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Population dynamics and the ecological stability of obligate pollination mutualisms

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Abstract Mutualistic interactions almost always produce both costs and benefits for each of the interacting species. It is the difference between gross benefits and costs that determines the net benefit and the per-capita effect on each of the interacting populations. For example, the net benefit of obligate pollinators, such as yucca and senita moths, to plants is determined by the difference between the number of ovules fertilized from moth pollination and the number of ovules eaten by the pollinator's larvae. It is clear that if pollinator populations are large, then, because many eggs are laid, costs to plants are large, whereas, if pollinator populations are small, gross benefits are low due to lack of pollination. Even though the size and dynamics of the pollinator population are likely to be crucial, their importance has been neglected in the investigation of mechanisms, such as selective fruit abortion, that can limit costs and increase net benefits. Here, we suggest that both the population size and dynamics of pollinators are important in determining the net benefits to plants, and that fruit abortion can significantly affect these. We develop a model of mutualism between populations of plants and their pollinating seed-predators to explore the ecological consequences of fruit abortion on pollinator population dynamics and the net effect on plants. We demonstrate that the benefit to a plant population is unimodal as a function of pollinator abundance, relative to the abundance of flowers. Both selective abortion of fruit with eggs and random abortion of fruit, without reference to whether they have eggs or not, can limit pollinator population size. This can increase the net benefits to the plant population by limiting the number

of eggs laid, if the pollination rate remains high. However, fruit abortion can possibly destabilize the pollinator population, with negative consequences for the plant population.

Keywords Fruit abortion · Functional response · Mutualism · Benefits · Costs

Introduction

Mutualism, at the individual or population level, occurs when there is a net increase in the reproduction and/or survival of each interacting species, when in the presence of its mutualistic partner. Most studies of mutualism involve identifying the species interacting, their benefits and costs, and their evolutionary relationships (Bronstein 1994a). Due to the importance of mutualistic interactions for the evolution and coevolution of species, much of the theoretical and empirical work on mutualism has occurred at the level of the individual, because changes in reproduction and/or survival of individuals lead to the evolution and coevolution of species. However, such changes in reproduction and survival not only influence evolution, but they also influence demography and population size and dynamics.

While there is much to still learn about the evolution of mutualism, we know even less about population processes occurring on ecological time scales that influence and are influenced by the ecological dynamics and population level processes of mutualism. Despite increasing attention in recent decades, the population dynamics of mutualists remain poorly understood (DeAngelis et al. 1979; Addicott 1981; Dean 1983; Wolin 1985; Addicott 1998; Bever 1999). There is little certainty about how the dynamics of mutualists influence each other's benefits and costs and vice versa. Such influences are crucial, because the magnitude of benefits and costs are not fixed traits of mutualism, in either ecological or evolutionary time, but instead can vary with population level variables, such as population size or density (Cushman and

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Whitham 1989; Breton and Addicott 1992; Bronstein 1994b; Morales 2000).

The potential influence of population size and dynamics on a mutualistic relationship is clearly exemplified by pollination mutualisms in which larvae of the pollinator consume seeds and fruit of plants. Such mutualisms include interactions between yucca plants and yucca moths (Riley 1892; Addicott 1986; Pellmyr et al. 1996), senita cacti and senita moths (Fleming and Holland 1998; Holland and Fleming 1999a,b), fig trees and fig wasps (Bronstein 1992; Herre 1996), *Trollius europaeus* and *Chiastocheta* flies (Pellmyr 1989, 1992; Hemborg and Despres 1999), and *Lithophragma* and *Greya* moths (Thompson and Pellmyr 1992; Pellmyr et al. 1996). In these mutualisms, adult insects benefit plants through pollination, but they also impose costs when eggs laid on flowers hatch and larvae consume the seeds of flowers pollinated by the adults. If pollinator populations are large relative to the number of flowers, then, because many eggs are laid, costs are large. On the other hand, if pollinator populations are small, then gross benefits to plants are low due to lack of pollination. Theory suggests that plants may have mechanisms to maximize pollination, while limiting the costs of seed predation (Trivers 1971; Axelrod and Hamilton 1981; Murray 1985; Bull and Rice 1991).

One mechanism that can reduce costs for a fruit crop is for plants to selectively abort immature fruit that contain many pollinator eggs and which, therefore, are highly likely to contain seed-eating larvae (Janzen 1979; Axelrod and Hamilton 1981; Murray 1985; Bull and Rice 1991; Bronstein 1992). When all fruit cannot be matured, for example due to limited resources (e.g., water and nutrients), seed loss for a fruit crop is reduced by selectively aborting those fruit that would most likely contribute the least to seed production. There is some evidence that selective abortion of fruit with eggs or larvae can reduce costs to plants in the short term (Fuller 1990; Pellmyr and Huth 1994; Richter and Weis 1995; Wilson and Addicott 1998; Addicott and Bao 1999). However, we are unaware of any study on the consequences of fruit abortion to pollinator population dynamics, or what the feedback effects might be on subsequent reproduction in the plant population. Fruit abortion, particularly when selective, may have consequences for the dynamics of the pollinator population by lowering recruitment and thus affecting the population size of the pollinator, since fruit abortion reduces the survival of pre-adult life stages of the pollinator (Fuller 1990; James et al. 1994; Richter and Weis 1995; Wilson and Addicott 1998; Holland and Fleming 1999a). This could have either positive or negative long-term effects on plant fruit production, depending on how it influences the relative effects of pollination and seed predation.

Reduced fruit set and fruit abortion are ubiquitous in nature (Stephenson 1981; Zimmerman and Pyke 1988). The hypotheses that most commonly explain the discrepancy between flower and fruit production include resource or pollen limitation, male function of flowers, and

bet hedging for temporal variation in resources and pollinators (Stephenson 1981; Sutherland and Delph 1984; Sutherland 1986). We hypothesize that an additional causal explanation for reduced fruit set and fruit abortion for plants with pollinating seed-predators may be as a mechanism to limit the abundance of the pollinator population, thereby preventing over-exploitation. However, even if this hypothesis is not correct, such fruit abortion certainly occurs, possibly having a significant direct effect on the pollinator and a feedback effect on fruit production. We consider not only selective abortion, but also random abortion, in which fruit are aborted regardless of the number of eggs. To our knowledge, this study is the first to explore the effects of reduced fruit set and fruit abortion on the pollinator population.

We first develop a simple analytical model of a plant population interacting with its pollinating seed-predator population and then extend it to a simulation model to address the following issues. Are gross benefits, costs, and net benefits to plants a function of pollinator population size? Are there consequences of fruit abortion for pollinator population dynamics and net benefits to the plant population? How do selective and random abortion compare as mechanisms to limit costs of seed predation? Our population-level models demonstrate that, under broad sets of circumstances, both selective and random abortion of fruit can limit pollinator populations and thereby limit costs of seed-predation while increasing the net benefit of fruit production. However, if fruit set is very low and there is no pollinator immigration, then each may lead to pollinator extinction and destabilization of the mutualism. We demonstrate this from an ecological standpoint. Our objective was not to examine the mechanisms for the evolution of fruit abortion, but instead to examine the ecological consequences of fruit abortion to pollinator population dynamics and fruit production. Nevertheless, we also discuss the evolutionary feasibility of fruit abortion.

Materials and methods

Population model of a pollinating seed-predator mutualism

We develop a model that captures the ecological dynamics of a pollinating seed-predator population interacting with the flowers in a plant population. The model describes fruit production by a fixed population of plants as a function of the population dynamics of an insect pollinator whose larvae prey on seeds and fruit. The model is based on senita and yucca mutualisms, but our approach to studying the ecological dynamics of mutualism has generality, and is not specific to these systems. First we examine the model under conditions that produce a constant dynamic equilibrium and then we allow for seasonal conditions.

Gross benefit, cost, and net benefit as a function of pollinator abundance

A functional response represents the effects of the size of one population on the rate of change of another. It can, in particular, represent the net benefit (= gross benefit minus cost) of a pollinator population to a plant population. We propose functional response

curves for both the number of flowers pollinated (gross benefits) and the number of those flowers that are preyed on by the pollinator's larvae (costs) as a function of pollinator population size, such that net benefits (fruit production) to the plant population are derived as a function of pollinator population size. A plant population has a number of flowers, F , that can be pollinated and oviposited on by the pollinator population, of size M . A ratio-dependent functional response based on Poisson probability of random search is reasonable (Thompson 1939; Gutierrez 1996), whereby the fraction of flowers pollinated depends positively on the ratio of pollinators-to-flowers, M/F . The higher M/F , the larger the fraction of flowers that are pollinated. The mathematical expression for the fraction of flowers pollinated (P) in the plant population during some unit of time, i.e., gross benefit, is

$$P = 1 - e^{-\gamma_1 M/F} \quad (1)$$

where γ_1 is a coefficient of the rate and effectiveness of pollination. The fraction of flowers pollinated increases as pollinator abundance increases, approaching one asymptotically as the ratio of pollinators-to-flowers increases (Fig. 1A).

