n(x + 1)/x$ pollen grains from the last $x$ plants visited (here $n = 2$ and $x = 2$). The pollinator delivers $n$ pollen grains from this mixture to the stigma (solid arrow) and picks up $n$ new grains from the anthers of the current plant (dashed arrow). As $n/x$ grains are delivered to a stigma per donor, all $x$ pollen donors contribute equally to the pollen load on the stigma.

assume that all $x$ donors contribute equal proportions to the $n$ pollen that are deposited at a single visit, that is $n/x$ grains per donor. All nonwilting flowers are visited by pollinators at the rate $r$; wilting flowers are never visited. In the absence of pollen-borne wilting substance, plants achieve the maximum flower opening time $t = 1$ (i.e., in general $0 \leq t \leq 1$) and attract $V$ visits by pollinators (i.e., $r = V/1 = V$ with only intrinsic wilting). When pollen that produces wilting substance has been delivered to the stigma, the substance accumulates on the recipient flower at the rate

$$a(s) = rns. \tag{1}$$

Because we assume that a flower is vulnerable to the wilting substance only when the stigma is receptive, we can investigate two different scenarios. Plants may either lack or have the ability to defend themselves by influencing the time $y$ of onset of receptivity (continuous trait $\geq 0$). Flowers unable to delay receptivity will become receptive at flower opening ($y = 0$), while those achieving a maximum delay will become receptive only at the natural end of a flower lifetime ($y = 1$), but they also pay a developmental cost $c_y$, which may arise through the mechanisms to delay receptivity (e.g., by physiological allocation in mounting a defense against pollen germination and pollen tube penetration of the pistil [Herrero 2003] or by the risk of losing pollen from the stigma or of remaining unpollinated if pollen is short lived).

With the above assumptions for both scenarios, we obtain the following two equations for the number of visits per flower $V$ in a plant population where the wilting substance is produced.

If flowers are unable to delay receptivity, the number of pollinator visits a flower receives depends only on the amount of wilting substance produced per pollen grain ($s$) and its accumulation rate,

$$V(s) = 1 + (r - 1)k^{a(s)}. \tag{2a}$$

The first summand (1) reflects the fact that at least one visit is necessary for the substance to be present. The term $k^{a(s)}$ (with $0 < k < 1$) implies that for higher values of wilting substance accumulation rate, flowers wilt immediately after the first visit.

If flowers can defend themselves at least partially by delaying receptivity, the number of pollinator visits a flower receives also depends on this delay in the timing of receptivity ($y$),

$$V(s, y) = 1 + (r - 1)y + \{r - [1 + (r - 1)y]\}k^{a(s)}. \tag{2b}$$

The first two summands account for the number of visits before the stigma becomes susceptible to the wilting substance, the second summand being the gain of visits from delaying receptivity for $y$ time units. The total amount of wilting substance accumulating on the stigma during the lifetime of a flower adds to

$$S(s) = nsV. \tag{3}$$

Note that the number of visits per flower is denoted $V$, implying that it has to be read as $V(s)$ or $V(s, y)$ depending on the scenario. For simplicity, in the following we will use equivalent abbreviations to account for the two scenarios.

### *Fitness of the Pollen Donor*

The fitness $W_s$ of an individual plant through its male function (pollen) depends on the total number of flowers its pollen is transferred to, its success in fathering viable offspring, and the costs involved in producing the wilting substance. The following derives male fitness for wild-type plants with pollen producing the amount $s$ of wilting substance and for mutant invaders producing $s'$ of wilting substance. Each plant is assumed to transfer $n/x$ pollen grains to each of $M$ other flowers. The value of $M$ is determined by the number of pollinator visits an individual plant receives and the number of flowers to which pollinators will subsequently transfer pollen of this individual, $M = Vx$. As pollen grains are deposited on the stigma in mixtures from different donors (either simultaneously when there is pollen carryover [$x = 2$] or over time when there is no pollen carryover [$x = 1$]), they compete for fertilizing the single ovule and for the resulting fitness benefit $B$. We assume that the outcome of this competition is determined by a fair lottery among all pollen deposited prior to the onset of wilting ($Vn$; Parker 1990). There is neither an effect of arrival time on siring success nor of the production of wilting substance. That is, the probability for a pollen donor to actually fertilize a seed equals the proportional contribution of this donor to the pollen load on the stigma, $(n/x)/(Vn)$. The fitness gain $B$ from fathering a seed, therefore, has to be discounted by this probability, which depends on the intensity of pollen competition. Thus, the fitness benefit $F$ per flower for a pollen donor, is given by

$$F(s) = B\frac{n/x}{Vn} = \frac{B}{Vx} = \frac{B}{M}. \tag{4}$$

Let us consider a mutant plant with pollen that produces a different amount of wilting substance $s'$ in a population with wild-type $s$. The fitness $W_s$ of this mutant is determined by the cost of producing the wilting substance (through reduced pollen production) and by the functions $M(s)$ and $F(s, s')$ or $M(s, y)$ and $F(s, s', y)$ depending on the scenario. When one out of all pollen grains deposited on the stigma produces this different amount $s'$, the total amount of wilting substance $S$ accumulating during the lifetime of this flower changes to (cf. eq. 3)

$$\begin{aligned} S(s') &= ns(V - 1) + n\left[\left(1 - \frac{1}{x}\right)s + \frac{1}{x}s'\right] \\ &= nsV + \frac{n}{x}(s' - s). \end{aligned} \tag{5}$$

The accumulation rate of wilting substance on a stigma can be calculated from the total amount arriving over the whole time period a flower is open, that is $a(s) = S(s)/t$. Thus, a flower containing mutant pollen accumulates the substance at (cf. eq. 2)

$$a(s') = \frac{S(s')}{V/r} = \frac{rS(s')}{V}. \tag{6}$$

The fitness benefit $F(s, s')$ or $F(s, s', y)$ a mutant receives per flower when fathering a seed can then be determined from equation (4), using $a(s')$ instead of $a(s)$ to calculate $V$ from equation (2a) or (2b), depending on the scenario.

Finally, we assume that the cost $c_s$ of making the wilting substance increases linearly with the amount of substance manufactured per pollen grain and that a plant produces as many pollen grains as are picked up by pollinators when there is no induced floral wilting ($rn$). Depending on whether plants can or cannot delay stigma receptivity by $y$ time units, we obtain for fitness $W_s$ of the mutant:

$$W_s(s, s') = W_0 + M(s)F(s, s') - c_s rns' \quad \text{and} \qquad (7a)$$

$$W_s(s, s', y) = W_0 + M(s, y)F(s, s', y) - c_s rns', \qquad (7b)$$

where $W_0$ equals the basic fitness component. Because we are interested in a more general case, we assume linear fitness functions.

### *Fitness of the Pollen Recipient*

In the coevolutionary scenario the fitness $W_y$ of an individual plant through its female function (seeds) is determined by the benefit of receiving a variety of pollen, the cost of being exposed to the now also harmful wilting substance, and the cost of delaying stigma receptivity. The following derives fitness of pollen recipients, both for wild-type plants delaying stigma receptivity by $y$ time units and for mutant invaders achieving a delay of $y'$.

