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Evolutionary stability of mutualism: interspecific population regulation as an evolutionarily stable strategy

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Interspecific mutualisms are often vulnerable to instability because low benefit : cost ratios can rapidly lead to extinction or to the conversion of mutualism to parasite–host or predator–prey interactions. We hypothesize that the evolutionary stability of mutualism can depend on how benefits and costs to one mutualist vary with the population density of its partner, and that stability can be maintained if a mutualist can influence demographic rates and regulate the population density of its partner. We test this hypothesis in a model of mutualism with key features of senita cactus (*Pachycereus schottii*) – senita moth (*Upiga virescens*) interactions, in which benefits of pollination and costs of larval seed consumption to plant fitness depend on pollinator density. We show that plants can maximize their fitness by allocating resources to the production of excess flowers at the expense of fruit. Fruit abortion resulting from excess flower production reduces pre-adult survival of the pollinating seed-consumer, and maintains its density beneath a threshold that would destabilize the mutualism. Such a strategy of excess flower production and fruit abortion is convergent and evolutionarily stable against invasion by cheater plants that produce few flowers and abort few to no fruit. This novel mechanism of achieving evolutionarily stable mutualism, namely interspecific population regulation, is qualitatively different from other mechanisms invoking partner choice or selective rewards, and may be a general process that helps to preserve mutualistic interactions in nature.

Keywords: fruit abortion; hermaphrodite; pollination; population dynamics; resource trade-offs; sex allocation

1. INTRODUCTION

Only recently has mutualism begun to receive the attention necessary to understand the ecological and evolutionary stability of interacting populations (Pellmyr & Huth 1994; Doebeli & Knowlton 1998; Thompson 1999; Ferriere *et al.* 2002; Holland *et al.* 2002; West *et al.* 2002*a*,*b*; Bergstrom & Lachmann 2003; Bronstein *et al.* 2003; Morris *et al.* 2003; Wilson *et al.* 2003). Insight into mutualism is being made through careful separation of costs and gross benefits from the net benefit experienced (by definition) by both partners (Addicott 1986; Pellmyr 1989; Axen & Pierce 1998; Ferriere *et al.* 2002; Holland *et al.* 2002). Costs can be internally constructed (e.g. plant nectar) or extracted (e.g. seed consumption by yucca moth larvae) by a mutualist. Benefits to a mutualist depend on the traits of its partner (e.g. nectar for pollinators or pollination by yucca moths). Interspecific linkage of costs and benefits often translates into benefits to one species being gained through costs paid by the partner.

A fundamental question of mutualisms remains the biological means by which interactions are stabilized. In theory, stability of mutualism requires that both partners maintain benefits that exceed costs. Otherwise, the interaction will erode into parasitism or predation, or possibly extinction of one or both partners. Such destabilization can occur through two general pathways. First, if a species extracts a benefit from its partner without providing benefits back to that partner, the interaction by definition is no longer mutualism. Second, in benefiting by extracting a cost from its partner, a species might increase its own benefit and its partner's cost to the point at which the partner no longer has a net benefit. In either case, if a species increases its benefit and its partner's cost beyond the limits of tolerance of its partner, it could cause extinction of its partner. If interactions are obligate, this could mean extinction of both species.

Destabilization can, in theory, be prevented if a species can prevent its partner from extracting excessive costs; that is, from being a true parasite or predator. Mechanisms achieving this control certainly can vary with the biology of interactions (Pellmyr & Huth 1994; Doebeli & Knowlton 1998; Ferriere *et al.* 2002; West *et al.* 2002*a*,*b*; Bergstrom & Lachmann 2003). However, in many mutualisms, the deciding factor that separates the mutualist from parasite or predator may simply be population density. Increasing or decreasing population density of a species may increase or decrease the costs and/or benefits to its partner (Holland *et al.* 2002), such that net (positive or negative) effects depend on how benefits and costs to a mutualist vary with population density of its partner species. For example, incremental increases in benefits might

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approach zero earlier than incremental increases in costs; further increases in population density incur only greater costs to the partner. If a mutualistic species is capable of influencing its partner's demographic rates, then natural selection might favour traits that exert interspecific regulation on population density.

We hypothesize that, when benefits and costs to a mutualist depend on its partner's population density, the mutualism can be stabilized by the mutualist exerting control over its partner's demographic rates and population density. We test this hypothesis for the pollinating seed-consuming mutualism between senita cacti and senita moths in which adult insects pollinate and larvae consume seeds (Holland & Fleming 1999). However, the model is applicable to other such mutualisms, e.g. yucca – yucca moth interactions (Pellmyr 2003). This theoretical study was motivated by the long-standing question of how such plants prevent larvae from consuming so many seeds that pollination benefits are negated by fecundity costs. We developed a model that explicitly relates pollinator population density to rates of pollination and seed eating; plant fitness (both male and female functions) to pollination and seed eating; and resource allocation trade-offs between flowers and fruit to pollinator population density. We analysed this ecological model to find evolutionarily stable strategies (ESSs) of plant resource allocation. We found that under reasonable conditions, excess flower production and fruit abortion is an ESS that increases plant fitness by regulating the pollinator population. Excess flower production and fruit abortion kept pollinator density below a critical level at which the mutualism would be destabilized.

