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THE ROLE OF NATURAL ENEMIES IN THE EXPRESSION AND EVOLUTION OF MIXED MATING IN HERMAPHRODITIC PLANTS AND ANIMALS

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Although a large portion of plant and animal species exhibit intermediate levels of outcrossing, the factors that maintain this wealth of variation are not well understood. Natural enemies are one relatively understudied ecological factor that may influence the evolutionary stability of mixed mating. In this paper, we aim for a conceptual unification of the role of enemies in mating system expression and evolution in both hermaphroditic animals and plants. We review current theory and detail the potential effects of enemies on fundamental mating system parameters. In doing so, we identify situations in which consideration of enemies alters expectations about the stability of mixed mating. Generally, we find that inclusion of the enemy dimension may broaden conditions in which mixed mating systems are evolutionarily stable. Finally, we highlight avenues ripe for future theoretical and empirical work that will advance our understanding of enemies in the expression and evolution of mixed mating in their hosts/victims, including examination of feedback cycles between victims and enemies and quantification of mating system-related parameters in victim populations in the presence and absence of enemies.

KEY WORDS: Enemy, host, mating system, outcrossing, self-fertilization.

Mating system (sensu stricto, i.e., relative production of inbred vs. outbred individuals) is a complex trait that reflects interactions among genetics, population structure, demography, and numerous environmental factors that influence mating success (Barrett and Eckert 1990). Evolutionary biologists have focused much attention on understanding the factors controlling mating system evolution because this trait has profound consequences for genetic variation within populations (Hamrick and Godt 1990), individual fitness (Charlesworth and Charlesworth 1987), population growth rate (Steets et al., 2007), and evolutionary change (Barrett 1990). Although not reviewed together since Jarne and Charlesworth’s work 14 years ago (JARNE and Charlesworth 1993), it is now clear that both plants and animals display a dramatic range of mating systems, as well as significant mixed mating, for example, 42% of plant species (Goodwillie et al. 2005) and 47% of hermaphroditic animal species surveyed to date have intermediate levels of outcrossing (0.2 < t < 0.8; Jarne and Auld 2006; Fig. 1). For the past few decades, researchers have tried to explain the mechanisms maintaining intermediate levels of outcrossing in plants (reviewed in Goodwillie et al. 2005), because classical
theory predicts mixed mating to be evolutionarily unstable (e.g., Lloyd 1979; Lande and Schemske 1985). Although current theory finds genetic mechanisms, such as inbreeding depression and population substructure, may explain some of the observed patterns, the conditions under which mixed mating is evolutionarily stable are fairly limited (e.g., Ronfort and Couvet 1995; Cheptou and Mathias 2001). Ecological aspects have also emerged as potential factors promoting mixed mating and, in plants, theoretical emphasis has been placed on variation in pollination ecology (e.g., Holsinger 1991; Schoen et al. 1996). Even so, two of the most complete studies that include ecological and genetic perspectives (Aquilegia canadensis: Herlihy and Eckert 2002; Collinsia verna: Kalisz et al. 2004) still fall short of a complete understanding of the causes of variation in mating system. Moreover, such a striking degree of similarity in the distribution of mating system variation in both plants and animals (Fig. 1) is suggestive of the role of similar selective factors in both groups. Natural enemies are one potential unifying ecological factor, but one that has received relatively little attention with respect to the evolution of mating systems.

Enemies (e.g., predators, herbivores, parasites, pathogens) are any biotic factor with negative fitness consequences for their victims (e.g., prey or hosts). Not only are enemies a ubiquitous force affecting both plant and animal fitness, but they have also been implicated as a prime factor in the evolution of sex (Hamilton et al. 1990) as well as contributing to the evolution of separate sexes from hermaphroditism (reviewed in Ashman 2002). Even though several theoretical considerations suggest that we should take seriously the notion that enemies may influence mating system evolution (Lively and Howard 1994; Agrawal and Lively 2001; Wolf et al., unpubl. ms.), there is currently little data to address the issue. In theory, enemies may impose selection on the mating system if the probability or severity of attack is influenced by the selfing rate of their victims (e.g., Lively and Howard 1994; Wolf et al., unpubl. ms.). Alternatively, enemies may influence the expression of traits important for mating system evolution (e.g., inbreeding depression, gamete discounting) and in this way may promote the evolutionary stability of mixed mating. Overall, current theory indicates that enemies may serve as significant selective agents on mating system, and thus, deserve a more complete treatment.

In this article, we aim for a conceptual unification of the role of enemies in influencing phenotypic variation in mating systems and mating system evolution in both hermaphroditic plants and animals. We begin by reviewing empirical evidence for the proximate effect of enemies on victim mating system and highlight potential evolutionary consequences of this interaction. Next, we synthesize theoretical and empirical evidence for the role of enemies in maintaining mixed mating via effects on important model parameters. In doing so, we identify the situations in which consideration of enemies alters expectations about the stability of mixed mating and identify areas in need of additional study, both empirical and theoretical.