We assume that the fitness benefit to the recipient increases with the amount of pollen grains available on the stigma up to a maximum $b$, for example, due to higher genetic quality of progeny resulting from competition among more and genetically more diverse pollen. Consequently, flowers able to delay stigma receptivity will gain higher fitness than flowers that wilt early, because they will be able to receive more pollinator visits and thus to collect more pollen despite the occurrence of wilting substance. When we further assume that the maximum $b$ is reached in a logistic fashion, that is, the advantage of receiving additional pollen is highest when the stigma has received only a few pollen grains, the fitness benefit is

$$\beta = b(1 - e^{(1-V)nl}), \qquad (8)$$

where $V$ is number of pollinator visits, $n$ the number of pollen grains deposited per visit, and $l$ a scaling factor.

We assume that the wilting substance is harmful for recipient plants and that this cost cannot be avoided by delaying stigma receptivity. Note that it is only in our second scenario (coevolution between wilting substance and delay of stigma receptivity onset) that we consider costs to the pollen recipient, that the toxicity per se of wilting substance will matter. Furthermore, we assume that the poisonous effect $P$ increases quadratically ($s^2$) with the amount of wilting substance the recipient is exposed to

$$P = pVns^2, \qquad (9)$$

where $p$ describes the harmfulness of a single pollen grain.

In sum, the fitness $W_y$ of a mutant with stigma receptivity $y'$ in a population with the wild-type $y$ is determined by

$$W_y(s, y') = W_0 + \beta(s, y') - P(s, y') - c_y y', \qquad (10)$$

where $W_0$ is the basic fitness component and $c_y$ denotes the cost of delaying stigma receptivity.

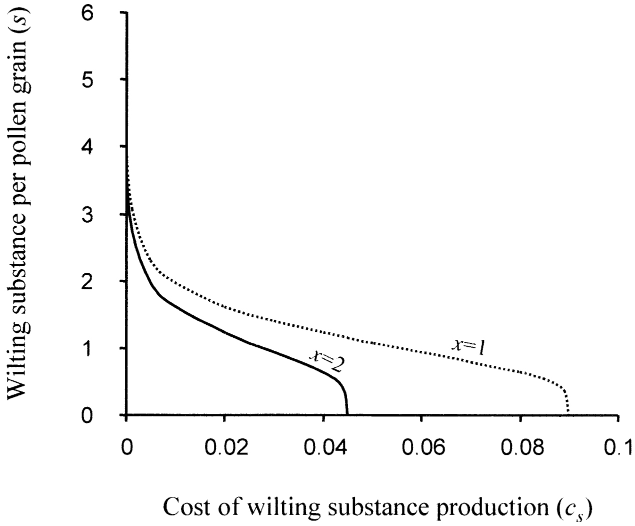

FIG. 2. ESS values of wilting substance per pollen grain ($s^*$, solid and dotted lines) in response to the cost to produce the substance ($c_s$), when pollen recipients cannot coevolve. The number of pollen donors contributing to the pollen load deposited during a pollinator visit is denoted by $x$, that is, only with $x = 2$ pollen carryover occurs. Stigma receptivity starts at the same time as flower opening, $y = 0$. Other parameter values are $n = 2$, $r = 3$, $k = 0.7$, $B = 1$ (see Table 1 and text for explanation).

### *Finding an Evolutionarily Stable Wilting Substance and Timing of Stigma Receptivity*

We first consider the evolution of wilting substance production by pollen donors when recipients cannot defend themselves, that is, the stigma becomes receptive when flowers open ($y = 0$). We then investigate the coevolutionary consequences when recipients can defend themselves by delaying stigma receptivity ($0 < y \leq 1$).

To search for the evolutionarily stable strategy (ESS) of wilting substance production in the absence of defense, ESS($s^*$), we use the standard approach for continuous strategies (Maynard Smith 1982; Bulmer 1994). There are two criteria for evolutionary stability, both of which have been taken into account in our analytical and numerical analyses (see Appendix 1, Figs. 2, 3). When both criteria are met, the population converges to the equilibrium $s^*$ (see Appendix 1).

To predict the joint ESS of wilting substance and timing of stigma receptivity, ESS($s^*$, $y^*$), that is, the outcome of coevolution of the two traits, we first determine the equilibrium trait values for both traits separately (Maynard Smith 1982; Bulmer 1994) and then proceed by solving the system of two equations with respect to both $s^*$ and $y^*$ (Tayler 1989; see Appendix 2; Fig. 4). Convergence stability of the joint equilibrium of both traits is investigated by analyses of the Jacobian in numerically derived points (Figs. 4a–d; Dieckmann and Law 1996; Leimar 2006).

## RESULTS

We derived numerical results for different cases (Figs. 2–4) and analytical results where possible (Appendix 1). In the numerical examples, parameter values were chosen to represent the general behavior of our system.

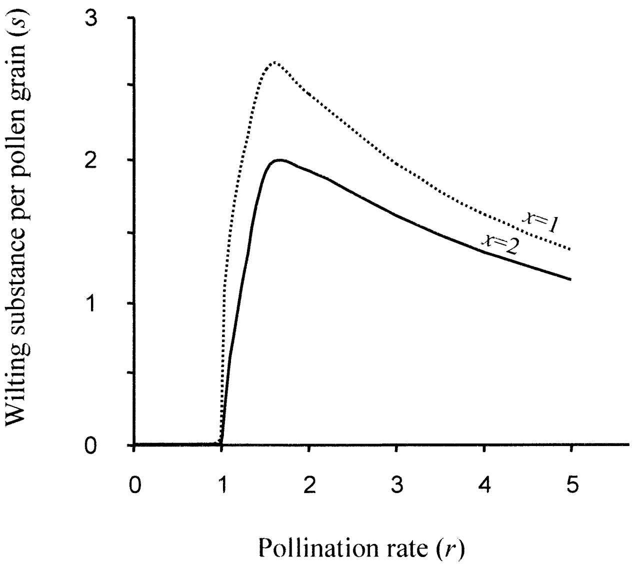

FIG. 3. ESS values of wilting substance per pollen grain ($s^*$, solid and dotted lines) in response to pollination rates ($r$), when pollen recipients cannot coevolve. As soon as pollination rates ($r$) are high enough to allow for more than one visit per flower, ESS values of wilting substance per pollen grain ($s^*$, solid and dotted lines) depart from zero. ESS values are higher for relatively low number of visits per time unit. In the absence of wilting substance, the maximum flower opening time is $t = 1$ and the number of visits during this time amounts to $V(s, y) = r$; $x$ is the number of pollen donors contributing to the pollen load deposited during a pollinator visit, that is, only with $x = 2$ pollen carryover occurs. Stigma receptivity starts at the same time as flower opening ($y = 0$). Set parameter values: $n = 2$, $k = 0.7$, $B = 1$, $c_s = 0.01$ (see Table 1 and text for explanation).