2. THE MODEL

(a) *Ecological model*

The symbols of models we develop below are defined in electronic Appendix A. Consider an individual plant (i) that produces a number of flowers (F_i) each time step, typically a day. Associated with the plant population is an obligate pollinator, of population size M, that lays its eggs in the flowers. Both benefits of pollination, expressed as the fraction of flowers pollinated (P_i), and costs of larval seed or fruit consumption, expressed as the fraction of flowers parasitized (D_i), are assumed to increase monotonically with pollinator density, M, and to asymptote to 1.0. P_i and D_i are assumed to increase and saturate with pollinator density, because at some M, pollinators are sufficiently abundant that almost all flowers are pollinated, or enough eggs are laid for almost all seeds to be eaten. We represent these functional responses as $P = 1 - \mathrm{e}^{-\gamma_1 f(M,F_i)}$ and $D = 1 - \mathrm{e}^{-\gamma_2 f(M,F_i)}$, where γ_1 and γ_2 are pollination and oviposition rates of an individual insect, respectively. A derivation of this type of functional response for pollination or parasitism can be found in Hassell (1975; see his Appendix 1), where it is shown that the function in the exponent, $f(M,F_i)$, has the general form $aM/(1 + aT_\mathrm{h}F)$, where a is the attack rate and T_h is the handling time. We consider only the two limiting forms that are proportional to M and M/F_i, yielding predator-dependent and ratio-dependent functional responses, respectively, analogous to prey-dependent and ratio-dependent functional responses in predator–prey theory (Abrams & Ginzburg 2000). We assume oviposition occurs on pollinated flowers and leads to larvae in fruit. Because not all seeds or fruit are consumed by larvae, $\gamma_2 \leqslant \gamma_1$, such that P_i increases faster than D_i. $P_i - D_i$ is the net effect of pollination and seed consumption on plant reproduction.

(b) *Incorporating male fitness, sex allocation and pollinator dynamics into the ecological model*

Hermaphrodite plants commonly produce excess flowers, resulting in low fruit : flower ratios (Sutherland & Delph 1984). Although numerous ecological and evolutionary explanations exist for this phenomenon (Ayre & Whelan 1989), here we ask only if excess flower production by hermaphroditic plants relying on pollinating seed-consumers might increase plant fitness by influencing M, and thereby $P_i - D_i$. Fitness of hermaphrodites depends on both male (pollen dispersal) and female (fruit production) functions of flowers. Hermaphrodite plant fitness, W_i, is expressed as

$$W_i = W_{\mathrm{F},i} + \overline{W}_\mathrm{F}\frac{W_{\mathrm{M},i}}{\overline{W}_\mathrm{M}}, \tag{2.1}$$

where $W_{\mathrm{F},i}$ and $W_{\mathrm{M},i}$ are female and male fitness of individual i, and $\overline{W}_\mathrm{F}$ and $\overline{W}_\mathrm{M}$ are mean female and male fitness of the population. Sex allocation involves the trade-off and partitioning of limited resources between flower (male fitness) and fruit (female fitness) production (Charlesworth & Charlesworth 1981; Campbell 2000; Klinkhamer & de Jong 2002). We do not assume specific forms of male and female fitness gain curves. We only assume that the plants can change flower production by partitioning resources between flower and fruit production.

$R_{\mathrm{t},i}$ is the total resource available for plant reproduction, expressed in arbitrary resource units. $R_{\mathrm{fl},i}$ is the fraction of $R_{\mathrm{t},i}$ allocated to flower production and $R_{\mathrm{fr},i}$ is the fraction of $R_{\mathrm{t},i}$ allocated to fruit production, such that $1 = R_{\mathrm{fl},i} + R_{\mathrm{fr},i}$. Flower production is expressed as $F_i = R_{\mathrm{t},i}R_{\mathrm{fl},i}\alpha$, where α is the conversion efficiency of resources into flowers. Potential fruit production is expressed as $G_i = R_{\mathrm{t},i}R_{\mathrm{fr},i}\beta$, where β is the conversion efficiency of resources into mature fruit. Actual fruit production is a function of flower production (F_i), fruit set ($F_{\mathrm{s},i}$) and fruit consumption (D_i). Fruit set, $F_{\mathrm{s},i}$, is the fraction of flowers beginning fruit development, given pollination (P_i) and resources available for fruit production (G_i). Fruit set is expressed as

$$F_{\mathrm{s},i} = \begin{cases} F_iP_i & \text{if} \quad F_iP_i < G_i \\ G_i & \text{if} \quad F_iP_i \geqslant G_i \end{cases}. \tag{2.2}$$

Seed or fruit production, or female fitness ($W_{\mathrm{F},i}$), is expressed as

$$W_{\mathrm{F},i} = F_{\mathrm{s},i}\left(1 - \frac{D_i}{P_i}\right). \tag{2.3}$$

In equation (2.3), D_i/P_i, the fraction of pollinated flowers that are parasitized, reflects the fact that eggs are laid on pollinated flowers. This is consistent with what is known about pollinating seed-consuming mutualisms, in that insects typically lay their eggs on flowers that they have pollinated (Pellmyr *et al.* 1996; Holland & Fleming 1999).

