

Interspecific population regulation and the stability of mutualism: fruit abortion and density-dependent mortality of pollinating seed-eating insects

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Two questions central to the population ecology of mutualism include: (1) what mechanisms prevent the inherent positive feedback of mutualism from leading to unbounded population growth; and (2) what mechanisms prevent instability from arising due to overexploitation. Theory and empiricism suggest that preventing such instability requires density-dependent processes. A recent theory proposes that if benefits and costs to a mutualist vary with the density of its partner, then instability can be prevented if the former species can control demographic rates and regulate (or limit) the population density of its partner. The ecological and evolutionary feasibility of this theory of interspecific population regulation has been demonstrated using quantitative models of mutualism between plants and pollinating seed-consuming insects. In these models, resource-limited fruit set and ensuing fruit abortion are mechanisms that can lead to density-dependent recruitment and population regulation of the insects. Yet, there has been little interplay between these theoretical results and empirical research. A recent study empirically examined the density-dependent effects of resource-limited fruit set and fruit abortion in the *Yucca*/moth mutualism. An analysis of the study led to the conclusion that, even though fruit abortion can account for >95% of moth mortality, it is largely a density-independent source of mortality that cannot regulate moth population density. Here, we re-analyze those empirical data and conduct further theoretical analyses to examine the nature of fruit abortion on moth recruitment. We conclude that resource-limited fruit set and fruit abortion can effectively regulate and limit moth populations, due to its density-dependent feedback on moth recruitment. Nonetheless, in any given interaction, multiple sources of mortality may contribute to the regulation and limitation of populations, and hence the stability of mutualism, including, larval competition and mortality due to locule damage in the *Yucca*/moth mutualism.

predation and competition, we know far more about those interactions than we do of mutualism. Two problems that remain central to theoretical and empirical research on the population ecology of mutualism include: (1) what biological mechanisms prevent the inherent positive feedback of mutualism from leading to unbounded population growth; and (2) what biological mechanisms prevent overexploitation of one mutualistic species by its partner, thereby averting the degradation of mutualism into parasitism or predation. Both questions are fundamental to understanding the ecological and evolutionary stability of mutualism.

Theory and empiricism suggest that both the ecological and evolutionary stability of mutualism depend on density-dependent processes, in particular the density dependence of the benefits and costs of mutualism (Addicott 1979, 1998, Breton and Addicott 1992, Nefdt and Compton 1996, Morales 2000, Holland et al. 2002). Recently, it has been proposed that density-dependent processes of mutualism can simultaneously explain both of the above questions in certain cases (Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004b). In particular, if the benefits and costs to reproduction and/or survival of a mutualistic species vary with the density of its partner (i.e. benefit and cost functional responses), then instability through overexploitation and unbounded population growth can be prevented, if the former species can exert some control over its partner's demographic rates and regulate its population density.

Understanding how interspecific interactions affect the abundance and dynamics of populations is a central focus of ecology. While there is still much to learn about

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Because instability results when there are no effective density-dependent restrictions on population growth, mechanisms by which mutualists exert such a density-dependent influence on their partner may contribute to stability. The ecological and evolutionary feasibility of this theory of interspecific population regulation (or limitation) has been demonstrated using quantitative models of fruit abortion's density-dependent feedback on recruitment of insects in pollinating seed-consuming mutualisms (Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004b).

Pollinating seed-eating interactions of *Yucca*/moth and senita/moth mutualisms involve interactions between hermaphroditic plants and insects that both pollinate and oviposit into flowers. Eggs hatch to produce larvae that consume developing seeds of fruit. If moth density is low, then benefits of pollination to plant reproduction are small. Yet, if moth density is high, then costs of larval seed consumption to plant reproduction are large, resulting in overexploitation and degradation into parasitism. Such instability may be prevented if plants have a mechanism to control demographic rates and regulate moth density around intermediate values. Fruit abortion by plants may be such a mechanism. Fruit abortion can reduce recruitment of adult moths because eggs and larvae in aborting fruit invariably die. Such mortality may have density-dependent feedbacks on moth recruitment. Theoretical results demonstrate that fruit abortion can regulate populations around intermediate values, thus preventing overexploitation and unbounded population growth (Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004b).