### *Evolutionary Outcomes of Varying Wilting Substance*

We find that producing wilting substance can be evolutionarily stable. Appendix 1 shows the conditions for stability and how the ESS($s^*$) depends on all parameters; Figures 2 and 3 exemplify its dependence on production cost $c_s$ and pollination rate $r$. Inducing floral wilting proves to be advantageous for pollen donors as soon as pollination rates are higher than one. The ESS amount of wilting substance increases with the net benefit to the pollen donor, balanced by the cost of producing the wilting substance. For high costs, the ESS amount will rapidly decrease to zero (Fig. 2). For low costs, the ESS amount will increase as long as a higher amount contributes to reducing the time during which the recipient flower is receptive to later-arriving pollen. A maximum benefit ($B/x$) is reached when the amount of wilting substance is so high that flowers start wilting immediately after a single pollinator visit (eq. 2a), and thus there are no benefits to gain from producing higher amounts of wilting substance.

The ESS amount of wilting substance is highest for a relatively low number of pollinator visits per unit time ($r$), as long as pollination rate exceeds one ($r > 1$, Fig. 3). Even though the benefit of producing wilting substance generally increases for a higher pollination rate because of the higher number of competitors that can be excluded if wilting is induced early (eqs. 2a, 4), this increase will gradually slow as the pollination rate and thus the number of competitors becomes higher. Production costs, on the other hand, will increase linearly with pollination rate due to the higher number of pollen produced (eqs. 7a, 7b). For this reason, the net gain of inducing wilting will be higher for low and intermediate pollination rates (as indicated by the steep rise and slow fall of the ESS curve in Fig. 3).

The ESS amount of wilting substance is strongly affected by how pollen is distributed (Figs. 2, 3). Pollen carryover (pollen from different $x = 2$ donors arrives simultaneously on the same flower), leads to a lower ESS amount of wilting substance. Indeed, when pollen is always transferred together with pollen from another individual, any investment in wilting substance will affect the fertilization success of pollen from competitors as much as that of the focus individual. A competitor will thus gain the benefit of a higher fertilization probability without paying the cost of producing the wilting substance. In this case, a mutant with a lower value of wilting substance can invade. Moreover, for higher costs of producing wilting substance, the substance can only evolve when there is no pollen carryover (Fig. 2).

### *Coevolution of Wilting Substance and Timing of Stigma Receptivity*

We find stable ESS combinations ($s^*$, $y^*$) for male and female strategies—the best pollen donor response $s^*(y)$ and the best pollen recipient response $y^*(s)$. That is, the amount of wilting substance produced by pollen and the delay of stigma receptivity can coevolve. While the general form of the female response could be derived analytically (Appendix 2), the male response curve and the joint ESS were determined numerically for various parameter combinations (Figs. 4a–d). Different parameter values, especially how toxic the wilting substance is and accordingly how large the fitness costs for females are, lead to three main cases. To better highlight the influence of toxicity level in the following, we only present examples in which we vary parameter values affecting pollen recipient fitness (Figs. 4a–d). However, which of the three cases results also depends on parameters influencing pollen donor benefits and costs (see below).

In the first case (Fig. 4a), the ESS amount of wilting substance is high and the stigma becomes receptive as soon as flowers open ($y^* = 0$). This solution is obtained when the wilting substance is very harmful. By delaying stigma receptivity, recipients can only delay the influence of the wilting substance but not prevent its damaging effect nor avoid the fitness costs. Selection favors recipients that receive as little wilting substance as possible even though this will result in less pollen on the stigma.

In the second case (Fig. 4b), high initial amounts of wilting substance result in the same ESS as in the previous case ($y^* = 0$, i.e., no defense), while for low initial amounts the stigma delays receptivity until late in the flower lifetime ($y^*$ close to 1). In the latter situation, it is evolutionarily stable for recipients to defend themselves against the negative effects of early wilting. Even though the toxic effects of the wilting substance cannot be avoided, its cost will be counteracted by the fitness benefit from competition among a larger number of diverse pollen grains. Simultaneously, a delayed onset of stigma receptivity lowers the benefit to the male of producing