If the number of flowers pollinated (F_iP_i) is less than the number of flowers that can set fruit given resources (G_i), fruit set is pollen limited, and equation (2.3) is

$$W_{\mathrm{F},i} = F_i(P_i - D_i) = R_{\mathrm{t},i}R_{\mathrm{fl},i}\alpha(\mathrm{e}^{-\gamma_2 f(M,F_i)} - \mathrm{e}^{-\gamma_1 f(M,F_i)}). \tag{2.4}$$

When fruit set is pollen limited, equalling F_iP_i, $F_i - F_iP_i$ unpollinated flowers abscise and no fruit abortion occurs. However, if the number of pollinated flowers (F_iP_i) is greater than the number of flowers that can set fruit given available resources (G_i), then fruit set is resource limited, and equation (2.3) is

$$W_{\mathrm{F},i} = G_i\left(\frac{P_i - D_i}{P_i}\right) = R_{\mathrm{t},i}R_{\mathrm{fr},i}\beta\left(\frac{\mathrm{e}^{-\gamma_2 f(M,F_i)} - \mathrm{e}^{-\gamma_1 f(M,F_i)}}{1 - \mathrm{e}^{-\gamma_1 f(M,F_i)}}\right). \tag{2.5}$$

When fruit set is resource limited, equalling G_i, $F_i - F_iP_i$ flower abscissions occur and $F_iP_i - G_i$ fruit abortions occur. Fruit abortion in this model is random, not selective, and occurs only if fruit set is resource limited. Given that $1 = R_{\mathrm{fl},i} + R_{\mathrm{fr},i}$, $F_i = R_{\mathrm{t},i}R_{\mathrm{fl},i}\alpha$ and $G_i = R_{\mathrm{t},i}R_{\mathrm{fr},i}\beta$, fruit set can be resource limited when the fraction of $R_{\mathrm{t},i}$ allocated to flower production is greater than $[\beta/(\beta + \alpha)]$. An important aspect of plant reproduction in equation (2.5) is fruit abortion. Fruit abortion has the consequence of reducing pre-adult survival of the pollinating seed-consumer population because eggs and larvae die in aborted fruit.

The differential equation for changes in pollinator density is

$$\frac{\mathrm{d}M}{\mathrm{d}t} = F_{\mathrm{s},i}\left(\frac{D_i}{P_i}\right) - \delta M = F_{\mathrm{s},i}\left(\frac{1 - \mathrm{e}^{-\gamma_2 f(M,F_i)}}{1 - \mathrm{e}^{-\gamma_1 f(M,F_i)}}\right) - \delta M, \tag{2.6}$$

where δM is the mortality rate of insects, $F_{\mathrm{s},i}(D_i/P_i)$ is the recruitment rate of adults, assuming that each parasitized fruit produces a single adult pollinator, and $F_{\mathrm{s},i}$ is given by equation (2.2). When $F_{\mathrm{s},i}$ is pollen limited, equation (2.6) becomes

$$\frac{\mathrm{d}M}{\mathrm{d}t} = F_i(1 - \mathrm{e}^{-\gamma_2 f(M,F_i)}) - \delta M, \tag{2.7}$$

where the first term is the number of flowers pollinated and parasitized. When $F_{\mathrm{s},i}$ is resource limited, equation (2.6) becomes

$$\frac{\mathrm{d}M}{\mathrm{d}t} = \frac{R_{\mathrm{t},i}R_{\mathrm{fr},i}\beta(1 - \mathrm{e}^{-\gamma_2 f(M,F_i)})}{1 - \mathrm{e}^{-\gamma_1 f(M,F_i)}} - \delta M, \tag{2.8}$$

where the first term reduces pollinator recruitment as a result of fruit abortion. Because equation (2.6) becomes equation (2.7) or equation (2.8), depending on M, fruit set has a density-dependent feedback on pollinator density. When fruit set is pollen limited, fruit abortion does not occur and pollinator density increases with flower production. However, when fruit set is resource limited, fruit abortion occurs, and pollinator density decreases with increasing flower production because $R_{\mathrm{fr},i}$ decreases. The larger F_iP_i is than G_i, the more fruit abortions occur and the greater the negative density-dependent feedback on pre-adult mortality.

Thus, fruit abortion may be a factor for population regulation of M. We have not explicitly included other mortality sources (e.g. predation), variation in egg–larva survival, or migration, but we have shown elsewhere that fruit abortion has the same dynamic effects when they are included (Holland & DeAngelis 2001, 2002; Holland *et al.* 2002). Also, the model follows pollinator population density, but not plant population density, because yucca and senita systems (Holland & Fleming 1999; Pellmyr 2003) involve long-lived iteroparous plants and semelparous pollinators with short generation times. Populations of these insects can fluctuate over short time periods in which (adult) plant population density remains relatively constant. We have incorporated flower phenology and plant population dynamics into ecological analyses of stability elsewhere (Holland & DeAngelis 2001; Holland *et al.* 2002).