Some of the seeds and fruit of the pollinated flowers are preyed on by larvae. We assume the fraction of pollinated flowers that are preyed on depends on the number of pollinators and flowers. With a larger abundance of pollinators relative to flowers, more eggs are laid, which results in a higher probability of larvae surviving and destroying seeds and fruit. The fraction of pollinated flowers whose seeds and fruit are destroyed (D) by larvae during some unit of time, i.e., costs, is

$$D = 1 - e^{-\gamma_2 M/F} \quad (2)$$

where γ_2 is a constant indicative of oviposition rate. Equation 2 implies that if the abundance of pollinators relative to flowers is sufficiently large, enough eggs are laid that nearly all seeds and fruit are destroyed by larvae (Fig. 1B). The specific Eqs. 1 and 2, are not very important themselves. The model results should be robust to a variety of functional responses that increase monotonically and asymptotically approach 1, as in Fig. 1.

We assume that each fruit that has been preyed on is destroyed by the larva and does not contribute to the net benefit to the plant population. Then, fruit production, W , a measure of net benefits, is

$$W = P(1 - D) = (e^{-\gamma_2 M/F} - e^{-(\gamma_1 + \gamma_2 M/F)}). \quad (3)$$

Fruit production, W , is a unimodal function of the size of the pollinator population relative to the number of flowers (Fig. 1C). The ratio, M/F , for which fruit production is maximum, W_{\max} , can be found by differentiating the right hand side of Eq. 3 with respect to M/F and setting the result to zero. This is

$$\left(\frac{M}{F}\right)_{\max} = \left(\frac{1}{\gamma_1}\right) \ln \left[\frac{(\gamma_1 + \gamma_2)}{\gamma_2} \right]. \quad (4)$$

For example, consider the specific parameter values $\gamma_1 = 4.0$ and $\gamma_2 = 2.0$. In this case, $(M/F)_{\max} = (1/4) \ln(3) = 0.275$.

This simple analytical model shows that gross benefits (P), costs (D), and net benefits (W) to a plant population are a function of the size of the pollinator population relative to the number of flowers. Gross benefits and costs are not constant, but instead change with M/F . Specifically, if M/F is large, then both gross benefits and costs are large, resulting in small net benefits. Similarly, if M/F is small, then both gross benefits and costs are small, resulting in small net benefits. On the other hand, for an intermediate M/F , gross benefits are still large, but costs are small, resulting in large net benefits. Because this model operates on the population level, we make no explicit inferences about the behavior of individual pollinators and their effects on individual flowers or fruit. Instead, P , D , and W are functions of pollinator abundance ("pollinator abundance" in reference to P , D , and W will imply relative to flower abundance, i.e., M/F). We only assume that, as pollinator abundance increases relative to the number of flowers, more flowers in the plant population are pollinated and more eggs

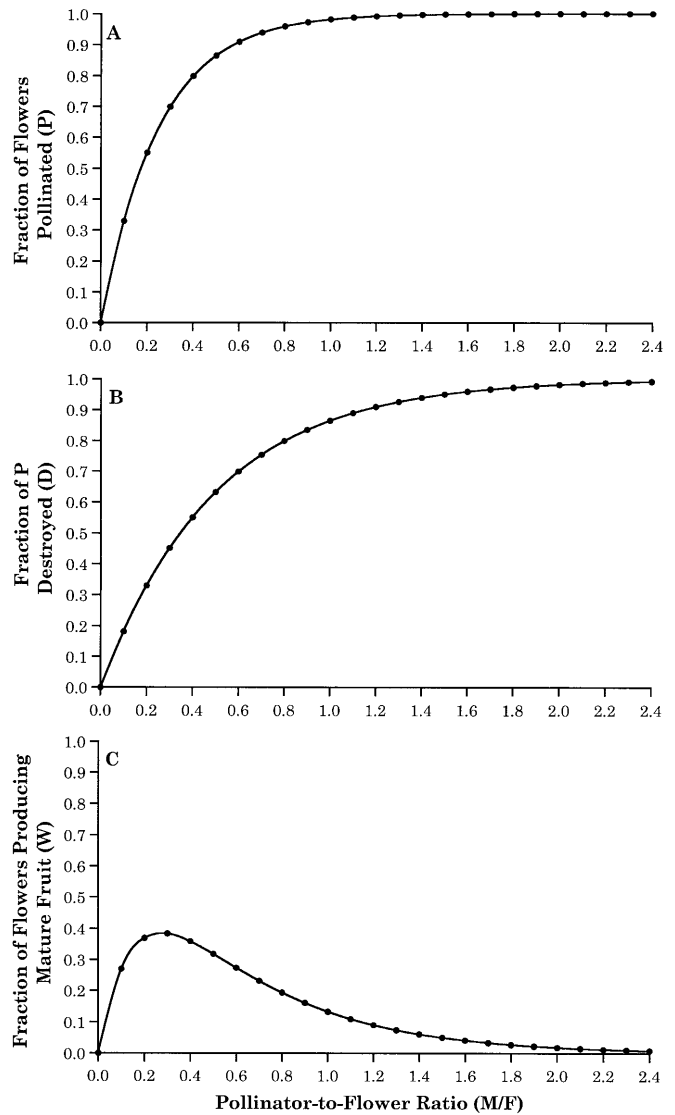


Fig. 1 Gross benefits (A), costs (B), and net benefits (C) to a plant population as a function of the population size of its obligate pollinating seed-predator. **A** Proportion of flowers pollinated, \bar{P} , in the plant population, **B** proportion of pollinated flowers destroyed as fruit by larval seed and fruit predators, \bar{D} , and **C** proportion of flowers maturing fruit, \bar{W} , in the plant population for different ratios of pollinators-to-flowers, M/F , in Eqs. 1–3. Parameter values for γ_1 and γ_2 are 4.0 and 2.0, respectively

are laid among those flowers. The above results were derived without any reference to the dynamics of the pollinator population. In the next section, a dynamic model for pollinators is analyzed at dynamic equilibrium.

Pollinator population dynamics and fruit abortion: dynamic equilibrium

The equation for fruit production in the preceding section demonstrated that the net benefit to the plant population is a unimodal function of mutualist abundance for pollinating seed-predator mutualisms. Clearly, too large a pollinator population can have negative effects on fruit production. In nature, however, pollinator populations are likely to have a tendency to increase in size.

To investigate pollinator dynamics and their effects on fruit production, we developed a general equation for the population of

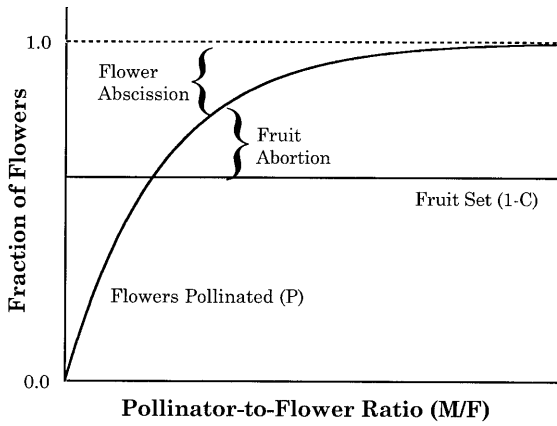


Fig. 2 Graphical representation of fruit abortions and flower abscissions given some level of fruit set ($1-C$) and flower pollination (P). The fraction of flowers abscissing and fruit aborting equals C such that fruit abortion equals $C-(1-P)$

pollinating seed-predators. We explore the behavior of the pollinator population and then examine if the dynamics of the pollinator population can be regulated by reduced fruit set and fruit abortion. Because fruit abortion is a source of mortality to eggs and larvae of the pollinator (James et al 1994; Richter and Weis 1995; Wilson and Addicott 1998; Holland and Fleming 1999a), it may be capable of limiting the pollinator population and preventing it from growing so large that all seeds and fruit are preyed upon. Fruit set, G , is the proportion of flowers retained on plants after the early phase of fruit development and prior to destruction by larvae, where

$$G = \begin{cases} P & \text{if } P < 1-C \\ 1-C & \text{if } P \geq 1-C \end{cases} \quad (5)$$

In Eq. 5, $1-C$ represents the maximum fraction of flowers per day that set fruit. If all flowers were pollinated, then C would equal the abortion rate of immature fruit. Otherwise, C is the combination of unpollinated flowers that abscise and immature fruit that abort, such that total fruit set is no more than $1-C$ (Fig. 2). If the fraction of flowers pollinated, P , is less than $1-C$, then Eq. 5 implies that no fruit abortions occur and only unpollinated flowers abscise (Fig. 2).