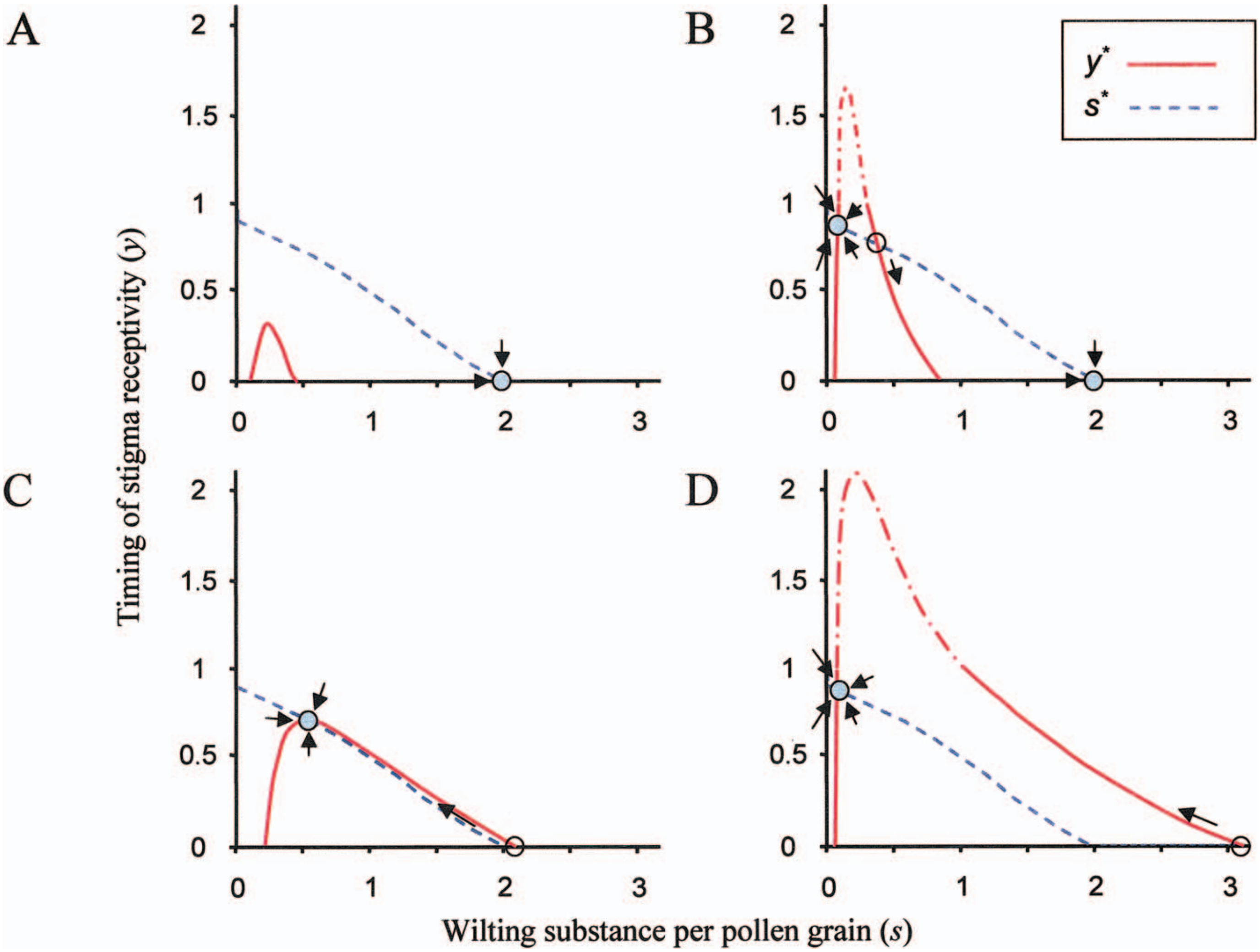

FIG. 4. Coevolution of the amount of wilting substance ($s$) and the timing of stigma receptivity ($y$), indicated by the joint ESS values of both traits. The timing of stigma receptivity is defined as a delayed onset, that is, the stigma can become receptive immediately when the flowers opens ($y = 0$), or when the flower has reached its maximum lifespan ($y = 1$; dash-dotted curves indicate where females should, theoretically, delay receptivity even further). Filled circles: evolutionary stable equilibria of both traits. Open circles: unstable equilibria. All stable ESS($s^*$, $y^*$) with $y \neq 0$ are convergence stable (see Appendix 2), as indicated by the arrows. In the four examples (A–D) parameter values are varied for female fitness only. The poisonous effect of wilting substance per pollen grain ($p$) and the partial net benefit of females (the maximum benefit of receiving a variety of pollen, $b$, versus the cost of delaying stigma receptivity, $c_y$) are (A) high ($p = 1$) and medium ($b = 1$, $c_y = 0.1$); (B) medium-high ($p = 0.5$) and high ($b = 1$, $c_y = 0.04$); (C) low ($p = 0.1$) and low ($b = 1$, $c_y = 0.2$); (D) low ($p = 0.05$) and high ($b = 1$, $c_y = 0.04$). Set parameter values: $x = 2$, $n = 2$, $r = 3$, $k = 0.7$, $B = 1$, $c_s = 0.005$, $l = 0.5$ (see Table 1 and text for explanation).

wilting substance, because most pollen has already been deposited when the wilting substance can start influencing the flower. Thus, at this second ESS the production of wilting substance is lowered substantially. This situation occurs when the wilting substance has medium to high toxicity, and the benefit/cost to females of delayed stigma receptivity (i.e., their partial net gain) is high.

In the third case (Figs. 4c,d), delayed stigma receptivity is evolutionarily stable but the exact timing of this delay varies depending on female partial net gain. Because the wilting substance has low toxicity and thus causes little harm, recipients are selected to defend themselves. When the partial net benefit of keeping the flowers receptive is high, selection for delayed stigma receptivity is strong (Fig. 4d). This also results in coevolution of lower values of wilting substance, as the male benefit of producing the wilting substance is reduced. For diminishing partial net benefit of keeping flowers receptive, females should decrease their defence accordingly, that is, become receptive earlier (Fig. 4c). This, in turn, will increase the optimal production of wilting substance. We did not find any stable solutions for relatively low female defense ($y^*$ closer to 0) and high values of wilting substance.

Male benefit/cost ratios and to some extent the occurrence of pollen carryover influence the outcome of coevolution. Higher male net benefit results in higher stable values of wilting substance production (Fig. 2), that is, the stable male curve ($s^*$) in Figure 4 moves upward for every value of stigma receptivity ($y$). This increases the probability of obtaining the first case (Fig. 4a) over the others (Figs. 4b–d), making it less likely for recipients to evolve defense. The occurrence of pollen carryover reduces the optimal amount of wilting substance (Figs. 2, 3). With pollen carryover, the probability of an evolutionarily stable solution where recipients delay stigma receptivity increases (Fig. 4b–d).

## DISCUSSION

Optimal floral receptive lifespan reflects the balance of fitness benefits (total floral display attractiveness to pollinators, amount and diversity of pollen received, and amount of exported pollen; e.g., Bingham and Orthner 1998; Harder and Johnson 2005) and costs (floral maintenance, Ashman and Schoen 1994; attractiveness to flower and seed predators, infection by pollinator-transmitted diseases, Shykoff et al. 1996). Through its fitness benefits, floral longevity and receptivity ultimately influence quantity and quality of the progeny produced.

Previous models investigated floral longevity as a response to intrinsic floral maintenance costs and the probability of receiveing compatible pollen (Ashman and Schoen 1994; Schoen and Ashman 1995). Floral longevities found in nature, however tended to be consistently shorter than predicted by the models. This may be due to an underestimation of the costs for floral maintenance. Alternatively, floral longevities may be shorter than predicted under optimal maintenance costs because of extrinsic influence on floral longevity. We propose that under some circumstances floral receptivity may be reduced by donor manipulation through pollen-induced wilting. Indeed, experimental pollinations in several species (Marshall and Ellstrand 1985; Cowan et al. 2000; Snow et al. 2000) showed a first-male advantage, implying that the first pollen donor often obtains higher fitness against later-arriving pollen. Several mechanisms may mediate this first-male advantage, including rate of pollen germination and growth under male control or female control, head start, layering, and the effect of a pollen-borne wilting substance, as proposed here. Regardless of the exact mechanism, we argue that we need to account for the fact that floral longevity of the pollen recipient will affect the relative success of pollen donors in species with multiple pollinator visits and post-pollination wilting.

We investigated in a game-theoretical model whether floral longevity, and in particular receptivity of pollen-receiving structures, may be manipulated by pollen donors as a strategy to secure paternity. Our results indicate that pollen-borne substances that induce wilting can evolve as a result of conflict between pollen donors and recipients over floral receptivity and that recipients can evolve resistance to pollen-borne wilting substances by delaying the onset of stigmatic receptivity after the flower opens. Importantly, this shows that male manipulation can evolve even when pollen carryover leads to the arrival of pollen from more than one competitor at the same time, which may happen frequently in plants (e.g., Schaal 1980; Thomson and Plowright 1980; Cresswell et al. 1995). Analogous to the ''tragedy of the commons'' (Hardin 1968), the male benefit of reducing female receptivity in plants with pollen carryover will be lower compared to a situation when females receive sperm from different males in consecutive matings (as is typical for most animals). This slight constraint on male fitness gain, however, should facilitate the evolution of female counter-adaptation, which in turn favors the production of male wilting substance. Thus, our model predicts the evolution of male manipulations of female reproductive physiology to secure paternity even when pollen is deposited simultaneously. It would be interesting to test this prediction in animals in which forms of carryover occur, for example, through passive sperm dispersal in sessile marine invertebrates (Bishop et al. 2000).