Despite the feasibility of this theory in quantitative models, until recently there has been no empirical evaluation or interplay with it. Beyond egg and larval mortality in fruit abortions, no empirical study has examined the nature of fruit abortion on pre-adult mortality. A recent empirical study examined fruit abortion's effects on density-dependent mortality of moths in the *Yucca*/moth mutualism (Shapiro and Addicott 2004). This study, hereafter S&A, reported a rigorous set of analyses, results of which provide insight into random versus selective fruit abortion, and cues for selective fruit abortion. In particular, fruit abortion can account for >95% of moth mortality, and selective abortion may not necessarily increase mortality substantially above that of random abortion. These empirical results are largely consistent with theoretical results (Holland and DeAngelis 2001). However, initial empirical analysis led to the conclusion that fruit abortion's effects on mortality are density-independent, or at best only weakly density dependent, and hence are "unlikely to generate density-dependent, population regulating mortality of moth eggs" (Shapiro and Addicott 2004, p. 458). Although this was a reasonable conclusion to draw from the particular analyses performed, here we

present additional analyses of the same data that provide an alternative empirical test of the density-dependent nature of fruit abortion.

This paper empirically and theoretically examines the nature of fruit abortion on the recruitment of moth populations. Our analyses include: (1) mathematical analysis of fruit abortion that incorporates the biological means by which plant reproductive biology gives rise to fruit abortion and pre-adult moth mortality; (2) re-analysis of empirical data on fruit set, fruit abortion, and pre-adult mortality in the *Yucca*/moth mutualism (Shapiro and Addicott 2004); and (3) density-dependent analysis of moth recruitment and population regulation and limitation through incorporation of the mathematics of resource-limited fruit set and fruit abortion into a population dynamic equation. We conclude that fruit abortion and resource-limited fruit set are effective means of regulating and limiting moth populations through density-dependent feedback on moth recruitment, but that in nature other density-dependent factors may also contribute to moth density and the stability of pollinating seed-eating mutualisms.

Theoretical analysis of fruit set, fruit abortion and density-dependent moth mortality

Fruit abortion is a deterministic process associated with the reproductive biology of hermaphroditic plants that produce excess flowers and have resource-limited fruit set (Stephenson 1981). Hermaphroditic plants, including *Yucca* and senita, are well recognized to have fruit-to-flower ratios less than unity due to low survivorship of flowers through fruit maturation. The ecological and evolutionary causes of low fruit-to-flower ratios can vary in space and time, among populations, and among species, including for example resource limitation, pollen limitation, and excess flower production for pollen dispersal (Ayer and Whelan 1989.). Despite such irregularity in causes, low flower-to-fruit survivorship results from a general set of mechanisms underlying the reproductive biology of hermaphroditic plants (Stephenson 1981, Wyatt 1981, Holland et al. 2003). These processes determine fruit abortion and their potential effects on density-dependent recruitment in moth populations. Here, we summarize the reproductive biology of hermaphroditic plants in relation to fruit set and fruit abortion. We then present simple graphical and analytical formulations of fruit set and fruit abortion that demonstrate the dependence of fruit abortion on moth density.

Fruit set (or "retention;" Shapiro and Addicott 2004) is the stage of flower-to-fruit survivorship at which plants match the number of pollinated flowers with resources available for fruit maturation. Fruit abortion is the shedding of immature fruit. Fruit abortion is the

same as random or selective “abscission” of S&A. Flower abscission, on the other hand, is the shedding of unpollinated and incompatibly pollinated flowers. Our use of “fruit set” here is consistent with S&A’s use of the term fruit “retention.” S&A quantified fruit set (retention) in terms of the fraction of flowers visited, as measured by oviposited flowers. Technically fruit set (retention) is a fraction of all flowers, not just those visited. This minor difference in the denominator marginally inflates fruit set values reported by them, but does not confound their results or those here. Fruit abortion remains the same, as it is dependent on pollination as estimated by the fraction of flowers visited.