We evaluated the model numerically, using both predator- and ratio-dependent functional responses, with constant flower production (F_i) and model parameters ($\gamma_1, \gamma_2, \alpha, \beta, \delta$). Right-hand sides of equations (2.7) and (2.8) were set to zero to solve for M for any F_i. Model results are numerical, because equation (2.6) has no closed solution. An approximation to this model can be solved analytically (see electronic Appendix B). We report numerical solutions because they are quantitatively correct.

(c) *Evolutionary model*

We evaluated whether an ESS occurs for excess flower production, and if it depends on male fitness gain curves. In a homogeneous plant population, male fitness is identical to female fitness. However, in a mixed strategy population, relative male fitness is related positively to relative flower production. Different functions exist for how male fitness may vary with flower production (Campbell 2000; Klinkhamer & de Jong 2002). We first rewrite equation (2.1) as

$$W_i(\mathrm{Inv}) = W_{\mathrm{F},i}(\mathrm{Inv}) + \overline{W}_{\mathrm{F}}(\mathrm{Res})\frac{W_{\mathrm{M},i}(\mathrm{Inv})}{\overline{W}_{\mathrm{M}}(\mathrm{Res})}, \tag{2.9}$$

where Res and Inv are resident and invader strategies, and then we analyse the evolutionary stability for three different male fitness functions. We refer to the first male fitness function incorporated into equation (2.9) as 'standard' male fitness, for which invader flower production is divided by resident flower production. The second male fitness function is 'decelerating' as a function of flower production. We express this function as $W_{\mathrm{M},i} = aF_i^b$, where F_i is flower production by Res or Inv and $b < 1$. Finally, we incorporate a 'saturating' male fitness function into equation (2.9). This function is $W_{\mathrm{M},i} = F_i(1 - \mathrm{e}^{-\gamma_1 f(M,F_i)})$, where F_i is flower production by Res or Inv. γ_1 is the rate of pollen collection, which is assumed to be equivalent to rates of pollination, because flower visitation behaviour of pollinating seed-consumers almost always includes both pollination and pollen collection (Holland & Fleming 1999; Pellmyr 2003). Note that the saturating male fitness function incorporates the demographic feedback of fruit abortion on male fitness by altering pollinator number, M.

We determined the fitness of residents in a homogeneous population for values of $R_{\mathrm{fl},i}(\mathrm{Res})$ from 0.0 to 1.0 at intervals of 0.02. For each $R_{\mathrm{fl},i}(\mathrm{Res})$ value, a series of invaders with strategies, $R_{\mathrm{fl},i}(\mathrm{Inv})$, covering the same range, were introduced and the $W_i(\mathrm{Inv})$ of each determined. For each resident strategy $R_{\mathrm{fl},i}(\mathrm{Res})$, it was determined for which $R_{\mathrm{fl},i}(\mathrm{Inv})$ value invader fitness was less than, equal to or greater than resident fitness.

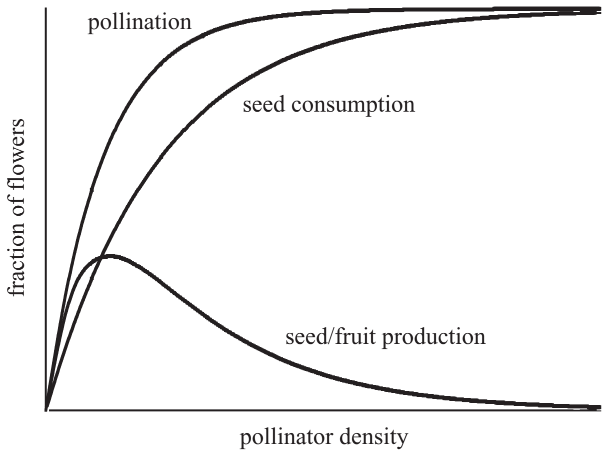

Figure 1. Benefits of pollination, costs of larval seed or fruit consumption, and net effects of seed or fruit production as a function of pollinator abundance [$f(M,F)$], for pollinating seed-consuming mutualisms such as yucca – yucca moth and senita – senita moth interactions.

3. RESULTS

(a) *Ecological model*

The net effect of pollinating seed-consumers on plant reproduction depends on both the functional responses of benefits of pollination and costs of larval fruit consumption, or $F_i(P_i - D_i) = F_i(\mathrm{e}^{-\gamma_2 f(M,F_i)} - \mathrm{e}^{-\gamma_1 f(M,F_i)})$ (figure 1). At low M, fruit production is low, as few flowers are pollinated. At high M, many flowers are pollinated but fruit parasitism is high. Intermediate M results in the greatest fruit production. Because both P_i and D_i are functions of M, plants may control benefits, costs and net fitness effects of the interaction by altering M.