Before deriving an equation for pollinator population dynamics, we briefly describe the life cycle of senita and yucca moths. Short-lived adult insects oviposit into flowers. Eggs hatch and produce larvae that consume seeds and fruit. Larvae then exit fruit and, in the case of senita moths, enter cactus branches to pupate or, in the case of yucca moths, drop to the ground to pupate in the soil. Moths emerge from pupal cases and the cycle repeats itself. The primary differences between senita and yucca moths are that senita moths pupate in plants, can have multiple cohorts in a flowering season, and fruit usually support one larva. In developing the dynamic model of the pollinator population below, we assume that for each destroyed fruit, only one larva reaches the pupal stage and that the flowering season is long relative to the life cycle of the pollinator, as in the senita mutualism.

The abundance and dynamics of the pollinator population are determined by survival and mortality of all life stages of the pollinator as well as immigration of adults from outside the local plant population. The number of adults in the population of pollinating seed-predators at a given step in time is derived from four sources: adults that have survived from the previous day, new adults emerging from the pupal life stage, adults emerging from diapause from the preceding year's flowering season, and adult immigrants. We can write a difference equation describing the size of the adult population, M_t , on daily time steps, t :

$$M_{t+1} = S_a M_t + F_{t-t_{lag}} G_{t-t_{lag}} D_{t-t_{lag}} S_p + M_{diap,t} + M_{imm,t} \quad (6)$$

In the first term of Eq. 6, S_a is the daily survival of adults. The second term is the number of new adults emerging from pupae. $F_{t-t_{lag}}$ is the number of flowers produced each day, with each flower available for pollination and oviposition for only one day. The t_{lag} represents the fact that a time period, t_{lag} , is required for an adult pollinator to develop through egg, larval, and pupal life stages. Thus, new adults in the population at $t+1$ are derived from flowers that were pollinated and oviposited on day $t-t_{lag}$. The factor $G_{t-t_{lag}}$ is the fraction of flowers setting fruit on day $t-t_{lag}$ as described by Eq. 5. $D_{t-t_{lag}}$ is the fraction of pollinated flowers that are destroyed as fruit by larvae, which also represents the survival of larvae. The factor S_p represents survival during the pupal stage. An assumption implicit in this term, and at this stage of the model, is that fruit abortion resulting from reduced fruit set is random; all pollinated flowers, whether or not they have larvae, have an equal chance of being aborted as fruit. The third term, $M_{diap,t}$ adults emerging from diapause, is assumed to be non-zero only over the early part of the flowering season. The fourth term, $M_{imm,t}$ is the number of adult immigrants entering the local plant population, which is assumed to occur at a constant rate. Inherent in Eq. 6 is the assumption that, aside from the limitation of flowers, there is no density-dependent regulation of the pollinator population (i.e., no density-dependent self-regulation or limitation by predators or parasitoids).

From Eqs. 5 and 6 it can be seen that, if the fraction of flowers pollinated is greater than the fraction of flowers setting fruit, then fruit abortion occurs and reduces the survival of the pollinator's eggs and larvae. This is so because those aborting flowers that contain an egg or eggs are a source of mortality for the pollinator population. If, for the moment, we assume that all rates in Eq. 6 are constant through time (the flowering season is long compared to the transient dynamics of the pollinator population), including flower production and immigration, then the dynamic equilibrium of the pollinator population, M^* , in terms of a pollinator-to-flower ratio (M^*/F), is

$$\frac{M^*}{F} = \left(\frac{1}{1-S_a} \right) \left[G^* (1 - e^{-\gamma_2 M^*/F}) S_p + \frac{M_{imm}}{F} \right] \quad (7)$$

where G^* is given by either $1-C$ or P depending on the inequalities in Eq. 5.

This implicit equation for M^*/F is transcendental and cannot be solved analytically, but the solution can be graphed using two parts of Eq. 7 (Fig. 3). The point of intersection of these two lines is the abundance of pollinators at dynamic equilibrium. Only one equilibrium abundance of pollinators exists and it can be shown to be stable (Fig. 3). Whatever the non-zero initial population of pollinators is, as time increases, the number of adults in the pollinator population will approach this dynamic equilibrium. A decrease in fruit set, G , (corresponding to an increase in fruit abortion and flower abscission, C) lowers the point where the two lines intersect, which then reduces the equilibrium abundance of pollinators by shifting M^*/F to the left. For a dynamic equilibrium and for parameter values consistent with what is known about these mutualisms, some level of random fruit abortion can limit the pollinator population size and increase the net benefit, unless immigration is $\geq 2 \times$ the local pollinator population (Holland and DeAngelis, unpublished data). This result and its implications are discussed in the Discussion, but our goal here is to proceed to the more realistic case of seasonal dynamics.

Pollinator population dynamics and fruit abortion: seasonal cycles

In most real pollination systems, there is pronounced seasonality in flower production, which may influence pollinator population dynamics. Hence, it is unlikely that pollinator populations reach dynamic equilibria [note, however, that if equilibria are achieved, it is more likely in specialized, obligate pollination mutualisms than in diffuse, facultative ones (Addicott et al. 1990; Waser et al. 1996). In fact, Addicott's (1998) empirical work suggests yucca moths are relatively constant in number from year-to-year]. We now incorporate seasonal cycles in flower production in order to

Fig. 3 Graphical representation of Eq. 6 for the population size of adult pollinators with two different parts of the equation plotted against pollinator-to-flower ratio, M^*/F . Note that there is only one point of intersection between the two parts, and thus, only one dynamic equilibrium point. As G^* is reduced, the M^*/F is lowered

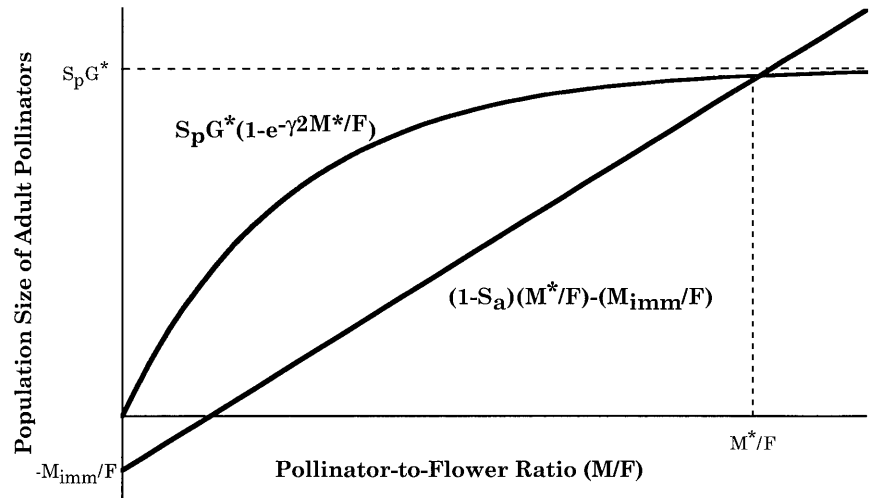
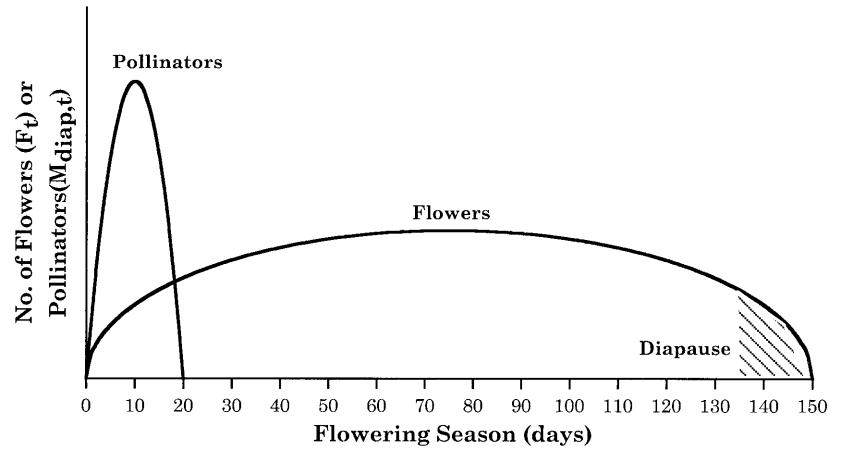


Fig. 4 Number of flowers, F_t , implied by Eq. 8 and emerging pollinators from diapause, $M_{diap,t}$ implied by Eq. 10 through time for a plant population interacting with an obligate pollinator population. Note that this is the flowering phenology of an individual plant, but that the model applies to a population. The *hatched area* from 135–150 days represents the time period during the flowering season when larvae of oviposited eggs do not pupate, but instead, enter diapause. Parameter values for simulations were $F_{mid}=200$, $t_{max}=150$, and $t_{mid}=10$



determine if pollinator populations can be regulated by fruit abortion, and whether this regulation increases fruit production.