**Effect of Enemies for Victim Outcrossing**

Enemies may directly influence the mating system of their victims by altering victim resource status and allocation to modular growth form or by altering interactions between the victim and other community members (e.g., pollinator interactions for plants or mate availability for animals). To date, only a few researchers have explored the role of enemies in influencing mating system expression in plants (Krupnick and Weis 1999; Elle and Hare 2002; Ivey and Carr 2005; Steets et al. 2006; L. Penet et al., unpubl. data), and no studies have been conducted in animals. However, at this point even studies conducted on plants offer no consistent message. For example, in Impatiens capensis, vegetative herbivory caused both a reduction in the number of simultaneously open flowers on a plant (i.e., floral display) and an alteration in the composition of the pollinating fauna, such that damaged plants were visited more often by pollinators that foraged in a manner that promoted outcrossing, resulting in a 37% increase in the outcrossing rate of open flowers (Steets et al. 2006). However, whole-plant outcrossing rate of I. capensis is a function of the proportional production of closed, selfing cleistogamous flowers as well as the open, potentially outcrossing chasmogamous flowers. Because herbivory also reduced the relative production of

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**Figure 1.** The distribution of outcrossing rate (t) estimates of hermaphroditic animals and plants. Animal t estimates (142 spp.) are from independently published studies compiled by Jarne and Auld (2006). Plant t estimates (342 spp.) are from Goodwillie et al. (2005) and combine biotically and abiotically pollinated plants. Figure adapted from Jarne and Auld (2006).
chasmogamous flowers, the net effect of herbivory was to reduce whole-plant outcrossing rate by 28% (Steets and Ashman 2004; Steets et al. 2006). Similarly, Ivey and Carr (2005) found that herbivory reduced outcrossing in *Mimulus guttatus*; however, the mechanism for this change remains unknown. In single ramets of *Fragaria virginiana*, florivory reduced outcrossing rate due to a reduction in pollinator visitation and increased autogamy (L. Penet et al., unpubl. data). Finally, Elle and Hare (2002) and Krupnick and Weis (1999) both found that herbivores did not significantly affect host outcrossing rate; however, in both studies there was a trend for enemies to increase outcrossing. In *Datura wrightii* this was due to an herbivory-induced reduction in floral display (Elle and Hare 2002). Overall, these studies demonstrate that enemies have the potential to affect plant outcrossing rate; however, the direction of effect varies with system and the mechanism underlying the change. Studies that examine unexplored mechanisms of enemy-induced changes in plant mating systems are needed. For example, in plants enemies can affect pollen competitive ability (e.g., damaged plants produce lower quality pollen; Quesada et al. 1995), such that self-pollen from damaged donors may lose in competition with outcross pollen from undamaged donors, leading to reduced selfing among damaged individuals. To date, similar direct evidence in animal systems is nonexistent. Nevertheless, pathogens or predators may cause a reduction in mate searching (e.g., Mathis and Hoback 1997; Rohr and Madison 2001) and/or mate attraction (e.g., Milinski and Bakker 1990), which may be expected to reduce outcrossing in animals.

The proximate effect of enemies for victim outcrossing may have consequences for mating system evolution. For example, Masuda et al. (2001) found that heteromorphic flower production (i.e., cleistogamous and chasmogamous flowers) can be evolutionarily stable when chasmogamous flowers self-fertilize some of their ovules via geitonogamy. As geitonogamy results in the production of inbred seeds, these seeds may suffer inbreeding depression. Thus, the advantage of outcrossing via chasmogamous flowers is balanced by the disadvantage of inbreeding depression and can result in a stable mixed mating system (e.g., Masuda et al. 2001). As enemies can reduce geitonogamy among chasmogamous flowers (Steets et al. 2006), they may select for individuals specializing on chasmogamous flower production.

**Maintenance of Mixed Mating by Enemies via Effects on Model Parameters**

From a theoretical perspective, mixed mating may be defined as a single evolutionarily stable strategy in which individuals self-fertilize some portion of their offspring ($s$) and outcross the rest ($t = 1 - s$) or as a genetic polymorphism of discrete or continuous strategies that have different selfing rates ($s_1, s_2, \ldots, s_n$; i.e., evolutionarily stable state, sensu Maynard Smith 1982 or evolutionary branching, sensu Geritz et al. 1998; Cheptou and Mathias 2001). To maintain either form of mixed mating, there must be selection against complete selfing or outcrossing, such as a negative feedback mechanism or environmental variation that causes the selective value of selfing to fluctuate in time or space. Below we explore how enemies may influence the stability of mixed mating by creating negative feedback on the selfing rate or by causing variation in the selective value of selfing due to effects on model parameters including inbreeding depression, genetics of resistance, mate availability, gamete discounting, and biparental inbreeding (Table 1).

**INBREEDING DEPRESSION**

Recent theoretical treatments indicate that enemies may have a strong influence on mating system evolution due to effects on inbreeding depression (Table 1, panel A). Lively and Howard (1994) and Wolf et al. (unpubl. ms.) find that enemies can promote stable mixed mating in their victims because the relative fitness associated with selfing and outcrossing is influenced by interactions with enemies. Alternatively, heterogeneous enemy pressure (Burdon et al. 1989; Louda 1989; Linhart 1991; Rand 2002) may set up conditions that could select for stable mixed mating by causing spatiotemporal or gender-based variation in expression of inbreeding depression. Below we review these theories and highlight empirical evidence relevant to each.