Hereafter, we refer to strategies of the fraction of resources allocated to flower production (x-axis, figure 2) simply as the 'flower production strategy', or $R_{\mathrm{fl},i}$. Potential fruit production decreases and flower production increases as resource allocation to flower production increases (figure 2). The intersection of these lines determines the exact flower production strategy at which fruit set can switch from pollen to resource limitation. For parameter values of figure 2, fruit set can be resource limited for flower production strategies using more than 33% (that is, $\beta/(\beta + \alpha) = 1/(1 + 2)$) of resources. Pollinator abundance and the number of flowers pollinated determines if fruit set is resource or pollen limited, and if fruit abortion occurs.

Pollinators become more abundant with increasing flower production strategies, $R_{\mathrm{fl},i}$, over the interval from 0 to 0.33 because seeds and fruit supporting their population increase (figure 2). Pollinator abundance decreases for $R_{\mathrm{fl},i} > 0.33$ because fruit set becomes resource limited, resulting in fruit abortion and pre-adult mortality. Even though fruit abortion reduces pollinator abundance for $R_{\mathrm{fl},i} > 0.33$, pollinators are abundant enough that fruit set remains limited by resources rather than pollen. Thus, M is relatively high for low flower production strategies, but declines to very low values with increasing $R_{\mathrm{fl},i}$ (figure 2). Results of ratio-dependent (figure 2*a*) and predator-dependent (figure 2*b*) functional responses were largely the same, with a central difference. For ratio dependence, pollinators persist at low flower production because the per-flower oviposition rate increases as flowers decrease in number, whereas for predator dependence, pollinator abundance does not begin to increase until the flower resource base becomes sufficiently large to counter their mortality rate.

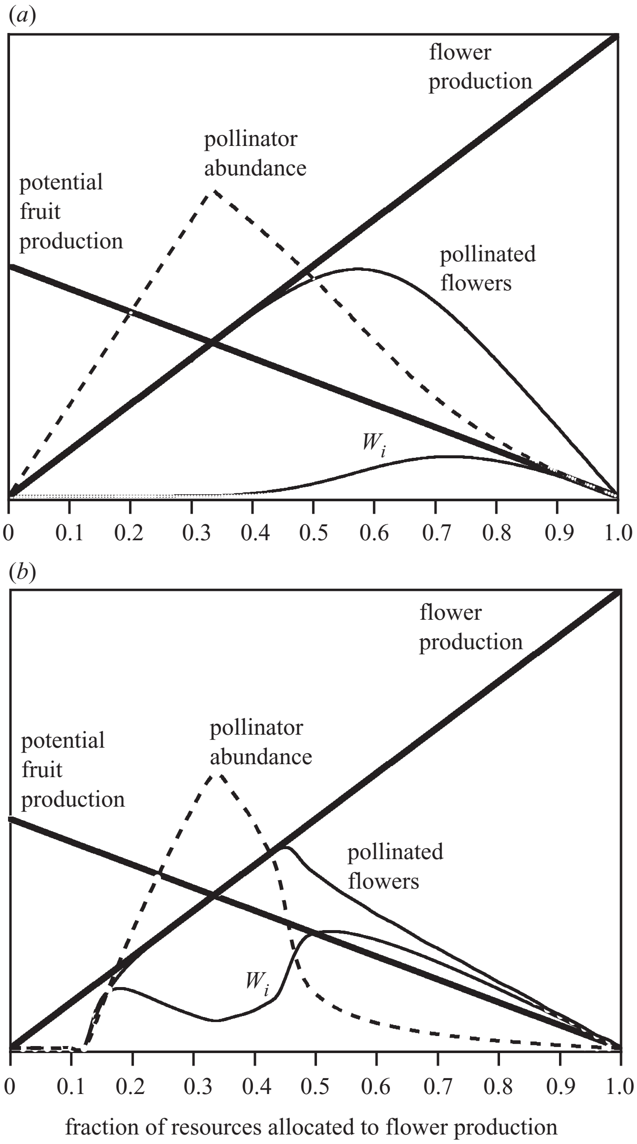

Figure 2. Ecological model of plant fitness based on the fraction of resources allocated to flower production (i.e. flower production strategies, $R_{\mathrm{fl},i}$) for pollinating seed-consuming mutualisms for (*a*) ratio-dependent, and (*b*) predator-dependent functional responses. Parameter values were $R_{\mathrm{t},i} = 200$, $\alpha = 2$, $\beta = 1$, $\gamma_1 = 6$, $\gamma_2 = 3$ and $\delta = 0.5$ for the ratio-dependent case, and $R_{\mathrm{t},i} = 200$, $\alpha = 2$, $\beta = 1$, $\gamma_1 = 0.03$, $\gamma_2 = 0.01$ and $\delta = 0.5$ for the predator-dependent case.