We used the same simple dynamic model developed above for pollinators interacting with the flowers, but we assumed a distinct flowering season in which flower production increased early in the season, decreased and terminated at the end of the season (Fig. 4). Our model could simulate the interaction over a single flowering season or over many years. The number of flowers, F_t , produced on a given day during a flowering season was described by the function

$$F_t = F_{mid} \sqrt{1 - \frac{[t - 0.5(t_{max})]^2}{(0.5t_{max})^2}} \quad (8)$$

F_{mid} is the peak number of flowers produced at the midpoint of the flowering season and t_{max} is the length of the flowering season.

At the end of each flowering season larvae of pollinators enter diapause until the beginning of next year's flowering season (Fig. 4). The number of larvae entering diapause and surviving to be pollinators during the next season is assumed to be the summation of all larvae that have survived from eggs laid during the last 15 days of the flowering season.

$$M_{diap} = \sum_{t=t_{max}-15}^{t_{max}} F_t G_t D_t S_p \quad (9)$$

These larvae enter diapause and then emerge during the first 20 days of the next flowering season. We assumed that the survival of these larvae to be pollinators of next year's flowers was the same as pupal survival. Adult pollinators entering the local population of plants through diapause, $M_{diap,t}$, emerge daily over the

early part of the flowering season (Fig. 4), which we described using the parabolic function

$$M_{diap,t} = M_{diap,mid} - \frac{M_{diap,mid}}{t_{mid}^2} (t - t_{mid})^2 \quad (10)$$

where $M_{diap,mid}$ is the peak abundance and occurs at the midpoint of the emergence period (t_{mid}). $M_{diap,mid}$ varies with M_{diap} , and was determined by setting Eq. 9 equal to the integral of Eq. 10. M_{imm} was assumed to be low and constant through time. It is not likely that local plant populations of yucca and senita have high rates of pollinator immigration given their behavior, size, and short adult life-span (Pellmyr et al. 1997; Massey and Hamrick 1998; Holland and Fleming 1999a).

The model is consistent with larvae of pollinators entering diapause at the end of a flowering season and emerging as adult pollinators at some point in the future during the next flowering season (Fig. 4). We assumed some synchrony between the flowering season and emergence and diapause of pollinators, as is expected of specialized pollination mutualisms (Addicott et al. 1990; Waser et al. 1996). However, asynchrony was also built into the model because some adult pollinators (those of eggs oviposited prior to the last 15 days of the flowering season that emerge after the flowering season ends) were alive after flowering ceased. These pollinators contributed neither to fruit production nor to recruitment into the pollinator population. Finally, we set the time to pass from egg through pupal life stages at 26 days. Adult survival (S_a) was set to produce an average adult lifetime of 3 days, which is consistent with what is known of senita and yucca moths (Rau 1945; Kingsolver 1984; Powell 1984; Holland and Fleming 1999a).

We modeled fruit production by the plant population at time t (W_t) using Eqs. 1–3, but fruit production (W_t) is now not in dynamic equilibrium, and so must be explicitly expressed in terms of the number of flowers produced $t-t_{\text{lag}}$ days ago and by the number of flowers setting fruit, G , so that

$$W_t = F_{t-t_{\text{lag}}} G_{t-t_{\text{lag}}} (1 - D_{t-t_{\text{lag}}}) \quad (11)$$

For simplicity we used fruit production as a measure of net benefits and assumed each fruit only supported one larva, as in the senita mutualism. Alternatively, seed production could be used as an indicator of the net benefit and multiple larvae could develop per fruit, as in the yucca mutualism. Nonetheless, the latter situation should be dynamically similar to the former.

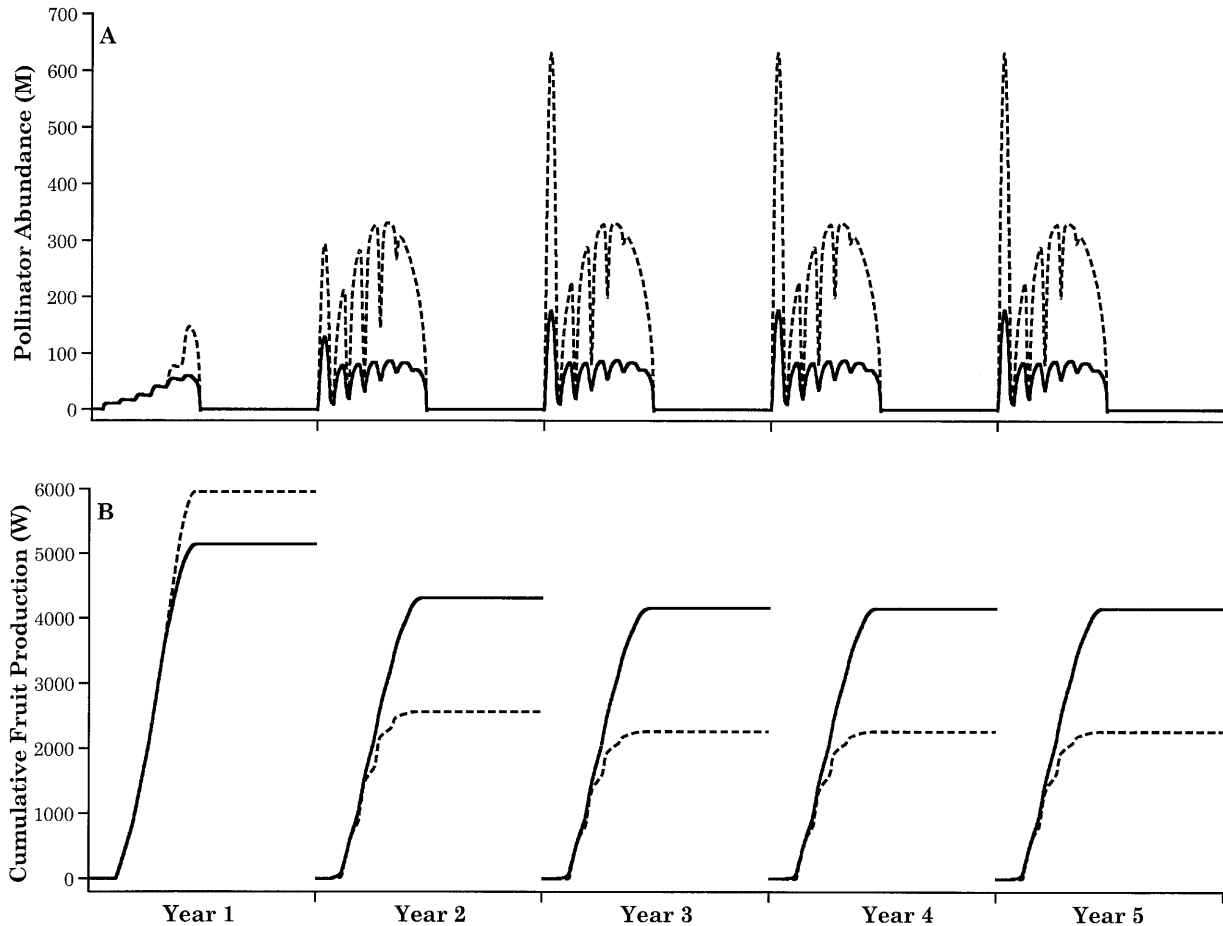
Results

Numerical simulations provided the number of pollinators and the number of fruit produced for different levels of fruit set, $G = 1 - C$. In these simulations, the peak of flower production was set to $F_{\text{mid}} = 200$ in Eq. 10, although this was completely arbitrary, and any number could be used. We first compared results of simulations

through five sequential years of flowering seasons for two levels of fruit set, the first equal to 1.0 ($C = 0$) where there were no fruit abortions and only unpollinated flowers abscised, and the second equal to 0.4 ($C = 0.6$) where fruit abortions did occur (Fig. 5). No assumption was made about the cause of reduced fruit set (i.e., whether fruit set was resource limited or not). In the first year of flowering, the initial recruitment of pollinators was only through immigration. During this flowering season, pollinator populations for both levels of fruit set increased in abundance toward their respective dynamic equilibria. At the end of the flowering season, however, the pollinator population of the plant population with reduced fruit set was being limited by fruit abortions. For this reason, pollinator abundance was smaller than that of the pollinator population without reduced fruit set. Fruit production was greater in year 1 for the plant population without reduced fruit set. In addition, the number of larvae entering diapause and emerging in year 2 was greater for the plant population without reduced fruit set.