The two ecological factors largely responsible for fruit set and fruit abortion are pollination and resource availability for fruit maturation. If the fraction of flowers pollinated is less than maximum fruit set possible given resource availability, then fruit set is pollen limited (Fig. 1A). The fraction of flowers setting fruit equals the fraction pollinated, while remaining unpollinated flowers abscise from plants. Alternatively, if the fraction of flowers pollinated is greater than maximum fruit set possible given resource availability, then fruit set is resource limited (Fig. 1A). Fruit abortion is the fraction of pollinated flowers that do not set fruit due to limited resources for fruit maturation (Fig. 1B). Whether random or selective, fruit abortion matches fruit set to resources available for fruit and seed production.

The reproductive biology of hermaphroditic plants, and the relations among pollination, fruit set, and fruit abortion graphically depicted in Fig. 1 are represented mathematically as follows (Holland and DeAngelis 2001, Holland et al. 2004b). The fraction of flowers (F) setting fruit, that is fruit set (F_s), is described by

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

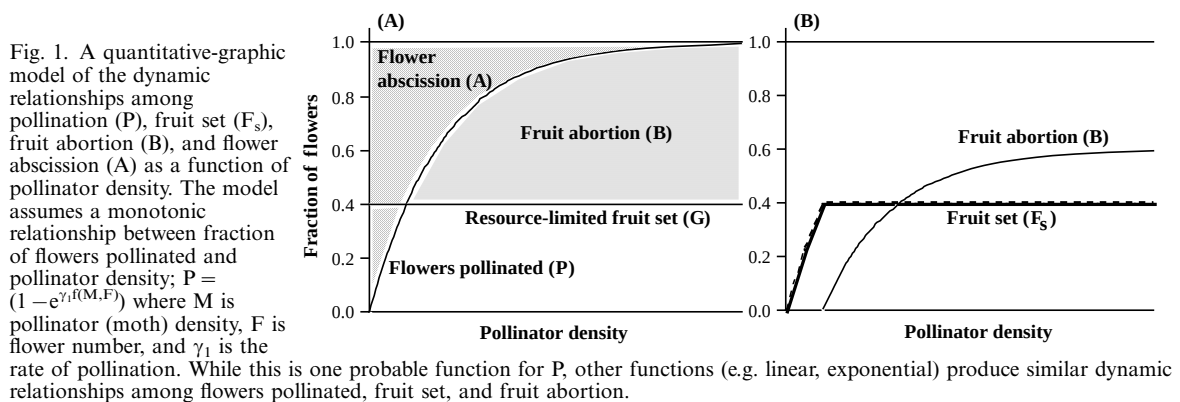
where P is the fraction of flowers pollinated, and G is the maximum possible fruit set given available resources (Fig. 1). If $P < G$, then $F_s = P$; flower abscission, A , equals $1 - P$; and fruit abortion, B , equals zero. If $P \geq G$,

then $F_s = G$, where $1 - G = A + B$; flower abscission remains $A = 1 - P$; but $B \neq 0$; instead $B = P - G$. Yet, fruit abortion asymptotes at $1 - G$ for high pollinator densities. Nonetheless, the fraction of flowers that are pollinated determines whether fruit abortion occurs.

Resource availability establishes the exact magnitude of fruit set when pollen is not limiting. We do not explore the ecological and evolutionary issues of excess flower production and resource availability for fruit set and fruit abortion here, as they have been examined elsewhere (Holland and DeAngelis 2001, Holland et al. 2004b) and both *Yucca* and senita have routinely resource-limited fruit set in space and time (Holland and DeAngelis 2001, Holland and Fleming 2002). Instead, we focus on the dynamic relationships among pollination, moth density, fruit set, and fruit abortion.