In this homogeneous plant population, fitness of all individuals is the same ($W_{\mathrm{F},i} = \overline{W}_{\mathrm{F}}$, $W_{\mathrm{M},i} = \overline{W}_{\mathrm{M}}$). Also, male fitness equals female fitness because pollen from each plant will pollinate the same expected number of flowers that produce fruit. Thus, $W_i = W_{\mathrm{F}} + W_{\mathrm{M}} = 2W_{\mathrm{F}}$. Figure 2 shows how plant fitness varies with pollinator density and flower production strategies. For the case of ratio-dependent functional responses, flower production strategies $R_{\mathrm{fl},i} > 0.40$ resulted in high pollinator densities, which lead to high larval fruit consumption and little to no fruit production (figure 2*a*). However, as resource allocation to flower production increased beyond $R_{\mathrm{fl},i} > 0.40$, fruit production and total plant fitness increased to optima,

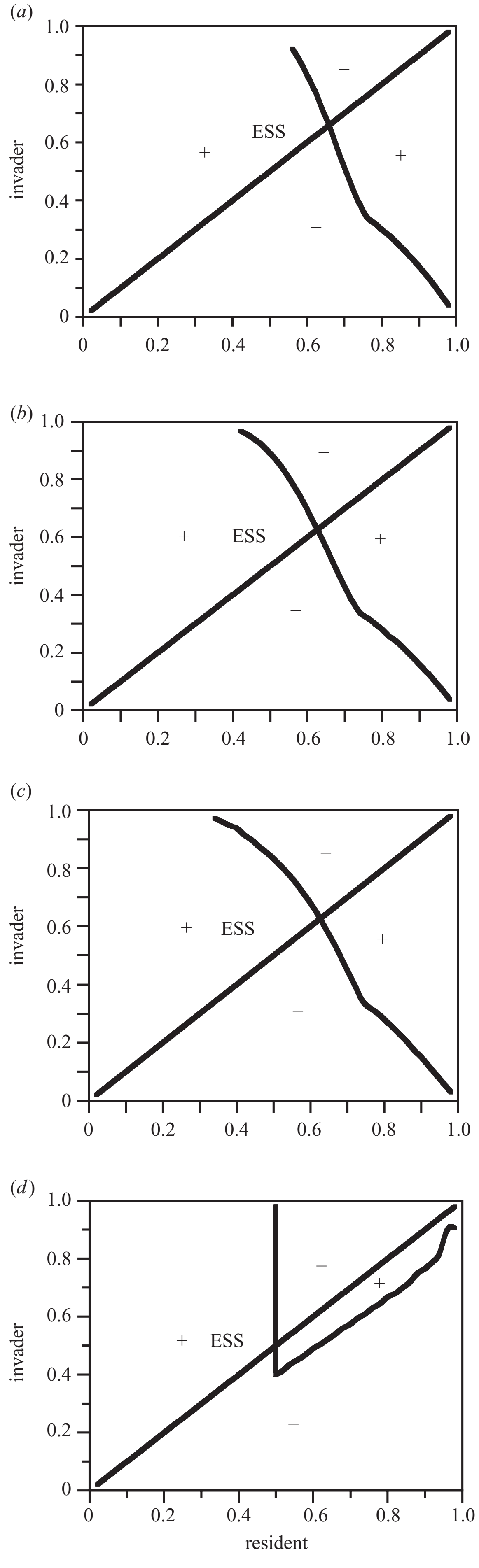

Figure 3. Invader versus resident strategies of flower production (fraction of resources allocated to flower production) for ratio dependence for: (*a*) standard; (*b*) decelerating; and (*c*) saturating male fitness as a function of flower production, and (*d*) standard male fitness for predator dependence. Plus signs are invadable areas, negative signs are uninvadable. The two lines in each plot are zero fitness contour lines. The ESS is at the point of intersection of the two zero fitness contour lines. Parameter values are the same as in figure 2, except that in (*b*) $a = 0.75$ and $b = 0.5$ for $W_{\mathrm{M}} = aF_i^b$. Note, the small kinks in the zero fitness contour line at an invader strategy of 0.333 occur because resource-limited fruit set and fruit abortion begin, hence a more rapid increase in the fitness contour line.

then declined for very high flower production strategies because M was exceptionally low. Such dynamics and results are largely consistent with those of predator dependence, with one important distinction (figure 2*b*). Under predator dependence, for some parameter values, plant fitness is a bimodal, rather than a unimodal, function of the fraction of resources allocated to flower production. There is a small fitness peak at low $R_{\mathrm{fl},i}$ values (*ca*. 0.17), and then a large fitness peak at intermediate to high $R_{\mathrm{fl},i}$ values (*ca*. 0.53). The trough in the fitness gradient results from pollinator density reaching such high levels that many flowers receive ovipositions, and hence high larval consumption. The fitness peaks occur because pollinators are sufficiently abundant to pollinate existing flowers, but not so abundant that high *per capita* flower oviposition occurs. Regardless of whether predator- or ratio-dependent functional responses were used, excess flower production and ensuing fruit abortion keep the pollinator population density below a threshold that would lead to little to no seed production and the probable extinction of the plant population. By increasing flower production, plants can regulate pollinator abundance, and their benefits and costs, and thereby optimize their fitness.