Our model provides a novel hypothesis for plant reproductive biology. To our knowledge, the function of pollination-induced wilting has not been investigated in terms of donor manipulation of recipient reproduction and potential conflict between maternal and paternal interests before. This novel conflict-driven hypothesis can help to explain variation in floral longevities and receptivity schedules in addition to concurrent adaptive hypotheses. Alternative explanations are that pollination-induced wilting may be a recipient strategy to reallocate resources to fruit production, limit the risk of contracting sexually transmitted diseases (Shykoff et al. 1996), redirect pollinators to unpollinated flowers within the inflorescence (Lloyd and Webb 1986), or optimize floral display in response to pollinator abundance (Harder and Johnson 2005; see also Bingham and Orthner 1998). The critical expectations under sexual conflict include a negative correlation between male ability to induce postpollination changes and female fitness, an association across species between the prevalence of multiple pollinator visits, and the occurrence of the trait, rapid evolution of these traits, and potentially local coadaptation between the sexes. However, it must be noted that some of the traits may also evolve under other forms of selection, and there currently is no golden rule to demonstrate conflict in any given system (Arnqvist and Rowe 2005; Bernasconi et al. 2006b). An initially adaptive response may provide the mechanistic basis to a conflict-driven manipulation, for instance, if pollen-coat substances evolved to mimic pathogen properties as a mechanism to elicit wilting and abscission of receptive structures.

Two situations may lead to lower selection on production of a wilting substance: (1) if initial pollen loads are often nonsaturating; and (2) if first-male advantage is at least partly mediated through other mechanisms than the wilting substance (see below). Pollen-induced wilting of receptive structures will negatively affect fitness of the recipient either by causing pollen limitation or if reducing the genetic variability of the pollen load leads to fewer or less-viable offspring (e.g., Schlichting et al. 1987, 1990; Paschke et al. 2002). Here, we assumed constant seed set (one ovule per flower) and mainly explored the latter case. Extensions of the model are needed to explore the case that pollen loads are nonsaturating (pollen limitation). One interesting aspect, however, is that from the donor perspective, it might sometimes be beneficial pay to induce wilting before the arrival of enough pollen for full seed set, because this may increase the number of offspring he sired although lowering total seed set. In flowers with multiple ovules, if fruits with few fertilized ovules are aborted, then pollen grains already on a stigma may instead benefit from the receipt of additional pollen to avoid abortion. This should also lower selection on pollen to cause pollen limitation. However, selective fruit abortion may also be a means of female counter-adaptation.

Postpollination wilting has been documented in most orchids and in more than 60 genera in other families. However, there are also species in which pollen deposition does not quicken stigmatic senescence (van Doorn 1997). Lack of postpollination wilting in these species may be explained if ''manipulative pollen'' only evolves in taxa where recipient structures are predisposed (e.g., ethylene sensitive), in a way similar to sensory bias exploitation (Arnqvist and Rowe 2005), or if the benefits accruing to donors by inducing wilting vary among taxa. The extent of benefits accruing in a pollen donor by reducing residual receptivity of the recipient plant will increase, the lower the probability that pollen arriving on subsequent visits is related to the recipient (i.e., as a consequence of pollinator behavior) and the higher the probability that simultaneously arriving pollen are related to each other (i.e., as a consequence of pollen packaging, e.g., when pollen grains are transferred as tetrads or groups such as in orchids). Because substances on the pollen surface are under diploid control, pollen from the same donor will resemble each other and this relatedness will also benefit the donor through cooperation in inducing rapid wilting. Future models may thus explore the consequences of varying the probability that pollen from the same (or a genetically related) donor arrives repeatedly on the stigma (e.g., when pollen carryover is high and populations are small, or because pollen grains are transferred as groups).

Regulation of receptivity schedules may also depend on whether plants are hermaphroditic, an aspect not considered in our model. Selfing in combination with pollen-induced wilting may either result in self-recognition (no donor-recipient conflict when these are one genetic individual) or modify the risk of inbreeding. In hermaphroditic flowers, pollen-induced wilting may reduce pollen export (e.g., by making the flower as a whole less attractive to pollinators) and thus lower fitness via the recipient's male function. The latter cost would not apply to protandrous plants, which release own pollen before their female function becomes receptive. Indeed, a major implication of our argument is that if donor and recipient interests over residual longevity of recipient flowers diverge, this may help to explain why protandry is more common than protogyny in hermaphroditic animal-pollinated plants (Lloyd and Webb 1986).

### *Coevolution of Wilting Substance and Timing of Stigma Receptivity*

We explored coevolutionary responses by females and found conditions favoring delayed stigmatic receptivity in response to manipulation by pollen donors. These results highlight an important parallel to models developed for animals with respect to the role of harm in maintaining manipulations and counter-manipulations. In animals, males are known to prevent females from remating through various mechanisms, including postcopulatory mate guarding, mating plugs, or substances in the ejaculate such as *Acp* proteins in *Drosophila.* Male mechanisms to prevent remating are often harmful for females (Chapman et al. 2003). It has been suggested that the damage itself can be beneficial to males, because it may induce females to actively modify their receptivity period or mating rates to limit harm, thereby increasing male fitness (Johnstone and Keller 2000; Morrow and Arnqvist 2003; Lessels 2005). In a game-theoretical model Johnstone and Keller (2000) explored whether a male strategy to reduce female receptivity can evolve even if it causes costs to females. Toxicity as a means of inhibiting remating could be maintained over a wide range of conditions.

In our model, the pollen-borne wilting substance is assumed to manipulate the signaling system in the pistil. If recipient plants cannot defend themselves, the wilting substance will always force flowers to wilt early, independently of how toxic the substance is (pleiotropic effect of harm; Parker 1979; Morrow and Arnqvist 2003). In our first scenario (no coevolutionary response by recipients), any toxic effect (i.e., any effect that reduces female fitness) of the wilting substance is unrelated to male fitness. By contrast, in the second scenario (coevolution of a female defense strategy), toxicity of the pollen wilting substance per se becomes important for male fitness because recipient plants will modify their defense strategy in relation to the toxicity level. If the wilting substance is highly toxic, the best female option is to reduce the receptivity period, that is, not to defend themselves against manipulative pollen, a finding consistent with Johnstone and Keller (2000). The higher probability for a harmful male manipulative trait to stay beneficial over evolutionary time suggests that, in general, manipulative traits that inflict damage should be more common than other such traits.

Johnstone and Keller (2000) concluded that a greater last-male advantage would result in stronger selection on toxin transfer and greater levels of harm. In plants, first-male advantage is often observed, however, we assumed that arrival time does not affect siring success. The incorporation of interpollination interval effects is indeed another simplifying assumption open to future modifications. Clearly, a wilting substance should not be advantageous at low visitation rates if only the earliest arriving pollen grains will be able to compete with each other. We expect that the consequences of interpollination interval will depend on whether first-male advantage is proximately caused by the wilting substance itself or through other independent mechanisms.