**Enemies intensify inbreeding depression**

Lively and Howard (1994) demonstrated that parasites can favor outcrossing or mixed mating even under conditions that would otherwise favor selfing (i.e., when inbreeding depression is less than 1/2). The model makes two important assumptions regarding the relationship between parasites and self-fertilization. First, it assumes that individuals produced through self-fertilization not only suffer from reduced fitness due to inbreeding depression, but also suffer from increased deleterious effects of parasites, either because they are more likely to be infected (i.e., lower resistance) and/or because they suffer greater fitness reduction when infected (i.e., lower tolerance) as compared to outcrossed individuals. In effect, the parasites intensify the realized inbreeding depression in their hosts because they reduce the relative fitness of individuals produced through selfing. Further, the model assumes that the parasite transmission rate or probability of infection ($T$) is influenced by the population selfing rate ($T = s^2$, where $s$ is the mean selfing rate of the population, and $T$ controls the shape of the relationship between $s$ and $T$), such that parasites become more abundant as the selfing rate increases. The consequence of these assumptions is a negative feedback mechanism. As the selfing rate increases, the probability of infection increases, and the relative fitness of individuals produced through selfing decreases. The evolutionarily
Table 1. The potential effect of enemies on victim mating system via effects on model parameters. Parameters include (A) inbreeding depression, (B) genetics of resistance, (C) mate availability, (D) male gamete discounting, and (E) biparental inbreeding. See text for details.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Enemy influence on parameter</th>
<th>Empirical evidence for enemy effect</th>
<th>Can enemy effect stabilize mixed mating?</th>
<th>Prediction based on following theory</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Inbreeding depression (δ)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None; Animals: None</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Varies spatiotemporally</td>
<td>Sexually transmitted enemies ↓ δ</td>
<td>Plants: Hayden et al. 2004 Animals: None</td>
<td>Yes</td>
<td>Wolf et al., unpubl. ms.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None; Animals: None</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Heterogeneous enemy environment leads to heterogeneous δ</td>
<td>Plants: None; Animals: None</td>
<td>Yes, if $\delta_{\text{female}} &gt; 0.5 \delta_{\text{male}}$ and $\delta_{\text{total}} &lt; 0.5$</td>
<td>Cheptou and Mathias 2001; Cheptou and Schoen 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None; Animals: None</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Varies with gender function</td>
<td>Enemies ↑ $\delta_{\text{female}}$ more than $\delta_{\text{male}}$</td>
<td>Plants: None; Animals: None</td>
<td>Yes, if $\delta_{\text{female}} &gt; 0.5 \delta_{\text{male}}$ and $\delta_{\text{total}} &lt; 0.5$</td>
<td>Rausher and Chang 1998</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None; Animals: None</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B. Genetics of resistance</strong></td>
<td></td>
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<td><strong>C. Mate availability (MA)</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>General</td>
<td>Enemies ↑ MA</td>
<td>Plants: reviewed in Knight et al. 2005 Animals: None</td>
<td>No</td>
<td>Lloyd 1979</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: reviewed in Knight et al. 2005 Animals: None</td>
<td>Yes</td>
<td>Lloyd 1979</td>
</tr>
<tr>
<td>Varies spatiotemporally</td>
<td>Heterogeneous enemy environment leads to heterogeneous MA availability</td>
<td>Plants: Mothershead and Marquis 2000; Steets et al. 2006 Animals: Van Duren and Videler 1996; Mathis and Hoback 1997</td>
<td>Yes</td>
<td>Morgan and Wilson 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None; Animals: None</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>D. Male gamete discounting (MGD)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Enemies ↑ MGD</td>
<td>Plants: None Animals: None</td>
<td>Yes</td>
<td>Holsinger 1991; Johnston 1998</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None Animals: None</td>
<td>Yes</td>
<td>Holsinger 1991; Johnston 1998</td>
</tr>
<tr>
<td><strong>E. Biparental inbreeding (BI)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Enemies ↑ BI</td>
<td>Plants: None Animals: None</td>
<td>Yes</td>
<td>Uyenoyama 1986</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plants: None Animals: None</td>
<td>Yes, if BI is greater than 0</td>
<td>Uyenoyama 1986</td>
</tr>
</tbody>
</table>

stable selfing rate ($s^*$) is determined by the level of inbreeding depression prior to infection ($d$), the effect of the parasites on selfed individuals ($E$), and the parameter controlling the relationship between selfing rate and transmission rate ($z$) ($s^* = [(1/2 - d)/E(1 - d)]^{1/15}$). Similar to classical theory (Fisher 1941; Nagylaki 1976; Lloyd 1979; Lande and Schemske 1985), Lively and Howard (1994) find that complete outcrossing is evolutionarily stable when inbreeding depression is greater than $1/2$, regardless of parasite infection. However, when inbreeding depression is less than $1/2$, parasites counteract the
transmission advantage of self-fertilization, and can favor mixed mating by creating a positive relationship between the population mean selfing rate and the realized level of inbreeding depression.

Although the model by Lively and Howard (1994) was written with parasites in mind, it applies to any type of enemy that creates a positive relationship between the selfing rate and realized inbreeding depression. This relationship should hold, for instance, if inbred individuals are more vulnerable to enemies due to low vigor and have a larger fitness reduction when infected or if inbred populations are more susceptible to epidemics because of low genetic diversity. Among empirical studies, there is some support for these predictions. First, enemies have been shown to increase the level of inbreeding depression in several plant species (Carr and Eubanks 2002; Hayes et al. 2004; Ivey et al. 2004; Ivey and Carr 2005). For example, in *Mimulus guttatus* inbred plants respond to herbivory with a greater reduction in flower production and aboveground biomass compared to outbred plants (Carr and Eubanks 2002; Ivey et al. 2004; Ivey and Carr 2005). However, increased expression of inbreeding depression with enemy pressure is not universal (e.g., Núñez-Farfán et al. 1996; Haag et al. 2003).