In the *Yucca*/moth and senita/moth mutualisms, plant reproduction is dependent upon moths for pollination, as the plants are entirely or almost completely self-incompatible. The relationship between the fraction of flowers pollinated (P) and pollinator (moth, M) density [i.e., pollination functional response, $P = f(M, F)$] determines whether fruit set is pollen or resource limited, and thus the quantity of fruit abortions. When moth density is low, fruit set is pollen limited and no fruit abortions occur (Fig. 1B). However, once moths reach a density at which resources (rather than pollination) limit fruit set, then fruit abortions begin to occur and continue to asymptotically increase with moth density (Fig. 1B). The number of fruit abortions by *Yucca* and senita plants is a density-dependent function of moth abundance (Fig. 1B). Thus, given that (1) fruit abortion is density-dependent function of pollination, and (2) pollination is density-dependent function of moth density, then (3) fruit abortion is dependent upon moth density.

Based on plant reproductive biology, we conclude on a theoretical basis that as long as pollination and oviposition are correlated to some degree, then resource-limited fruit set and fruit abortion can impose density-dependent mortality on moth populations. Indeed, active pollination and flower oviposition are tightly-coupled, evolved behaviors of mutualistic moths in pollinating



seed-eating mutualisms (Pellmyr et al. 1996). Below, we empirically examine how resource-limited fruit set and fruit abortion vary with moth density, and consequently, how moth mortality varies with fruit abortion. In the following section, we theoretically examine whether resource-limited fruit set and fruit abortion can regulate and/or limit moth populations, including whether the asymptote of fruit abortion at $1 - G$ for high moth densities prevents population regulation, as suggested by S&A.

Empirical analysis of fruit set, fruit abortion and density-dependent moth mortality

The recent study by S&A has made important insights into the ecology and evolution of the *Yucca*/moth mutualism. In particular, the study shows that selective abortion may not substantially increase moth mortality above that of random abortion, which is consistent with theory (Holland and DeAngelis 2001). Furthermore, their results indicate that 95% of pre-adult mortality can be accounted for by fruit abortion. Here, we re-analyze and re-interpret a portion of those data with respect to resource-limited fruit set, fruit abortion, and density-dependent pre-adult mortality of moth populations. The data we re-analyze come from Fig. 1 of S&A. Methods employed in the collection of these data can be found in the original studies (Addicott 1998, Shapiro and Addicott 2004).

S&A evaluated density-dependent pre-adult mortality resulting from fruit abortion by analyzing fruit set (retention) and k -values for resource-limited fruit set

$[k_{r1} = \log_{10}(1/\text{retention})]$ as a function of ovipositions per visited flower (see their Fig. 2a). These analyses were interpreted to mean that “egg mortality due to resource limitation did not increase with the average number of ovipositions per visited flower, because retention (fruit set) was not influenced by numbers of eggs per flower” (p. 454). This led to the conclusion that it is “unlikely that abscission (fruit abortion) by yuccas can generate density-dependent mortality over more than a small range of densities” (p. 459), and hence, fruit abortion does not likely regulate moths and prevent overexploitation of plants. As we discuss below, fruit set (retention) is not the most appropriate response variable for such analyses of fruit abortion and mortality.

The fruit abortion hypothesis for interspecific population regulation does not suggest that plants reduce their fruit set (retention) on ecological time scales within flowering seasons to increase fruit abortion and pre-adult mortality, as analyzed in Fig. 2 of S&A. The fruit abortion hypothesis does suggest, however, that mortality and steady-state population size of moths vary with fruit abortion. Consequently, there may be an evolutionarily stable strategy of excess flower production, and hence resource-limited fruit set and fruit abortion, to maximize plant fitness through the regulation of moth density. The use of fruit set (retention) as a response variable provides insight into yucca reproduction; however, it does not examine the density dependence of moth mortality on fruit abortion. Fruit set as a response variable shows that it is routinely less than unity and that it does not vary with ovipositions per flower. This is consistent with plant reproductive biology and the above theoretical analyses. If hermaphroditic plants produce