In conclusion, we find an ESS for a pollen-borne substance that induces premature wilting of the female recipient structures, thus lowering female fitness. This indicates that male-manipulative traits also can evolve in species where mating (i.e., pollen deposition) is not strictly sequential. We also find an ESS for a coevolutionary response by recipients that evolve to delay onset of receptivity. Female counter-adaptation was more likely to evolve when toxicity of the pollen-borne substance was low, suggesting that inflicting harm can increase the probability that a male-manipulative trait stays beneficial and evades counter-manipulation over evolutionary time. This, together with empirical findings that pollen deposition induces wilting and that receptive structures often have delayed maturation schedules, suggests that sexual antagonism over remating may be taxonomically more widespread than previously understood (Chapman et al. 2003; Bernasconi et al. 2004; Arnqvist and Rowe 2005).

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## Literature Cited

Aizen, M. A. 1993. Self-pollination shortens flower life-span in *Portulaca umbraticola* Hbk (Portulacaceae). Int. J. Plant Sci. 154:412–415.

Arathi, H. S., A. Rasch, C. Cox, and J. K. Kelly. 2002. Autogamy and floral longevity in *Mimulus guttatus*. Int. J. Plant Sci. 163: 567–573.

Armbruster, W. S., E. M. Debevec, and M. F. Willson. 2002a. Evolution of syncarpy in Angiosperm: theoretical and phylogenetic analyses of the effects of carpel fusion on offspring quantity and quality. J. Evol. Biol. 15:657–672.

Armbruster, W. S., C. P. H. Mulder, B. G. Baldwin, S. Kalisz, B. Wessa, and H. Nute. 2002b. Comparative analysis of late floral development and mating-system evolution in tribe Collinsiae (Scrophulariaceae S.L.). Am. J. Bot. 89:37–49.

Arnqvist, G., and L. Rowe. 2005. Sexual conflict: monographs in behavior and ecology. Princeton Univ. Press, Princeton, NJ.

Ashman, T.-L. 2004. Flower longevity. Pp. 349–362 *in* L. D. Nooden, ed. Cell death in plants. Elsevier, London.

Ashman, T.-L., and D. J. Schoen. 1994. How long should flowers live? Nature 371:788–791.

Barrett, S. C. H. 2003. Mating strategies in flowering plants: the outcrossing-selfing paradigm and beyond. Philos. Trans. R. Soc. Lond. B 358:991–1004.

Bernasconi, G. 2003. Multiple paternity in flowering plants and its evolutionary consequences. Persp. Plant Ecol. Evol. Syst. 6: 147–156.

Bernasconi, G., M. Paschke, and B. Schmid. 2003. Diversity effects in reproductive biology. Oikos 102:217–220.

Bernasconi, G., T.-L. Ashman, T. R. Birkhead, J. D. D. Bishop, U. Grossniklaus, E. Kubli, D. L. Marshall, B. Schmid, I. Skogsmyr, R. R. Snook, D. Taylor, I. Till-Bottraud, P. I. Ward, D. Zeh, and B. Hellriegel. 2004. Evolutionary ecology of the pre-zygotic stage. Science 303:971–974.

Bernasconi, G., D. J. Lang, and B. Schmid. 2006a. Microgrametophyte population sizes and plant reproductive output in the insect-pollinated *Prunella grandiflora* (Lamiaceae). New Phytol. doi:10.1111/j.1469-8137.2006. 01920x.

Bernasconi, G., L. S. Corley, and M. K. N. Lawniczak. 2006b. ''Trick or treat'': the battle of the sexes. J. Evol. Biol. 16: 1003–1005.

Bingham, R. A., and A. R. Orthner. 1998. Efficient pollination of alpine plants. Nature 391:238–239.

Bishop, J. D. D., A. J. Pemberton, and L. R. Noble. 2000. Sperm precedence in a novel context: mating in a sessile marine invertebrate with dispersing sperm. Proc. R. Soc. Lond. B 267: 1107–1113.

Bulmer, M. 1994. Theoretical evolutionary ecology. Sinauer Associates, Inc, Sunderland, MA.

Campbell, D. 1998. Multiple paternity in fruits of *Ipomopsis aggregata* (Polemoniaceae). Am. J. Bot. 85:1022–1027.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends Ecol. Evol. 18:41–47.

Clayton, S., and M. A. Aizen. 1996. Effects of pollinia removal and insertion on flower longevity in *Chloraea alpina* (Orchidaceae). Evol. Ecol. 10:653–660.

Cowan, A. A., A. H. Marshall, and T. P. T. Michaelson-Yates. 2000. Effect of pollen competition and stigmatic receptivity on seed set in white clover (*Trifolium repens* L.). Sex. Plant Reprod. 13: 37–42.

Christiansen, F. B. 1991. On conditions for evolutionary stability for a continuously varying character. Am. Nat. 138:37–50.

Cresswell, J. E., A. P. Bassom, S. A. Bell, S. J. Collins, and T. B. Kelly. 1995. Predicted pollen dispersal by honey-bees and three species of bumble-bees foraging on oil-seed rape: a comparison of three models. Funct. Ecol. 9:829–841.

da Costa-Nunes, J. A., and U. Grossniklaus. 2003. Unveiling the gene-expression profile of pollen. Genome Biol. 5:205.

Dahl, Å. E., and M. Fredrikson. 1996. The timetable for development of maternal tissues sets the stage for male genomic selection in *Betula pendula* (Betulaceae). Am. J. Bot. 83:895–902.

De Jong, T. J. and P. G. L. Klinkhamer. 2005. Evolutionary ecology of plant reproductive strategies. Cambridge. Univ. Press, Cambridge, U.K.

De Jong, T. J., H. van Dijk, P. G. L. Klinkhamer. 2005. Hamilton's rule, imprinting and parent-offspring conflict over seed mass in partially selfing plants. J. Evol. Biol. 18:676–682.

Delph, L. F., and K. Havens. 1998. Pollen competition in flowering plants. Pp. 149–173 *in* T. R. Birkhead and A. P. Møller, eds. Sperm competition and sexual selection. Academic Press, New York.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34:579–612.

Douglas, K. L., and R. W. Cruden. 1994. The reproductive biology of *Anemone canadensis* (Ranunculaceae): breeding system and facilitation of sexual selection. Am. J. Bot. 81:314–321.

Ellstrand, N. C. 1984. Multiple paternity within the fruits of the wild radish, *Raphanus sativus*. Am. Nat. 123:819–828.

Fiebig, A., R. Kimport, and D. Preuss. 2004. Comparisons of pollen coat genes across Brassicaceae species reveal rapid evolution by repeat expansion and diversification. Proc. Natl. Acad. Sci. USA 101:3286–3291.

Galen, C., J. A. Shykoff, and R. C. Plowright. 1986. Consequences of stigma receptivity schedules for sexual selection in flowering plants. Am. Nat. 127:462–476.

Ganeshaiah, K. N., and U. R. Shaanker. 1988. Regulation of seed number and female incitation of mate competition by a pH-dependent proteinaceous inhibitor of pollen grain germination in *Leucaena leucocephala*. Oecologia 75:110–113.