Second, selfing can increase the probability of infection. For example, inbreeding is known to increase infection rate in many vertebrates (e.g., Coltman et al. 1999; Meagher 1999; Acevedo-Whitehouse et al. 2003). However, among several studies of hermaphroditic plants and animals examining the influence of victim mating system on enemy abundance within a population, the results are mixed (Table 2). The majority of populations (17/27) show no significant relationship between victim inbreeding and infection, 26% of populations (7/27) demonstrate the predicted positive relationship between victim selfing rate and enemy abundance or intensity of infection, and 11% of populations (3/27) show the reverse pattern (Table 2). Two studies to date have also examined the relationship between infection rate and inbreeding among populations (Trouvé et al. 2003; Puurtinen et al. 2004; Table 2, panel B). In both cases there was a trend for infection rate to increase with population selfing rate; however, this relationship was only statistically significant in the Puurtinen et al. (2004) study. Greater understanding of the genetics underlying the victim–enemy interaction may help to explain the neutral and negative responses; theory finds that when victim–enemy interactions are controlled by interactions between specific resistance and virulence genes (e.g. gene-for-gene interactions), inbreeding does not necessarily alter resistance (Koslow and DeAngelis 2006). Although empirical support for selfing increasing victim infection or attack rate are not conclusive, there is evidence in at least some systems that the probability or severity of infection or attack may differ among inbred and outbred individuals or among populations with different levels of inbreeding. Therefore, there could be a relationship between the realized level of inbreeding depression and selfing rate that is mediated by enemies, as postulated by Lively and Howard (1994).

**Sexually transmitted enemies reduce inbreeding depression**

Sexually transmitted diseases are ubiquitous among animals (Morand 1993; Morand and Faliex 1994; Lockhart et al. 1996; Knell and Webberley 2004). In plants, enemies transmitted among flowers by pollinating agents (e.g., bees, wind) are considered sexually transmitted (Parker 1992; Kaltz and Schmid 1995; Antonovics 2005). Wolf et al. (unpubl. ms.) modeled the effect of sexually transmitted enemies on victim mating system evolution. Given the mode of transmission of these enemies, traits that promote outcrossing also have the potential to increase the probability of infection. Further, selfing populations are unlikely to maintain sexually transmitted enemies, so the transmission rate may be influenced not just by individual selfing rate, but also by the population mean selfing rate. Therefore, Wolf et al. (unpubl. ms.) assume that outcrossing individuals are more likely to be infected by sexually transmitted enemies than selfing individuals and that the probability of a host coming into contact with a sexually transmitted enemy increases with the population outcrossing rate ($\beta = \ell$, where $\beta$ is the probability that an outcrossing individual is infected, $\ell$ is the outcrossing rate, and $z$ is a shape parameter). Like traditional models (Fisher 1941; Nagylaki 1976; Lloyd 1979; Lande and Schemske 1985), complete selfing is favored when inbreeding depression is less than 1/2. However, sexually transmitted enemies can favor mixed mating as an evolutionaryarily stable strategy under conditions that would otherwise favor complete outcrossing (i.e., when inbreeding depression is greater than 1/2). As in the case of nonsexually transmitted enemies (i.e., Lively and Howard 1994), sexually transmitted enemies create a negative feedback mechanism, but with the opposite relationship between selfing rate and the relative fitness of selfed and outcrossed offspring. Here, as the population selfing rate decreases, sexually transmitted enemies increase in abundance. A mutant with higher rates of selfing would have a reduced chance of infection relative to outcrossing individuals, preventing the population from evolving to complete outcrossing.