In year 2, pollinator numbers were much higher for the plant population without fruit abortions and reduced fruit set (Fig. 5). Consequently, many more fruit were destroyed by the pollinator's larvae and fruit production was much lower than for the plant population with fruit abortions. In all subsequent years, periodic cycles and intra-annual damped oscillations occurred for both populations of pollinators. This occurred because the number

Fig. 5 **A** Pollinator abundance, M_{diap} , and **B** cumulative fruit production per year, W , for 5 years of two different plant populations, one with fruit set, G , equal to 1.0 ($C = 0$; *hatched line*) and the other with fruit set equal to 0.4 ($C = 0.6$; *solid line*). Parameter values were $S_a = 0.5$, $S_p = 0.85$, $\gamma_1 = 4.0$, $\gamma_2 = 2.0$, $M_{\text{imm}} = 5$ starting on day 21, and as in Fig. 4



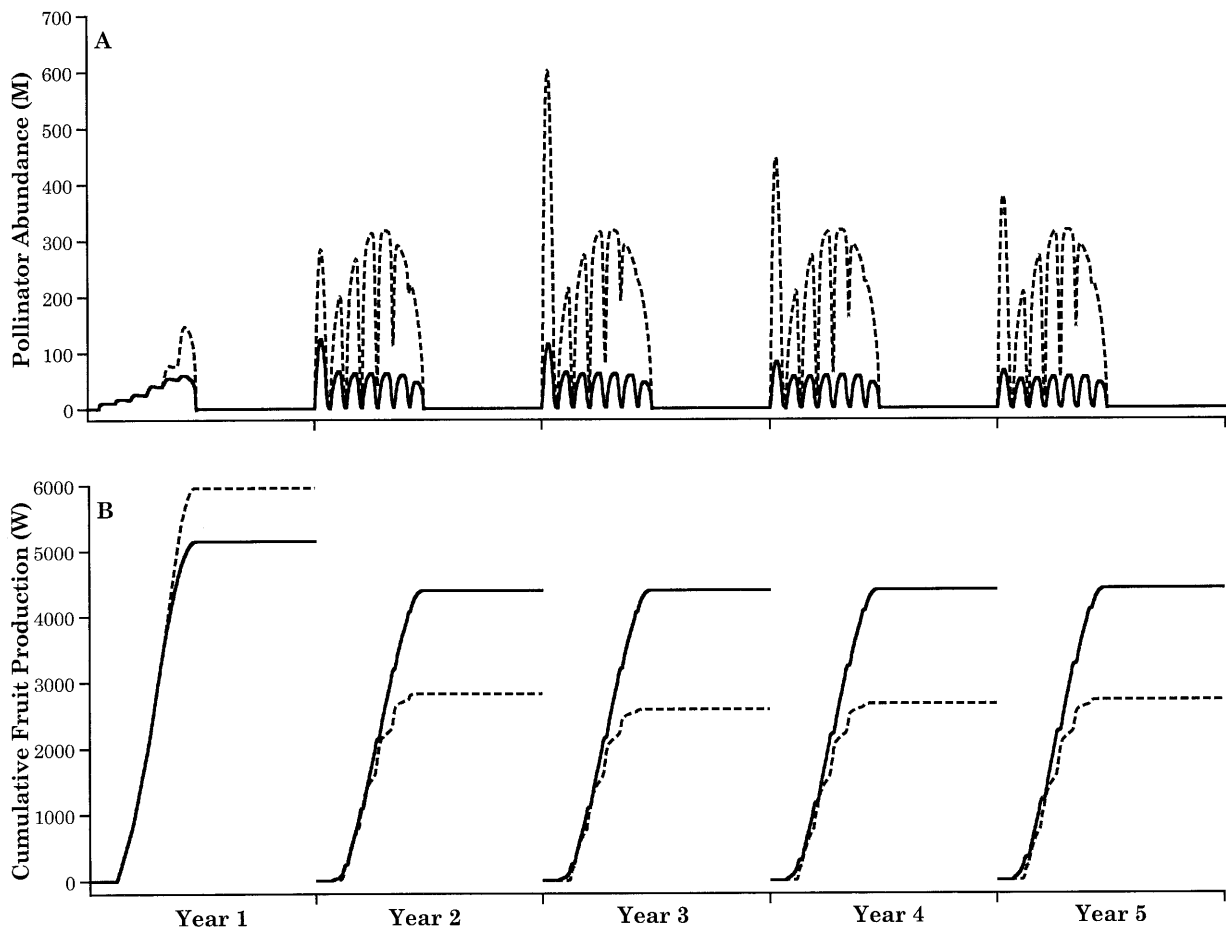


Fig. 6 Stochastic model of **A** pollinator abundance, M_{diap} , and **B** cumulative fruit production per year, W , for 5 years of two different plant populations, one with fruit set, G , equal to 1.0 ($C=0$; hatched line) and the other with fruit set equal to 0.4 ($C=0.6$; solid line). Parameter values were the same as in Fig. 5, except S_p in Eq. 9 was set to vary randomly from 0.5 to 0.95

of pollinators entering diapause and emerging the following year became periodic with the same values each year. Because this equilibrium of diapausing larvae was smaller for the plant population with fruit abortions, pollinator numbers did not become so large during the flowering season that many fruit were destroyed by larvae. Hence, fruit production remained greater for the plant population with fruit abortion and reduced fruit set. Even when the number of pollinators emerging from diapause varied stochastically, pollinators could still be limited by fruit abortion and fruit production was greater for the plant population with reduced fruit set (Fig. 6).

In the preceding analysis, we demonstrated that fruit abortion can regulate both the inter- and intra-annual dynamics of pollinators, limit the number of pollinators emerging from diapause, and increase fruit production (Figs. 5, 6). This analysis was for two specific levels of fruit set. We next examined how pollinator populations and fruit production compared for the entire range of different levels of fruit set and fruit abortion (Fig. 7). The equilibrium number of pollinators emerging from dia-

pause decreased with increased reduction in fruit set, 1–C. This reduction in pollinator numbers resulted in an increase in fruit production for a wide range of levels of fruit set. However, when fruit set was exceptionally low ($C \geq 0.85$), pollinator populations were primarily maintained through immigration. This abundance of pollinators was smaller than that number without fruit abortion and resulted in lower fruit production in comparison to no fruit abortions ($C=0$). While it may appear counter-intuitive, fruit production actually increased monotonically over a wide range of values of reduced fruit set and fruit abortion.