Gori, D. F. 1983. Post-pollination phenomena and adaptive floral changes. Pp. 31–49 *in* C. E. Jones and R. J. Little, eds. Handbook of experimental pollination biology. van Nostrand Reinhold, New York.

Harder, L. D., and S. D. Johnson. 2005. Adaptive plasticity of floral display size in animal-pollinated plants. Proc. R. Soc. Lond. B 272:2651–2657.

Harder, L. D., and J. D. Thomson. 1989. Evolutionary options for maximazing pollen dispersal of animal-pollinated plants. Am. Nat. 133:323–344.

Hardin, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

Herrero, M. 2003. Male and female synchrony and the regulation of mating in flowering plants. Philos. Trans. R. Soc. B 358: 1019–1024.

Herrero, M., and A. Arbeola. 1989. Influence of the pistil on pollen tube kinetics in peach (*Prunus persica*). Am. J. Bot. 76: 1441–1447.

Higashiyama, T., S. Yabe, N. Sasaki, Y. Nishimura, S. Miyagishima, H. Kuroiwa, and T. Kuroiwa. 2001. Pollen tube attraction by the synergid cells. Science 293:1480–1483.

Hormaza, J. I., and M. Herrero. 1994. Gametophytic competition and selection. Pp. 372–400 *in* E. G. Williams, A. E. Clarke, and R. B. Knox, eds. Genetic control of self-incompatibility and reproductive development in flowering plants. Kluwer, Dordrecht.

Johnstone, R. A., and L. Keller. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins and the cost of mating. Am. Nat. 156:368–377.

Jones, M. L. 2002. Ethylene responsiveness in carnation style is associated with stigma receptivity. Sex. Plant Reprod. 15: 107–112.

Leimar, O. 2006. Multidimensional convergence stability and the canonical adaptive dynamics. *In* U. Dieckmann and J. A. J. Metz, eds., Elements of adaptive dynamics. Cambridge Univ. Press, Cambridge, U.K. *In press*.

Lessells, C. M. 2005. Why are males bad for females? Models for the evolution of damaging male mating behavior. Am. Nat. 165: S46–S63.

Levin, D. A. 1990. Sizes of microgametophyte populations in pistils of *Phlox drummondii*. Am. J. Bot. 77:356–363.

Lloyd, D. G., and C. J. Webb. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. NZ J. Bot. 24:135–162.

Marshall, D. L., and N. C. Ellstrand. 1985. Proximal causes of multiple paternity in wild radish, *Raphanus sativus*. Am. Nat. 126:596–605.

Maynard Smith, J. 1982. Evolution and theory of games. Cambridge Univ. Press, Cambridge, U.K.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature 6:15–18.

Meagher, T., and L. Delph. 2001. Individual flower demography, floral phenology and floral display size in *Silene latifolia*. Evol. Ecol. Res. 3:845–860.

Morrow, E. H., and G. Arnqvist. 2003. Costly traumatic insemination and a female counter-adaptation in bed bugs. Proc. R. Soc. Lond. B 270:2377–2381.

Murdy, W. H., and M. E. B. Carter. 1987. Regulation of the timing of pollen germination by the pistil in *Talinum mengesii* (Portulacaceae). Am. J. Bot. 74:1888–1892.

Niesenbaum, R. A. 1999. The effects of pollen load size and donor diversity on pollen performance, selective abortion, and progeny vigor in *Mirabilis jalapa* (Nyctagynaceae). Am. J. Bot. 86: 261–268.

O'Neill, S. D. 1997. Pollination regulation of flower development. Annu. Rev. Plant Physiol. Plant Mol. Biol. 48:547–574.

Parker, G. A. 1979. Sexual selection and sexual conflict. Pp. 123–166 *in* M. S. Blum and N. A. Blum, eds. Sexual selection and reproductive competition in insects. Academic Press, New York.

———. 1990. Sperm competition games: raffles and roles. Proc. R. Soc. Lond. B 242:120–126.

Paschke, M., C. Abs, and B. Schmid. 2002. Effects of population size and pollen diversity on reproductive success and offspring size in the narrow endemic *Cochlearia bavarica* (Brassicaceae). Am. J. Bot. 89:1250–1259.

Paschke, M., G. Bernasconi, and B. Schmid. 2005. Effects of inbreeding and pollen donor provenance and diversity on offspring performance under environmental stress in the rare plant *Cochlearia bavarica*. Basic Appl. Ecol. 6:325–338.

Pimentel de Carvalho, A. C., and D. Message. 2004. A scientific note on the toxic pollen of *Stryphnodendron polyphyllum* (Fabaceae, Mimosoideae) which causes sacbrood-like symptoms. Apidologie 35:89–90.

Preston, R. E. 1991. The intrafloral phenology of *Streptanthus tortuosus* (Brassicaceae). Am. J. Bot. 78:1044–1053.

Primack, R. B. 1985. Longevity of invidual flowers. Annu. Rev. Ecol. Syst. 16:15–37.

Proctor, H. C., and L. D. Harder. 1995. Effect of pollination success on floral longevity in the orchid *Calypso bulbosa* (Orchidaceae). Am. J. Bot. 82:1131–1136.

Rathcke, B. J. 2003. Floral longevity and reproductive assurance: seasonal patterns and an experimental test with *Kalmia latifolia* (Ericaceae). Am. J. Bot. 90:1328–1332.

Rice, W. R., and B. Holland. 1997. The enemies within: intragenomic conflict, interlocus contest evolution (ICE) and the intraspecific Red Queen. Behav. Ecol. Sociobiol. 41:1–10.

Schaal, B. A. 1980. Measurement of gene flow in *Lupinus texensis*. Nature 284:450–451.

Schemske, D. W., and L. P. Pautler. 1984. The effects of pollen composition on fitness components in a neotropical herb. Oecologia 62:31–36.

Schlichting, C. D., A. G. Stephenson, L. D. Davis, and J. A. Winsor. 1987. Pollen competition and offspring variance. Evol. Trends Plants 1:35–40.

Schlichting, C. D., A. G. Stephenson, and L. E. Small. 1990. Pollen loads and progeny vigor in *Cucurbita pepo*: the next generation. Evolution 44:1358–1372.

Schoen, D. J., and T.-L. Ashman. 1995. The evolution of floral longevity: resource allocation to maintenance versus construction of repeated parts in modular organisms. Evolution 49: 131–139.

Service, P., and R. E. Vossbrinks. 1996. Genetic variation in ''first'' male effects on egg laying and remating by female *Drosophila melanogaster*. Behav. Genet. 26:39–48.

Shaanker, R. U., and K. N. Ganeshaiah. 1989. Stylar plugging by fertilized ovules in *Kleinhovia hospita* (Sterculiaceae): a case of vaginal sealing in plants. Evol. Trends Plants 3:59–64.

Shykoff, J. A., E. Bucheli, and O. Kaltz. 1996. Flower lifespan and disease risk. Nature 379:779.