A requirement for the maintenance of mixed mating under the Wolf et al. (unpubl. ms.) model is that the frequency or probability of sexually transmitted enemy attack is higher for outcrossing individuals than for selfing individuals. There is empirical evidence that this may occur in some plant systems. The anther smut, *Microbotryum violaceum*, is transmitted from flower to flower via pollinators. In dioecious *Silene alba*, more inbred plants have higher resistance to *M. violaceum* than outbred plants (Ouborg et al. 2000). In addition, the receipt of spores is correlated with the receipt of outcross pollen in dioecious *Silene dioica* (Elmqvist et al. 1993; Giles et al. 2006). Because *S. alba* and
Table 2. Empirical evidence from hermaphroditic plant (A) and animal (B) systems for an association between victim selfing rate and enemy abundance/intensity of interaction. Study species, type of enemy investigated, population identity (given when authors investigated multiple populations; *among* indicates relationship is among multiple populations rather than within a single population), relationship between host selfing rate/genetic diversity and enemy abundance/intensity of interaction, study type (whether the study measured outcrossing rate and enemy attack in populations without manipulating inbreeding level (C), presented selfed and outcrossed plants with different enemy environments (M), or generated individuals with different inbreeding coefficients to investigate relationship (I)), and reference are given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Enemy</th>
<th>Population</th>
<th>Relationship</th>
<th>Study type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cucurbita pepo ssp. texana</td>
<td>Herbivore</td>
<td>—</td>
<td>+</td>
<td>I</td>
<td>Hayes et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Herbivore</td>
<td>—</td>
<td>+</td>
<td>M</td>
<td>Stephenson et al. 2004</td>
</tr>
<tr>
<td></td>
<td>Pathogen</td>
<td>—</td>
<td>+</td>
<td>M</td>
<td>Stephenson et al. 2004</td>
</tr>
<tr>
<td>Datura stramonium</td>
<td>Generalist herbivore</td>
<td>—</td>
<td>0</td>
<td>M</td>
<td>Núñez-Farfán et al. 1996</td>
</tr>
<tr>
<td></td>
<td>Specialist herbivore</td>
<td>—</td>
<td>0</td>
<td>M</td>
<td>Núñez-Farfán et al. 1996</td>
</tr>
<tr>
<td>Erigeron glaucus</td>
<td>Herbivore</td>
<td>—</td>
<td>– or 0(^1)</td>
<td>M</td>
<td>Strauss and Karban 1994</td>
</tr>
<tr>
<td>Ipomoea hederacea</td>
<td>Generalist herbivore</td>
<td>—</td>
<td>+</td>
<td>M</td>
<td>Hull-Sanders and Eubanks 2005</td>
</tr>
<tr>
<td></td>
<td>Specialist herbivore</td>
<td>—</td>
<td>–</td>
<td>M</td>
<td>Hull-Sanders and Eubanks 2005</td>
</tr>
<tr>
<td>Mimulus guttatus</td>
<td>Pathogen</td>
<td>M5</td>
<td>0</td>
<td>M</td>
<td>Carr et al. 2003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M13</td>
<td>0</td>
<td>M</td>
<td>Carr et al. 2003</td>
</tr>
<tr>
<td></td>
<td>Herbivore</td>
<td>M5</td>
<td>0</td>
<td>M</td>
<td>Carr and Eubanks 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M13</td>
<td>+</td>
<td>M</td>
<td>Carr and Eubanks 2002</td>
</tr>
<tr>
<td>Pinus elliottii</td>
<td>Fungus</td>
<td>—</td>
<td>0</td>
<td>I</td>
<td>Matheson et al. 1995</td>
</tr>
<tr>
<td>Biophthora pfeifferi</td>
<td>Parasite</td>
<td>—</td>
<td>–</td>
<td>C</td>
<td>Charbonnel et al. 2002(^2)</td>
</tr>
<tr>
<td>Helisoma anceps</td>
<td>Parasite</td>
<td>—</td>
<td>+</td>
<td>C</td>
<td>Mulvey et al. 1987(^2)</td>
</tr>
<tr>
<td>Lymnaea ovata</td>
<td>Parasite</td>
<td>Feldmeilen</td>
<td>+</td>
<td>C</td>
<td>Wiehn et al. 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Horgen</td>
<td>0</td>
<td>C</td>
<td>Wiehn et al. 2002</td>
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<td></td>
<td></td>
<td>Mythenquai</td>
<td>0</td>
<td>C</td>
<td>Wiehn et al. 2002</td>
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<td>Lymnaea stagnalis</td>
<td>Parasite</td>
<td>Among</td>
<td>+</td>
<td>C</td>
<td>Puurtinen et al. 2004(^2)</td>
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<td></td>
<td></td>
<td>A</td>
<td>0</td>
<td>C</td>
<td>Puurtinen et al. 2004</td>
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<td></td>
<td></td>
<td>B</td>
<td>0</td>
<td>C</td>
<td>Puurtinen et al. 2004</td>
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<td></td>
<td></td>
<td>C</td>
<td>0</td>
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<td>Puurtinen et al. 2004</td>
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\(^1\)Response depended upon the level of herbivore infestation in maternal plants.
\(^2\)Homozygosity, rather than selfing rate, was measured.

S. dioica are dioecious, self-fertilization is not possible. However, hermaphroditic species, such as S. virginica and S. caroliniana also serve as hosts for sexually transmitted M. violaceum (Antonovics et al. 1996; 2003). What remains to be seen is whether selfing individuals of S. virginica or S. caroliniana are less infected by M. violaceum than outcrossing individuals. Future empirical studies that estimate outcrossing rate in the presence and absence of a sexually transmitted enemy can help to test the predictions of the Wolf et al. (unpubl. ms.) model.

Traditional models predict that complete outcrossing will evolve in the presence of high inbreeding depression (Fisher 1941; Nagylaki 1976; Lloyd 1979; Lande and Schemske 1985). However, in the presence of a sexually transmitted enemy, the model by Wolf and colleagues (unpubl. ms.) predicts that populations will exhibit mixed mating because partial self-fertilization may reduce the chance of infection. In a survey of 150 plant species, the majority had intermediate selfing rates and high levels of inbreeding depression (>1/2; Goodwillie et al. 2005). However,
whether sexually transmitted enemies have an influence in these species is currently unknown. Future empirical work that directly measures inbreeding depression and outcrossing rate in uninfected and infected victim populations would be particularly enlightening.

**Spatiotemporal variation in inbreeding depression**

Theory holds that temporal or spatiotemporal variation in inbreeding depression can favor a mixed mating system if inbreeding depression alternates between high (\( > 1/2 \)) and low (\( < 1/2 \)) values such that automatic selection alternately favors outcrossing or selfing, respectively (Cheptou and Mathias 2001). Even if mean inbreeding depression is low, a model by Cheptou and Schoen (2002) predicts that mixed mating can be evolutionarily stable if inbreeding depression is high in occasional years because the years in which selfing produces offspring of low fitness disproportionately influence mating system evolution. Although both biotic and abiotic factors have the potential to create variation in inbreeding depression (reviewed in Armbruster and Reed 2005), enemies may be an important source of such variation because their abundance varies both spatially and temporally and years of extremely high infection levels (outbreaks) are common for both pathogen and herbivore populations (Burdon et al. 1989; Lively 1991; Rand 2002). A few empirical studies have demonstrated that enemies can exacerbate inbreeding depression of their victims. For example, beetle herbivory causes average inbreeding depression to increase from 0.4 to 0.63 in Cucurbita pepo ssp. texana (calculated from Hayes et al. 2004). If inbreeding depression were to vary in time due to temporal variation in herbivory, then mixed mating may be maintained via this mechanism (Table 1, panel A; Cheptou and Mathias 2001).