Random versus selective abortion of fruit

In the preceding case, we assumed that all fruit had an equal probability of being destroyed by larvae. Alternatively, the probability of seeds and fruit have being destroyed by larvae depends on the number of eggs laid per flower. Pollinators may be more strongly regulated by selectively aborting those immature fruit with more eggs. Here, we compare the effects of selective and random abortion on pollinator population dynamics and fruit production. We also compare the effect of varying the pollination rate (γ_1) and oviposition rate (γ_2) relative to one another for both selective and random abortion. For simplicity in comparing random and selective abortion, and

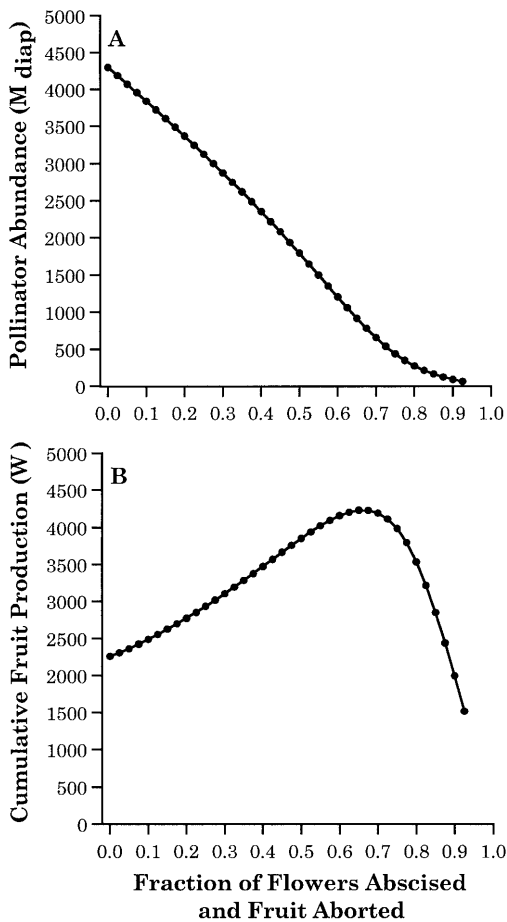


Fig. 7 A Pollinator abundance, M_{diap} , and B cumulative fruit production, W , at dynamic equilibrium for different levels of fruit set. Note that the abscissa is C , the number of flowers abscised and fruit aborted, such that fruit set equals $1-C$ and fruit abortion equals the difference between the proportion of flowers pollinated and $1-C$. Parameter values are the same as in Fig. 5

pollination (γ_1) and oviposition (γ_2) rates, we removed adult immigration from Eq. 6 and assumed constant flower production such that pollinators reached a dynamic equilibrium. This is reasonable, given that we have already shown that, even when confronted with seasonal flowering, pollinator immigration, and stochasticity, fruit abortion can limit pollinator abundance and increase fruit production (Figs. 5, 6). In these simulations, fruit with a greater number of eggs were preferentially aborted prior to fruit with fewer or no eggs.

To compare the two types of abortion and the pollination and oviposition rates, we modeled selective abortion and random abortion for three different scenarios of pollination relative to oviposition: (1) when the pollination rate (γ_1) is greater than the oviposition rate (γ_2), (2) when pollination (γ_1) and oviposition (γ_2) rates are equal, and (3) when the pollination rate (γ_1) is less than the oviposition rate (γ_2) (Fig. 8). (Recall that oviposition is on pollinated flowers only; absolute number of oviposited flowers that produce larvae is less than or equal to the absolute number of pollinated flowers). For all three scenari-

os and for both selective and random abortion, pollinator abundance decreased with reduction in fruit set and pollinators went to extinction and destabilized the mutualistic relationship when the reduction in fruit set became too large (Fig. 8A,C,E). This effect of fruit abortion on pollinator abundance resulted in an increase in fruit production as fruit set decreased, but when fruit set became sufficiently low, no fruit were produced because pollinators went to extinction (Fig. 8B,D,E). Selective abortion can more effectively limit the abundance of pollinators with less abortion of fruit, and therefore, fruit production is greater for selective abortion than for random abortion. However, for low levels of fruit set pollinator extinction is more likely for selective abortion than for random abortion (Fig. 8). Despite these differences in random and selective abortion, when fruit set is large and few flowers are aborted and abscised, then selective and random abortion appear to have similar effects on pollinators and fruit production (Fig. 8), depending on the relative rates of pollination and oviposition.

Despite the overall similarities in the effects of fruit abortion and reduced fruit set on pollinators and fruit production, some important differences occurred depending on the relative rates of pollination (γ_1) and oviposition (γ_2). For example, as the rate of pollination decreased relative to oviposition, fruit set ($1-C$) had to decrease to maximize fruit production for both selective and random abortion. Furthermore, for both selective and random abortion, this maximum for fruit production decreased as the rate of pollination decreased relative to oviposition (Fig. 8B,D,F). When pollination was greater than oviposition, selective abortion led to pollinator extinction for higher levels of fruit set than did random abortion. On the other hand, when pollination is less than oviposition, random abortion led to pollinator extinction for higher levels of fruit set than selective abortion. These results suggest that limiting pollinators and maximizing fruit production by plants depends simultaneously on pollination rates, oviposition rates, and the level of fruit set.

We must point out the congruence between our model predictions and fruit set in the senita and yucca pollination mutualisms. In the yucca mutualism, many ovipositions and pollinations occur on one flower (Aker and Udovic 1981; Pellmyr and Huth 1994; Addicott and Tyre 1995). While the costs imposed to the plant continue to increase with more ovipositions, the benefit from pollination diminishes due to the limited number of ovules that can be fertilized by pollination. Hence, the yucca mutualism may be characterized as the rate of pollination < oviposition. In contrast, the pollination rate by senita moths is likely to be equal to or greater than the rate of oviposition since senita cactus flowers rarely have more than one egg per flower (Holland and Fleming 1999a). Our models predict that when pollination < oviposition, as in the case of the yucca mutualism, plants must have lower levels of fruit set than when pollination equals oviposition or pollination was greater than oviposition, as in the senita mutualism (Fig. 8B,D,F). Indeed, yucca plants

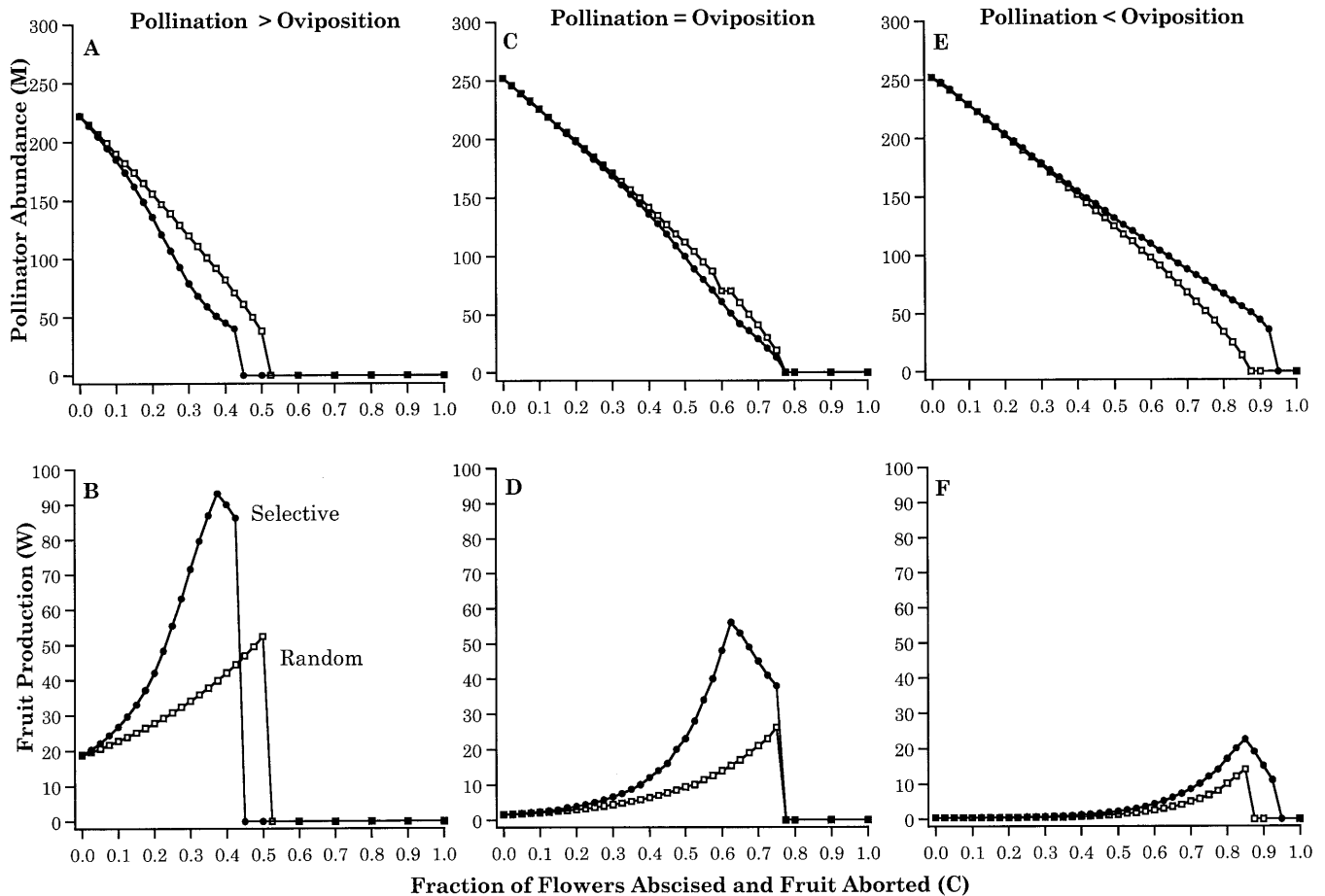


Fig. 8 Pollinator abundance, M , (A, C, and E) and fruit production, W , (B, D, and F) at dynamic equilibrium for different levels of flower abscission and fruit abortion (C) for random (empty squares) and selective (filled circles) fruit abortion. Pollinator abundance and fruit production were modeled for the pollination rate greater than the oviposition rate (A, B), pollination equals oviposition (C, D), and pollination less than oviposition (E, F). Parameter values were $F=F_{t-lag}=150$, $S_p=0.85$, $S_a=0.7$, and $\gamma_1=4.0$ and $\gamma_2=2.0$ for (A, B), $\gamma_1=4.0$ and $\gamma_2=4.0$ for (C, D), and $\gamma_1=3.0$ and $\gamma_2=7.0$ for (E, F)