(**b**) ***Evolutionary model***

The above results of the ecological model show that a strategy of excess flower production and ensuing fruit abortion is capable of regulating pollinator density, thereby maximizing plant fitness and preventing extinction of the plant population. Advantages of this strategy, however, do not mean that it is an ESS. In theory, stability of mutualism requires that a conspecific 'cheater' genotype, within either partner species, does not spread to fixation and eliminate the 'mutualistic' genotype. This problem mirrors similar barriers to the evolution of intraspecific cooperation (Axelrod & Hamilton 1981; Bull & Rice 1991). Cheaters are individuals that increase their fitness by reducing their cost : benefit ratio and thereby the benefit : cost ratio of their partner. They can do so by reducing benefits provided to their partner (and costs to themselves), or by increasing their own benefits (and costs to their partner). In either case, cheater fitness will increase and its phenotype may spread to fixation, reducing mutualism to parasite–host or predator–prey interactions. In a resident population of excess flower production, a cheater with low flower production may experience the benefits of moderate pollinator density without over-producing flowers and aborting fruit.

Such an invader strategy may replace a resident strategy of excess flower production.

Figure 3 shows pairwise invasibility plots (Geritz *et al.* 1997) of invader versus resident strategies of flower production for ratio-dependent functional responses for standard, decelerating and saturating male fitness functions, and for predator-dependent functional responses for standard male fitness. These male fitness functions are described in § 2c. The two lines in each plot are zero fitness contour lines; that is, where the fitness of invader and resident strategies are the same. The point of intersection of the two zero fitness contour lines is a singular strategy. Plus signs denote areas in which the resident strategy can be invaded because fitness of the invader strategy is greater than the resident strategy. Negative signs denote areas in which the resident strategy cannot be invaded because fitness of the invader strategy is lower than the resident strategy. If a vertical line drawn through the singular strategy lies entirely in areas with negative signs, then the singular strategy is an ESS. If the area just above the zero fitness line emanating from the origin has positive signs, and the area just below this line to the right of the singular strategy also has positive signs, then the singular strategy is a convergence stable strategy (CSS). If the singular strategy is convergence and evolutionarily stable, then the ESS–CSS is reached through progress evolutionary steps, whereby phenotypes closer to the singular strategy invade and replace those farther from it.

ESSs and CSSs of excess flower production exist for ratio dependence for the standard, decelerating and saturating male fitness (figure 3*a*–*c*) and for predator dependence for standard male fitness. Regardless of a variety of assumptions about male fitness gain curves, excess flower production and ensuing fruit abortion to regulate pollinator density does represent an ESS reached through convergence. Regulating pollinator density increases plant fitness and prevents extinction of the plant population. We evaluated how the ecological and ESS $R_{\text{fl},i}$ values varied and compared with one another for a variety of parameter values (electronic Appendix C). Changing parameter values altered the exact ecological and ESS $R_{\text{fl},i}$ values, as well as the discrepancy between them. However, all $R_{\text{fl},i}$ values, regardless of parameter values, were for strategies of excess flower production. Also, discrepancies between ecological and ESS $R_{\text{fl},i}$ values were not large, again regardless of the exact parameter values. In no case were $R_{\text{fl},i}$ values for low flower production or equal resource partitioning between flower and fruit production. For two reasons, cheater strategies of low flower production cannot invade an ESS of excess flower production. First, an invader with fewer flowers than the ESS strategy experiences greater per-flower oviposition than the ESS strategy, and hence lower fruit production and female fitness as a result of high larval fruit eating. Second, an invader with few flowers relative to the ESS strategy has lower male fitness as a result of lower flower production. In general and without consideration of parameter values or the exact functional response, strategies of excess flower production prevail over low flower production by increasing *both* male and female fitness functions of hermaphroditic plants. In particular, excess flower production allows plants to increase their female fitness function of fruit production by preventing costs of larval seed consumption from being so high that few to no fruit are produced.

4. DISCUSSION

We studied how the evolutionary stability of mutualism can depend on a mutualistic species having a mechanism to regulate the population growth rate and density of its partner. Into a single succinct formulation of mutualism between hermaphroditic plants and pollinating seed-consumers, we incorporated several key processes: sex allocation, trade-offs in resource allocation between flower and fruit production, benefits of pollination, costs of larval fruit eating, pollinator population dynamics and fruit abortion. We have shown that, in the absence of further pollinator evolution, the mutualism's stability depends on the strategy that a plant adopts in allocating resources between flower and fruit production. Low flower production strategies lead to high pollinator abundances and high larval fruit consumption, and hence little to no seed production and the probable extinction of the plant population. Strategies of excess flower production and ensuing fruit abortion lead to moderate pollinator population density, greater plant fitness and stability of the mutualism. Moreover, excess flower production increases *both* male fitness (pollen dispersal) *and* female fitness (fruit production). Fruit production actually increases, even though resources available for it decrease, because pollinator abundance is reduced to intermediate levels through increased larval mortality resulting from fruit abortion. Such a strategy of excess flower production and fruit abortion is evolutionarily stable, regardless of parameter values, male fitness gain curves or functional responses (ratio- or predator-dependent). Independent of the numerous hypotheses explaining excess flower production (Sutherland & Delph 1984; Ayre & Whelan 1989) and in contrast with the prediction from sex allocation theory that fruit production should decrease with flower production, this study and another (Ehrlén 1991) indicate that excess flower production can, under some ecological scenarios, evolve for the sole function of increasing female fitness of hermaphroditic plants.