Even if enemies do not directly create variation in inbreeding depression, they could indirectly influence the expression of inbreeding depression via their effects on population density. Specifically, a model by Cheptou and Dieckmann (2002) predicts that mixed mating may be maintained when inbreeding depression is either positively or negatively correlated with density due to reciprocal interactions between the selfing rate, inbreeding depression, and population density. These associations may arise if inbred and outbred individuals differ in their competitive abilities, so that the relative fitness of inbred individuals is influenced by population density, as well as by the proportion of competitors that are inbred (Cheptou and Dieckmann 2002). Although the model by Cheptou and Dieckmann (2002) did not explicitly consider enemies, enemies may create the association between victim density and inbreeding depression necessary to produce dynamics favoring mixed mating. For example, because enemies increase mortality (e.g., Crawley 1997) and increase inbreeding depression (Carr and Eubanks 2002; Hayes et al. 2004; Ivey et al. 2004; Ivey and Carr 2005), they could generate a negative correlation between inbreeding depression and density. Alternatively, enemies could generate a positive correlation between density and inbreeding depression because enemies may be more abundant in dense populations (e.g., Thompson 1978), and exacerbate the difference in competitive ability between inbred and outbred individuals. Finally, stochastic variation in population size due to varying enemy pressure (e.g., Carson and Root 2000; Schoener et al. 2002) could promote mixed mating by altering the expression of inbreeding depression (Cheptou and Dieckmann 2002).

**Gender-dependent variation in inbreeding depression**

Theoretical work by Rausher and Chang (1998), showed that when inbreeding depression in female fitness is greater than male fitness, and inbreeding depression for female fitness is greater than 1/2 but total inbreeding depression through both sex functions is less than 1/2, then stable mixed mating may be maintained (Table 1, panel A). Although there is some evidence that independent enemy pressure inbreeding depression can be substantially greater for female than male fitness components (del Castillo 1998; Chang and Rausher 1999), there are only two studies that directly address how enemies affect inbreeding depression in both male and female components of fitness (Hayes et al. 2004; Stephenson et al. 2004). Neither of these studies provide evidence for enemies maintaining mixed mating via this mechanism because enemies did not increase inbreeding depression through female fitness above 1/2 (Stephenson et al. 2004) or inbreeding depression through male function was greater than that through female function (Hayes et al. 2004). Despite the current lack of support, there is clearly a need to study the effect of enemies on inbreeding depression through both sex functions in other systems before we can draw any conclusions as to whether enemies can contribute to mixed mating via this mechanism.

**Genetics of resistance**

In a recent simulation model, Agrawal and Lively (2001) demonstrated that enemies can select for mixed mating when the probability that an individual will be infected is determined by its genotype at two bi-allelic resistance loci, as well as the parasite genotype at loci for evading resistance (Table 1, panel B). In general, higher parasite virulence was more effective at promoting host outcrossing than lower parasite virulence; however, the virulence level required to counter the transmission advantage of selfing was dependent on the genetic details of resistance (e.g., overdominance model vs. matching allele model), the amount of male gamete discounting, and the parasite selfing rate. As Agrawal and Lively’s (2001) model was a simulation, the mechanism promoting outcrossing and maintaining mixed mating is not entirely clear; however, it is likely a type of frequency-dependent selection. For example, when a host genotype is widespread in a population, the parasite genotype that can infect it also becomes common.
When infection is determined by a matching-allele model (i.e., one-to-one correspondence between parasite genotype and host genotype) and the parasite is highly selfing, homozgyous parasite genotypes will be common in the population. Therefore, hosts that partially outcross will be favored because they may produce some heterozygous progeny that can effectively escape infection by the parasite (Agrawal and Lively 2001). In addition, host outcrossing is also advantageous because it promotes recombination among resistance loci, which generates new combinations of alleles at these loci (Agrawal and Lively 2001). A low level of outcrossing provides enough recombination to evade enemies and balance the transmission advantage of selfing, and in this way, enemies can stabilize mixed mating.

Although we lack rigorous tests of Agrawal and Lively’s (2001) model, it does reveal that enemies have the potential to promote outcrossing and maintain mixed mating. We find some support for the Agrawal and Lively (2001) model and its assumptions that recombination is more efficient in outcrossing species (Nordborg 2000 and references therein). Empirical work that combines identification of molecular genetics of pathogen resistance with study of host mating system would greatly improve our understanding of whether mixed mating is promoted by enemies in the way envisioned by Agrawal and Lively (2001).