do have lower levels of fruit set than senita (8% vs 37% fruit set, on average; Holland and Fleming 1999b). Current understanding of pollination, oviposition, and fruit set in yucca and senita mutualisms is qualitatively consistent with theoretical predictions from our models. Furthermore, our model predictions are consistent with nature, in that some species of yucca do employ selective abortion.

Discussion

For pollinating seed-predator mutualisms, selective abortion of immature fruit with many pollinator eggs has been documented to increase short-term seed production for a fruit crop for some species of *Yucca* (e.g., Pellmyr and Huth 1994). However, such observations do not incorporate the mechanism's consequences to the long-

term ecological dynamics of the pollinator. Because fruit abortion is a mortality factor for the pre-adult life stages of the pollinator, it can have dynamic consequences for the pollinator population which can then alter future seed and fruit production. The objectives of this paper were to investigate how the population size of pollinators influenced the net benefits of fruit production, and whether fruit abortion altered pollinator population dynamics and, consequently, fruit production.

We have shown that, in the presence or absence of immigration, pollinator population dynamics are coupled with the production of flowers and fruit abortion by the plant population. Reduced fruit set and fruit abortion have the consequence of limiting the abundance of pollinators, which can increase the net benefits of fruit production. However, sufficiently low levels of fruit set can destabilize pollinator populations and cause their extinction, depending on the rate of immigration. Selective and random abortion have similar consequences to the pollinator population but selective abortion results in greater fruit production than random abortion. Nevertheless, selective and random abortion can be indistinguishable in terms of their effects on fruit production depending on the level of fruit set and the relative rates of pollination and oviposition.

Fruit abortion and reduced fruit set in obligate plant-pollinator mutualisms can act much like a homeostatic regulator, which can be responsive to changes in the de-

mography and population dynamics of pollinators. In nature a variety of demographic and environmental factors can lead to fluctuations in population size and growth rates (Nicholson and Bailey 1935; Andrewartha and Birch 1954). Thus, some factors may cause the pollinator population to fluctuate, such that the population size is shifted away from the abundance that results in greatest net benefits for that level of fruit set. For any given level of fruit set, the abortion rate of a plant population would also shift (Fig. 2; Eq. 5), in such a way that it counteracts the pollinator population's trend. For example, if pollinator abundance is reduced below the number that results in greatest net benefits for that level of fruit set, then this leads to fewer flower pollinations and ovipositions and fruit abortions consequently decrease, so that larval survival increases and the pollinator population grows. Conversely, if the pollinator population has a positive fluctuation, then more pollinations and ovipositions occur and fruit abortions increase, lowering the growth rate of the pollinator population. Therefore, reduced fruit set and fruit abortion appear to be mechanisms that can be responsive to the dynamics of ecological systems and, within limits, stabilize the pollinator population and increase the net benefit to the plant population.

Abundance of mutualists and outcomes of interactions

Theoretical studies on the population dynamics of mutualists have incorporated factors that limit population growth in an attempt to reconcile limited growth of populations in nature with the assumption that, because mutualists increase the reproduction and/or survival of each other, an increase in the abundance of one mutualist increases the abundance of the other (Vandermeer and Boucher 1978; Goh 1979; Travis and Post 1979; Addicott 1981; May 1981; Dean 1983; DeAngelis et al. 1986). Alternatively, because mutualisms impose costs as well as benefits, both expressible as functional responses, an increase in the abundance of one mutualist does not necessarily increase the net benefit to the other, and may even begin to limit the population growth of the other. In other words, most mutualistic species likely have functional responses for gross benefits, costs, and net benefits: benefits and costs to one mutualistic population change as a function of the abundance of its mutualistic partner. Thus, an increase in the abundance of one mutualist does not necessarily increase the abundance of its partner, because net benefits to the partner can saturate or diminish with an increasing abundance of its mutualist.

Prior empirical and theoretical work on how benefits and costs vary with population size or density have couched the problem in terms of how the benefits and costs to one species vary as a function of its own density (Addicott 1979; Wolin and Lawlor 1984; Wolin 1985; Breton and Addicott 1992; Morales 2000). While benefits and costs to one species can indeed vary as a function of its own density (Breton and Addicott 1992;

Morales 2000), our objective was to introduce and investigate the influence of the abundance of a mutualist's partner, that is, functional responses. Incorporating functional responses of benefits and costs into both theoretical and empirical studies provides a biologically intuitive and mechanistic basis for understanding how mutualistic interactions influence benefits, costs, and the stability and population dynamics of mutualists.

Our theoretical model shows that the net benefit to a plant population is a function of the abundance of pollinating seed-predators relative to flowers. Empirical research also suggests that the abundance of pollinators relative to flowers, and abundance of mutualists in general, can influence costs and net benefits in mutualisms (Addicott 1984; Cushman and Whitham 1989; Herre 1989; Breton and Addicott 1992; Bronstein 1994b; Nefdt and Compton 1996; Herre and West 1997; Morales 2000). Costs imposed by pollinating seed-eaters on a plant population can be reduced if some factor (e.g., fruit abortion, predation) reduces survival such that pollinator populations do not become so large that many eggs are oviposited. In our model, fruit abortion can limit costs and increase net benefits because the pollinator population size without fruit abortion is much greater than the population size with fruit abortion. Thus, net benefits are greater with fruit abortion. To our knowledge, this is the first study to simultaneously link gross benefits, costs, and net benefits to one mutualist as a function of the population size of its mutualistic partner and to derive a unimodal net benefit curve as a function of population size. Nevertheless, we must point out that it is not the unimodal net benefit curve itself that stabilizes the interaction, but rather the ability of the fruit abortion to limit the abundance of the pollinator population. Without such limits, the pollinator population could become sufficiently large that the interaction would be parasitic.

Evolutionary feasibility of fruit abortion

Although this study was on the ecological consequences of fruit abortion for pollinator dynamics and fruit production, and not on the evolution of fruit abortion, *per se*, we must acknowledge some evolutionary implications. Selective fruit abortion can increase the reproductive output for a fruit crop. Furthermore, fruit abortion in general, whether selective or random, can increase the lifetime reproduction of plants interacting with pollinating seed-predators. Thus, it seems feasible that selection could favor fruit abortion. However, it also appears that a mutant non-aborting plant would be favored in resident population of aborters, since it would accrue the benefits of reduced pollinator population size without aborting fruit. Holland and DeAngelis (unpublished data) have considered this problem, using a form of the dynamic equilibrium model described earlier (Eq. 7). They simulated multi-plant systems, in which individual plants with either a fruit abortion or non-abortion strategy were placed within a population of plants with the alternative

strategy, and in which pollinators could migrate freely among the plants. In both cases, the abortion strategy proved to increase fruit production over the non-abortion strategy, as long as the migration rate did not completely homogenize the pollinator population among plants. Holland and DeAngelis also showed that the question of whether an abortion strategy can evolve is a close analog to the question of the evolution of other plant adaptations that impose a cost on the individual with the strategy but can produce benefits that may be shared by “cheaters” (de Mazancourt et al. 1998, 1999; de Mazancourt and Loreau 2000a, b). If there is sufficient spatial localization of the benefits, then there is a possibility for the strategy to evolve and possibly to be an evolutionarily stable strategy.