To our knowledge, this study is the first to propose and demonstrate that evolutionary stability of mutualism, at least in the short term, can depend on a partner's population density and can be maintained by the evolution of traits that regulate a partner's population density. When benefits or costs of mutualism to a species depend on a partner's population density, such interspecific population regulation may control benefits, costs and fitness resulting from the interaction. It should be noted, however, that the purpose of this study was to analyse evolution of plant strategies that increase fitness and prevent extinction. It remains possible that the pollinator could evolve to overcome the limitations placed by the plant's strategy. This paper is the first of a pair of papers, the second dealing with coevolutionary responses of pollinators. For example, pollinating seed-consumers might evolve an oviposition strategy (reduced clutch size, uniform or clumped egg distribution (Holland & Fleming 1999; Ferdy *et al.* 2002)) that minimizes the regulating effects of excess flower production and ensuing fruit abortion. Such evolution of increased survival might render the ESS plant strategy less effective, causing a shift in the ESS to a higher flower production strategy, or possibly destabilization of the interaction. Our results do show, however, that plants can prevent immediate short-term destabilization through regulation of the pollinator population.

Although mechanisms of partner choice and partner fidelity, derived from game theory to explain the evolutionary stability of intraspecific cooperation, have been applied to interspecific mutualisms (e.g. Axelrod & Hamilton 1981; Bull & Rice 1991; Doebeli & Knowlton 1998), these have had limited success explaining stability of mutualism. These mechanisms are based on individuals being able to choose among partners (with different strategies, genotypes) with which to interact; repeated interactions with the same beneficial individuals (or genotypes) of a partner species; and differential reward and punishment of individuals (genotypes) that are more and less rewarding. Although these mechanisms may be feasible for intraspecific cooperation, they are not often observed in interspecific interactions. Many species involved in mutualistic interactions have only one interaction with particular partners. Many species have little to no ability to choose their partners, and many species have little flexibility in differentially rewarding and punishing particular partners. Mechanisms independent of, or in combination with partner fidelity and partner choice, may be needed for mutualism to be evolutionarily stable. We do not imply that such mechanisms are *in lieu* of partner choice or partner fidelity, only that such mechanisms may facilitate evolutionary stability of mutualism.

Mechanisms other than partner choice and partner fidelity may be needed because the benefits and costs, and hence net fitness effects, to an individual mutualist often depend on the abundance of partners with which an individual interacts. For example, selective fruit abortion by certain species of yucca has been interpreted as a mechanism of partner choice, in which the plant can punish moths that lay many eggs in individual flowers, thus selecting for more innocuous moth genotypes (Bull & Rice 1991; Pellmyr & Huth 1994). By selectively aborting fruit with many rather than few yucca moth larvae, yucca plants can increase net seed production of a flower crop. However, if yucca moths are so abundant that many fruit have many larvae, then net seed production will be low regardless of selective abortion. But, excess flower production, at times more than 90% than can be matured, is common among many species of *Yucca* (see, for example, Aker & Udovic 1981; Udovic 1981). This is consistent with our model results in that excess flower production, with either random or selective fruit abortion, can function to regulate the pollinating seed-consumer population, and hence benefits of pollination and costs of larval seed or fruit consumption. Therefore, selective fruit abortion can simultaneously be a mechanism of partner choice and a mechanism to regulate the abundance of moths interacting with yucca plants, which might then result in a lower expected cost to all plants in the population (Holland & DeAngelis 2001). In addition to selective fruit abortion in yucca – yucca moth interactions, other similar mechanisms that may limit partner abundance include, for example, senescing nodules in legume–rhizobium interactions (Denison 2000; West *et al.* 2002*a*,*b*), chemical toxins produced by plants that limit mycorrhizal growth (Smith & Read 1997), and limited thorn domicile production in plants that might reduce abundance of protector ants (Fonseca 1993). In each case, the individual plant can certainly limit the frequency of interaction with its partner by limiting the amount of hospitable resource it provides. However, an additional effect might be to limit the partner's population, such that a lower 'infection' rate results that is more tolerable by plants.

In the pollinating seed-consuming mutualism between senita and senita moths, there is no apparent mechanism of partner choice by which plants can punish or sanction moths (Holland *et al.* 2004). The only apparent means by which senita can control their benefits and costs is by regulating pollinator density through excess flower production and (non-selective) fruit abortion. We have shown that excess flower production can evolve to regulate pollinator population density and increase fruit production. Evolution of such mechanisms to regulate partner abundance does not rely on group selection, as we have shown that selection at the level of individuals can lead to ESSs that regulate partner abundance. A cheater genotype with low flower production cannot invade because (i) they have few flowers and hence low male fitness, and (ii) they experience high pollinator densities and hence high larval fruit consumption. Moreover, senita with few flowers have higher pollinator : flower ratios than senita with many flowers (Holland *et al.* 2004). Although there is little clarity on what prevents evolutionary instability that would result from unchecked larval seed consumption and the collapse of plant fecundity, we suggest that, for pollinating seed-consuming mutualisms and mutualisms in general, evolutionary stability often depends at least in part on individuals having mechanisms to control, regulate or limit partner abundance.

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