MATE AVAILABILITY

Reproductive assurance is thought to be a primary ecological factor favoring self-fertilization (e.g., Baker 1967; Morgan and Wilson 2005; Porcher and Lande 2005); thus, the availability of mates is important to mating system evolution. In plants, mate availability is often assessed via measurement of pollen limitation (Ashman et al. 2004; Knight et al. 2005). Low mate availability or pollen limitation will favor the evolution of selfing and can promote some forms of mixed mating. For example, delayed selfing, a form of mixed mating, is always predicted to be favored due to its ability to increase offspring production when mates are limited without reducing the production of outcrossed seeds (Lloyd 1979). Enemies can increase pollen limitation by reducing the size or density of the plant population (Vazquez and Simberloff 2004) or by altering flowering phenotype and pollinator behavior (reviewed in Knight et al. 2005). Similarly, in animals, enemies can reduce population size, and thus, mate availability. Levri and Lively (1996) demonstrated that trematode parasites alter the behavior of a dioecious snail (Potamopyrgus antipodarum) inducing them to forage at a different time of day. This behavioral shift increases predation on the snail by ducks, and likely reduces the number of mates available in the snail population. In addition, some trematode parasites are known to castrate their snail hosts (e.g., Krist and Lively 1998; Fredensborg et al. 2005), leading to a reduction in male-fertile mates. Finally, snails with resistant genotypes discriminate against mates on the basis of trematode parasite infection (Webster and Gower 2006), which may result in reduced mate availability for infected individuals. For both plants and animals, theory predicts that low mate availability will favor selfing (e.g., Tsitrone et al. 2003a; Porcher and Lande 2005); thus, we predict that an enemy-induced reduction in mate availability will also select for selfing (Table 1, panel C). Alternatively, enemies may reduce plant resources, such that reproduction is resource limited rather than pollen limited. For example, Parker (1987) demonstrated that healthy Arisaema triphyllum plants were strongly pollen limited whereas those infected with Uromyces were not, most likely because the infected plants did not have the resources to allocate to maturing more seeds. Future empirical studies should expand this work to understand the evolutionary consequences for mating system of these enemy-induced changes in pollen limitation and mate availability. In addition, because mate availability largely influences female gamete discounting (i.e., loss of outcrossed progeny relative to gain in selfed progeny; Lloyd 1992; Schoen and Lloyd 1992), an enemy-induced change in mate availability may also have consequences for this discounting cost. Thus, theoretical and empirical studies aimed at understanding how enemies affect mate availability and female gamete discounting would be particularly informative.

Enemy pressure is often heterogeneous (Burdon et al. 1989; Louda 1989; Linhart 1991; Rand 2002), which may result in variation in mate availability. Theory suggests that unpredictable outcross pollen availability can select for mixed mating (Schoen and Brown 1991; Morgan and Wilson 2005). Specifically, a model by Morgan and Wilson (2005) finds that when the pollination environment is variable, the fitness benefits of increased selfing during times of low mate availability outweigh the fitness costs of selfing when mate availability is high because of nonlinear averaging (i.e., Jensen’s inequality); thus, variation in mate availability can promote the evolution of mixed mating. Enemies may create conditions that promote variability in the pollination environment, and thus, selection for mixed mating (Table 1, panel C). For example, in plants, damage from enemies often reduces pollinator visitation (e.g., Strauss et al. 1996; Mothershead and Marquis 2000; Steets and Ashman 2004); thus, variation in enemy attack at any stage prior to or during flowering can produce conditions leading to unpredictable pollinator visitation. Likewise, in animals, variability in outcross mating opportunities can favor self-fertilization or mixed mating (Puurtinen and Kaitala 2002; Tsitrone et al. 2003a, b; Table 1, panel C). Puurtinen and Kaitala (2002) modeled sexual-system evolution in hermaphroditic animals with respect to mate-searching efficiency and demonstrated that selfing is favored when mate-searching efficiency is low. Given that enemies, such as predators, often decrease mate-searching activity of their prey (e.g., Van Duren and Videler 1996; Mathis and Hoback 1997; Rohr and Madison 2001), variation in enemy risk could select for individuals that possess the ability to self-fertilize when attack...
risk is high (i.e., when mate availability is low), but still reap the benefits of outcrossing when attack risk is low (i.e., when mate availability is high).

**MALE GAMETE DISCOUNTING**

Male gamete discounting is the loss of sperm (or pollen) available for outcrossing caused by an increase in selfing (Schoen and Lloyd 1992). Male gamete discounting has been incorporated into models of mating system evolution, and independent of the enemy environment, models predict that it can stabilize intermediate levels of outcrossing when discounting increases with the selfing rate (e.g., Holsinger 1991; Johnston 1998; Porcher and Lande 2005). Enemies have the potential to influence male gamete discounting in ways that could promote the maintenance of intermediate outcrossing (Table 1, panel D). For example, in plants enemies may reduce geitonogamous selfing (Steets et al. 2006) and potentially male gamete discounting. In addition, in animals and plants, enemy pressure may limit mate availability (see Mate Availability), resulting in increased autogamy and potentially reduced male-gamete-discounting costs. Depending on the level of gamete discounting that attacked individuals’ experience, theory predicts that stable mixed mating or complete outcrossing will be favored (Table 1, panel D; Holsinger 1991; Johnston 1998). Because our understanding of how enemies influence victim gamete discounting is still in its infancy, future research should explore whether the above-outlined mechanisms occur in plant and animal systems, and thus, whether enemies have the potential to stabilize victim mixed mating via effects on male gamete discounting.