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References

- Addicott JF (1979) A multispecies aphid-ant association: density dependence and species-specific effects. *Can J Zool* 57:558–569
- Addicott JF (1981) Stability properties of 2-species models of mutualism: simulation studies. *Oecologia* 49:42–49
- Addicott JF (1984) Mutualistic interactions in population and community processes. In: Price PW, Slobodchikoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp 437–455
- Addicott JF (1986) Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. *Oecologia* 70:486–494
- Addicott JF (1998) Regulation of mutualism between yuccas and yucca moths: population level processes. *Oikos* 81:119–129
- Addicott JF, Bao T (1999) Limiting the costs of mutualism: multiple modes of interaction between yuccas and yucca moths. *Proc R Soc Lond B* 266:197–202
- Addicott JF, Tyre AJ (1995) Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72:382–394
- Addicott JF, Bronstein J, Kjellberg F (1990) Evolution of mutualistic life-cycles: yucca moths and fig wasps. In: Gilbert F (ed) *Insect life cycles: genetics, evolution, and co-ordination*. Springer, Berlin Heidelberg New York, pp 143–161
- Aker CL, Udovic D (1981) Oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49:96–101
- Andrewartha HG, Birch LC (1954) *The distribution and abundance of animals*. University of Chicago Press, Chicago
- Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390–1396
- Bever JD (1999) Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecol Lett* 2:52–61
- Breton LM, Addicott JF (1992) Density-dependent mutualism in an aphid-ant interaction. *Ecology* 73:2175–2180
- Bronstein JL (1992) Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. In: Bernays EA (ed) *Insect-plant interactions*, vol IV. CRC, Boca Raton, pp 1–44
- Bronstein JL (1994a) Our current understanding of mutualism. *Q Rev Biol* 69:31–51
- Bronstein JL (1994b) Conditional outcomes in mutualistic interactions. *Trends Ecol Evol* 9:214–17
- Bull JJ, Rice WR (1991) Distinguishing mechanisms for the evolution of cooperation. *J Theor Biol* 149:63–74
- Cushman JH, Whitman TG (1989) Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. *Ecology* 70:1040–1047
- Dean AM (1983) A simple model of mutualism. *Am Nat* 121:409–417
- DeAngelis DL, Travis CC, Post WM (1979) Persistence and stability of seed-dispersed species in a patchy environment. *Theor Pop Biol* 16:107–125
- DeAngelis DL, Post WM, Travis CC (1986) *Positive feedback in natural systems*. Springer, Berlin Heidelberg New York
- Fleming TH, Holland JN (1998) The evolution of obligate pollination mutualisms: senita cactus and senita moth. *Oecologia* 114:368–375
- Fuller OS (1990) Factors affecting the balance of cooperation and conflict between the yucca moth, *Tegeticula yuccasella*, and its mutualist, *Yucca glauca*. Dissertation, University of New Mexico, Albuquerque
- Goh BS (1979) Stability in models of mutualism. *Am Nat* 113:261–275
- Gutierrez AP (1996) *Applied population ecology: A supply-demand approach*. Wiley, New York
- Hemborg AM, Despres L (1999) Oviposition by mutualistic seed-parasitic pollinators and its effects on annual fitness of single- and multi-flowered host plants. *Oecologia* 120:427–436
- Herre EA (1989) Coevolution of reproductive characteristics of 12 species of New World figs and their pollinator wasps. *Experientia* 45:637–647
- Herre EA (1996) An overview of studies on a community of Panamanian figs. *J Biogeogr* 23:593–607
- Herre EA, West SA (1997) Conflict of interest in a mutualism: documenting the elusive fig wasp-seed trade-off. *Proc R Soc Lond B* 264:1501–1507
- Holland JN, Fleming TH (1999a) Mutualistic interactions between *Upiga virescens* (Pyrilidae), a pollinating seed-consumer, and *Lophocereus schottii* (Cactaceae). *Ecology* 80:2074–2084
- Holland JN, Fleming TH (1999b) Geographic and population variation in pollinating seed-consuming interactions between senita cacti (*Lophocereus schottii*) and senita moths (*Upiga virescens*). *Oecologia* 121:405–410
- James CA, Hoffman MT, Lightfoot DC, Forbes GS, Whitford WG (1994) Fruit abortion in *Yucca elata* and its implications for the mutualistic association with yucca moths. *Oikos* 69:207–216
- Janzen DH (1979) How to be a fig. *Annu Rev Ecol Syst* 10:13–51
- Kingsolver RW (1984) Population biology of a mutualistic association: *Yucca glauca* and *Tegeticula yuccesella*. Dissertation, University of Kansas, Lawrence
- Massey LK, Hamrick JL (1998) Genetic diversity and population structure of *Yucca filamentosa* (Agavaceae). *Am J Bot* 85:340–345
- May RM (1981) Models of two interacting populations. In: May RM (ed) *Theoretical ecology: principles and applications*. Blackwell, Boston, pp 78–104
- Mazancourt C de, Loreau M (2000a) Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: should a palatable plant evolve? *Evolution* 54:81–92
- Mazancourt C de, Loreau M (2000b) Effect of herbivory and plant species replacement on primary production. *Am Nat* 155:735–734
- Mazancourt C de, Loreau M, Abbadie L (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79:2242–2252
- Mazancourt C de, Loreau M, Abbadie L (1999) Grazing optimization and nutrient cycling: potential impact of large herbivores in a Savanna system. *Ecol Appl* 9:784–797
- Morales MA (2000) Mechanisms and density dependence of benefit in an ant-membracid mutualism. *Ecology* 81:482–489

- Murray MG (1985) Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol J Linn Soc* 26:69–81
- Nefdt RJC, Compton SG (1996) Regulation of seed and pollinator production in the fig-fig wasp mutualism. *J Anim Ecol* 65:170–182
- Nicholson AJ, Bailey VA (1935) The balance of animal populations, part I. *Proc Zool Soc Lond*, pp 551–598
- Pellmyr O (1989) The cost of mutualism: interactions between *Trollius europaeus* and its pollinating parasites. *Oecologia* 78:53–59
- Pellmyr O (1992) The phylogeny of a mutualism: evolution and coadaptation between *Trollius* and its seed-parasitic pollinators. *Biol J Linn Soc* 47:337–365
- Pellmyr O, Huth CJ (1994) Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* 372:257–260
- Pellmyr O, Thompson JN, Brown JM, Harrison RG (1996) Evolution of pollination and mutualism in the yucca moth lineage. *Am Nat* 148:827–847
- Pellmyr O, Massey LK, Hamrick JL, Feist MA (1997) Genetic consequences of specialization: yucca moth behavior and self-pollination in yuccas. *Oecologia* 109:273–278
- Powell JA (1984) Biological interrelationships of moths and *Yucca schottii*. *Univ Calif Publ Entomol* 100:1–93
- Rau P (1945) The yucca plant, *Yucca filamentosa*, and the yucca moth, *Tegeticula* (Pronuba) *yuccasella* Riley: an ecologico-behavior study. *Ann Mo Bot Gard* 32:373–394
- Richter KS, Weis AE (1995) Differential abortion in the yucca. *Nature* 376:557–558
- Riley CV (1892) The yucca moth and yucca pollination. *Ann Rep Mo Bot Gard* 3:99–159
- Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annu Rev Ecol Syst* 12:253–79
- Sutherland S (1986) Patterns of fruit-set: what controls fruit-flow-er ratios in plants? *Evolution* 40:117–128
- Sutherland S, Delph LF (1984) On the importance of male fitness in plants: patterns of fruit-set. *Ecology* 65:1093–1104
- Thompson JN, Pellmyr O (1992) Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. *Ecology* 73:1780–1791
- Thompson WR (1939) Biological control and the theories of the interaction of populations. *Parasitology* 31:299–388
- Travis CC, Post WF (1979) Dynamics and comparative statics of mutualistic communities. *J Theor Biol* 78:553–571
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57
- Vandermeer JH, Boucher DH (1978) Varieties of mutualistic interaction in population models. *J Theor Biol* 74:549–558
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060
- Wilson RD, Addicott JF (1998) Regulation of mutualism between yuccas and yucca moths: is oviposition behavior responsive to selective abscission of flowers? *Oikos* 81:109–118
- Wolin CL (1985) The population dynamics of mutualistic systems. In: Boucher DH (ed) *The biology of mutualism: ecology and evolution*. Oxford University Press, New York, pp 248–269
- Wolin CL, Lawlor LR (1984) Models of facultative mutualism: density effects. *Am Nat* 124:843–862
- Zimmerman M, Pyke GH (1988) Reproduction in *Polemonium*: assessing the factors limiting seed set. *Am Nat* 131:723–738