Skogsmyr, I., and Å. Lankinen. 2000. Potential selection for female choice in *Viola tricolor*. Evol. Ecol. Res. 2:965–979.

Snow, A. A., and P. O. Lewis. 1993. Reproductive traits and male fertility in plants: empirical approaches. Annu. Rev. Ecol. Syst. 24:331–351.

Snow, A. A., T. P. Spira, and H. Liu. 2000. Effects of sequential pollination on the success of ''fast'' and ''slow'' pollen donors in *Hibiscus moscheutos* (Malvaceae). Am. J. Bot. 87:1656–1659.

Stanley, R. G., and H. F. Linskens. 1974. Pollen: Biology, Biochemisty, Management. Springer, Berlin.

Stanton, M. L. 1994. Male-male competition during pollination in plant populations. Am. Nat. 144:S40–S68.

Taylor, L. P., and P. K. Hepler. 1997. Pollen germination and tube growth. Annu. Rev. Plant Physiol. Mol. Biol. 48:461–491.

Taylor, P. D. 1989. Evolutionary stability in one-parameter models under weak selection. Theor. Popul. Biol. 36:125–143.

Thomson, J. D., and R. C. Plowright. 1980. Pollen carryover, nectar rewards and pollinator behavior with special reference to *Diervilla lonicera*. Oecologia 46:68–74.

van Doorn, W. G. 1997. Effects of pollination on floral attraction and longevity. J. Exp. Bot. 48:1615–1622.

Willson, M. F., and N. Burley. 1983. Mate choice in plants: tactics, mechanisms, and consequences. Princeton Univ. Press, Princeton, NJ.

Young, H. J., and L. Gravitz. 2002. The effects of stigma age on receptivity in *Silene alba* (Caryophyllaceae). Am. J. Bot. 89: 1237–1241.

Zinkl, G., and D. Preuss. 2000. Dissecting *Arabidopsis* pollen-stigma interactions: a species-specific interaction reveals novel mechanisms that confer mating specificity. Ann. Bot. 85:15–21.

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## APPENDIX 1

In this appendix, we describe the ESS analysis for the model that explores the evolution of a pollen-borne wilting substance in the absence of a resistance response of the recipient plant. From equation (7a) and using the equilibrium condition for an ESS,

$$\left.\frac{\partial W_s(s,\, s')}{\partial s'}\right|_{s'=s=s^*} = 0, \tag{A1}$$

we determined the equilibrium amount of wilting substance ($s^*$)

$$s^*_{1/2} = \frac{1}{rn\cdot\ln(k)}\cdot\ln\left\{-\frac{2c_s x + B\cdot\ln(k)}{2c_s x(r-1)} \pm \frac{1}{2c_s x(r-1)}\cdot\sqrt{B\cdot\ln(k)\cdot[4c_s x + B\cdot\ln(k)]}\right\}. \tag{A2}$$

There are two criteria for the evolutionary stability of this equilibrium: local stability and convergence stability. Local stability implies that the ESS, when it is adopted by all individuals in a population, should not be invasible by any other strategy in some neighborhood of the ESS (Maynard Smith and Price 1973; Maynard Smith 1982). The condition for this is

$$\left.\frac{\partial^2 W_s(s,\ s')}{\partial s'^2}\right|_{s'=s=s^*} = B\left[\frac{rn\cdot\ln(k)}{x}\right]^2\cdot\frac{k^{a(s^*)}[-1+(r-1)k^{a(s^*)}]}{[1+(r-1)k^{a(s^*)}]^4} < 0, \tag{A3}$$

which is always fulfilled if $r < 1$, while for $r > 1$ and as defined $0 < k < 1$ (i.e., $\ln[k] < 0$) it only holds if

$$s^* > -\frac{\ln(r-1)}{rn\cdot\ln(k)}. \tag{A4}$$

Convergence stability implies that the ESS can be invasible by mutant strategies closer to the ESS in a population dominated by a wild-type with a strategy at some distance from the ESS (Taylor 1989; Christiansen 1991). This second condition is met if

$$\begin{aligned}\left.\frac{\partial}{\partial s}\left(\frac{\partial W_s(s,\ s')}{\partial s'}\right)\right|_{s'=s=s^*} &= -\frac{r^2n^2\cdot\ln(k)^2\cdot Bk^{rns^*}}{x^2[V(s^*)]} \\ &\quad\times\langle(r-1)^2k^{rns^*}\cdot[1+2x-x(1-r)k^{rns^*}] \\ &\qquad+(r-1)(x-1)\rangle \\ &< 0,\end{aligned} \tag{A5}$$

which holds true if the second multiplier is greater than zero and this again implies that for $r > 1$ and as defined $0 < k < 1$ (i.e., $\ln[k] < 0$)

$$s^* > -\frac{\ln(r-1)}{rn\cdot\ln(k)}.$$

Thus, when criterium (A4) is fulfilled, the population converges to the equilibrium. These criteria have also been taken into account in our numerical analyses.

## APPENDIX 2

Here we describe the ESS analysis for the model that explores the coevolution of a pollen-borne wilting substance and resistance by delaying the timing of receptivity. To be able to predict the joint ESS of the two traits, we first solve the equilibrium trait values of both traits separately (Maynard Smith 1982; Bulmer 1994). From equation (10) and using the equilibrium condition for an ESS,

$$\left.\frac{\partial W_s(s,\ y')}{\partial y'}\right|_{y'=y=y^*} = 0, \tag{A6}$$

we determined the equilibrium for timing of stigma receptivity ($y^*$)

$$\begin{aligned}y^* = -\Bigg\{&\frac{k^{rns}}{1-k^{rns}} \\ &+\frac{1}{nl(r-1)(1-k^{rns})}\cdot\ln\left[\frac{c_y+(r-1)(1-k^{rns})pns^2}{bnl(r-1)(1-k^{rns})}\right]\Bigg\}.\end{aligned} \tag{A7}$$

From equation (10) and using the equilibrium condition for an ESS,

$$\left.\frac{\partial W_s(s,\ s',\ y)}{\partial s'}\right|_{s'=s=s^*} = 0, \tag{A8}$$

it unfortunately is not possible to derive an analytical expression for the equilibrium amount of wilting substance ($s^*$).

Convergence stability of the joint equilibrium of both traits is investigated by analyses of the Jacobian in numerically derived points (Fig. 4a–d). When a Jacobian fulfills all stability conditions, that is, when it is negative definitive, this also implies stability when there exist intertrait genetic correlations (Leimar 2006).

When the joint equilibrium ESS($s^*$, $y^*$) is on the $x$-axes (i.e., $y^* = 0$, implying that delaying stigma receptivity is not evolutionarily stable), the stability of ESS($s^*$, 0) cannot be determined by analyzing the Jacobian, because the fitness gradient is striving toward a value that is biologically non meaningful (i.e., $y < 0$, implicating that the stigma should become receptive before flowers have opened). In this case, we, analyze the stability of wilting substance production in the absence of defense, ESS($s^*$) (see Appendix 1).