**BIPARENTAL INBREEDING**

Structural aspects of organisms or their populations can also influence mating system. For example, breeding can occur between related individuals (biparental inbreeding) in clonal and nonclonal organisms with spatial population structure; however, it may be more likely in sedentary ones, which have more restricted gene flow (e.g., Schaal 1974; Grosberg 1991). Breeding between related individuals reduces the advantage of outcrossing because the fitness differential between selfed and outcrossed progeny is lowered. Because the frequency of biparental inbreeding likely increases with the selfing rate, theory holds that biparental inbreeding may promote frequency-dependent selection that can stabilize mixed mating (Uyenoyama 1986). This, however, will depend strongly on both the magnitudes of the genetic cost of outcrossing and inbreeding depression (Yahara 1992; Ronfort and Couvet 1995). The few studies that have estimated biparental inbreeding in natural populations find that it varies dramatically among species (reviewed in Goodwillie et al. 2005), but to date, no study has examined whether enemies contribute to this variation. Nevertheless, enemies have the potential to affect biparental inbreeding in their victims (Table 1, panel E). For example, in *Impatiens capensis* plants damaged by herbivores receive fewer visits by pollinators and are more frequently visited by small solitary bees rather than bumblebees relative to undamaged plants (Steets et al. 2006). Given that pollinator types can differ in their foraging distances (Schmitt 1980), this change in pollinator composition with damage could result in reduced global pollen flow and increased breeding among damaged, related neighbors, thereby increasing biparental inbreeding in these spatially structured populations (Knight and Waller 1987). Alternatively, enemies may reduce biparental inbreeding in the victim population if they enhance gene flow via effects on migration in animals or pollen movement in plants (Table 1, panel E). Based on Uyenoyama’s (1986) model, we predict that increased spatial structure and biparental inbreeding in the victim population may stabilize mixed mating whereas reductions in biparental inbreeding may favor complete outcrossing (Table 1, panel E). Given that biparental inbreeding may affect mating system evolution, a crucial area for research will be to relate spatial genetic structure and spatial patterns of damage to gene flow and mating system.

**Future Directions for Theoretical and Empirical Work**

This review makes clear that enemies have the potential to influence mating system evolution of their victims. However, much more work, both theoretical and empirical, is needed to understand the evolutionary consequences of this interaction. Despite their ubiquity, to our knowledge, enemies have only been explicitly incorporated into theory of victim mating system evolution a few times (Lively and Howard 1994; Agrawal and Lively 2001; Wolf et al., unpubl. ms.), and we would benefit from models that incorporate more ecological realism of the victim–enemy interaction. For example, theory incorporating generalist and specialist victim–enemy interactions for mating system evolution would be particularly informative as inbred and outbred plants can differ in their resistance to generalist and specialist enemies (Hull-Sanders and Eubanks 2005), and simultaneous selection pressure by both enemy types may have complex effects on the mating system. In addition, we lack rigorous tests of the theoretical approaches that have explicitly linked enemy pressure and victim mating system evolution (Lively and Howard 1994; Agrawal and Lively 2001; Wolf et al., unpubl. ms.). Empirical studies that measure model parameters, such as inbreeding depression, male gamete discounting, and victim and enemy selfing rates, in natural systems under different levels of enemy abundance are essential.

Theoretical studies that incorporate parameters known to be influenced by enemies would represent a major step forward. Given that the magnitude of inbreeding depression is a critical determinant in most models of mating system evolution (reviewed in Goodwillie et al. 2005), and that enemies can influence victim expression of inbreeding depression (see Inbreeding
Depression), future theoretical explorations should expand the work of Agrawal and Lively (2001) to also include inbreeding depression. In addition, expanding existing theory to incorporate feedback cycles would be valuable given the importance of balancing selection to the maintenance of mixed mating. Recent empirical studies indicate that the mating system of an enemy can influence victim–enemy dynamics (Christen et al. 2002; Christen and Milinski 2003). Specifically, outcrossing increases the infection success and growth of a tapeworm (Schistoscephalus solidus) into its primary (copepod; Christen et al. 2002) and secondary (stickleback; Christen and Milinski 2003) hosts, especially when parasites compete with one another (Milinski 2006). Given that enemies alter victim mating system expression and victim mating system expression influences both the enemy mating system and the intensity of victim–enemy interaction, this important feedback cycle needs to be incorporated into theory on victim mating system evolution. For example, theory that examines the coevolution of victim and enemy mating systems would be especially insightful.

In addition, as our empirical understanding of the role of enemies in influencing mating system evolution mainly comes from plants, expansion of this work to animal systems to better understand the generality of response and to direct future theory is needed. Although we have a wealth of knowledge on how enemies affect mate availability in animals and pollen limitation in plants, currently no empirical study has linked enemy-induced changes in mate availability to mating system evolution despite the potentially strong connection. Thus, future studies should aim to explore how enemy-induced changes in mate availability or pollen limitation influence selection on victim mating system. Studies that simultaneously test for the influence of enemies on multiple mating system parameters would be especially informative as this approach will allow researchers to discern the relative importance of the numerous pathways by which enemies may have evolutionary consequences for victim mating system.

Consideration of natural enemies has added a new dimension to our understanding of mating system evolution in both plants and animals. Although theoretical and empirical evidences are just beginning to accumulate, it largely points to an enemy effect on mating system and demonstrates that enemies can create dynamics that lead to the evolutionary stability of mixed mating. Additional theoretical and empirical work will further elucidate the impact of this ubiquitous ecological factor on the evolution of mixed mating.

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