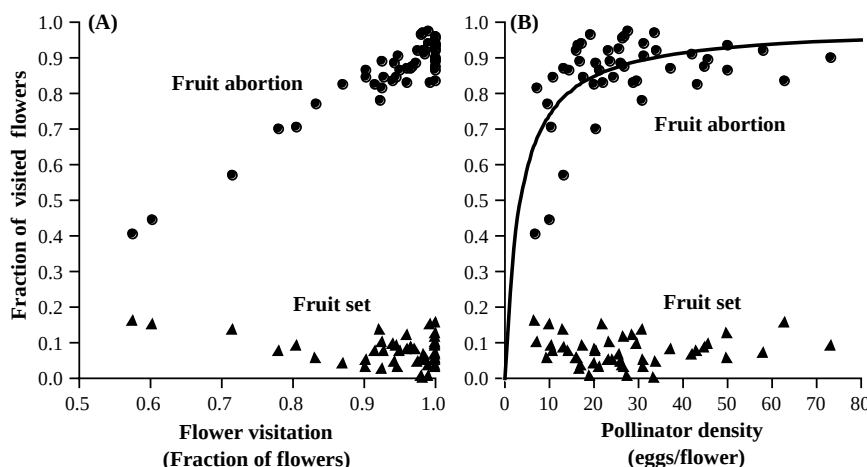


Fig. 2. Fruit set (triangles; fraction of visited flowers retained [i.e. retention]) and fruit abortion (circles; fraction of flowers visited minus fruit set) as a function of (A) flower visitation rates, V (fraction of flowers visited) and (B) pollinator density ($\sim$ eggs/flower). Fruit set and fruit abortion are fractions of the fraction of flowers visited (y-axis), such that the sum of fruit abortion and fruit set equals the fraction of flowers visited, as originally measured by S&A. Fruit abortion and fruit set will not always sum to 1.0, because the fraction of

flowers visited was not always 1.0. Pollinator density is assumed to scale with number of eggs oviposited. Regression of fruit abortion as a function of flower visitation was significant ($F_{1,44} = 103$, $p < 0.0001$, $r^2 = 0.70$; $b = 0.35$, $t = 10.2$, $p < 0.0001$; $[\log_{10}(100 \times \text{fruitabortion}) = 1.446 + 0.35 \times \text{asin}(\sqrt{V})]$). We used a Michaelis-Menton function to analyze the nonlinear relationship between fruit abortion, B , and pollinator density, M , [$B = aM/(b + M)$]. This nonlinear analysis of fruit abortion was significant ($F_{1,44} = 25.9$, $p < 0.001$, $r^2 = 0.37$; $a = 1.0$, $b = 3.39$). No significant relationship occurred between fruit set and flower visitation or pollinator density (Shapiro and Addicott 2004).

excess flowers and have limited resources available for fruit maturation, then fruit set is theoretically predicted to remain relatively invariable (Fig. 1), as empirically confirmed in Fig. 2 of S&A and replotted here in our Fig. 2.

The density-dependent nature of moth recruitment can be examined through the analysis of fruit abortion itself. Although definitive data are lacking, there is little doubt that fruit set was resource limited for the *Yucca* population reported in S&A. Only 7.9% of (visited) flowers set fruit even though no plant had less than 50% of its flowers visited at least once by moths. Because $F_s = G$ (that is, fruit set was resource limited), fruit abortion, B , equals $P - G$. We empirically estimated fruit abortion, B , from $B = P - G$. Resource-limited fruit set (retention), G , was measured for each plant (Shapiro and Addicott 2004), and the fraction of flowers pollinated, P , is approximated by the fraction of flowers with at least one oviposition, assuming behavioral coupling of pollination and oviposition by *Yucca* moths (Pellmyr et al. 1996). As predicted for resource-limited plants (Fig. 1), fruit set did not vary with the fraction of flowers visited (Fig. 2A) or with pollinator (moth) density (Fig. 2B) (see also Fig. 2 of Shapiro and Addicott 2004), as pollinators were never sufficiently rare that fruit set became pollen limited. Fruit abortion was density dependent, as predicted from theory (Fig. 1). Fruit abortion increased with both the fraction of flowers visited (Fig. 2A) and with moth density (Fig. 2B). In fact, fruit abortion asymptotes at a value in close proximity to that predicted by theory (Fig. 1): $1 - G = 0.92$, where mean fruit set, $\bar{G} = 0.079$. Accounting for 95% of pre-adult mortality, fruit abortion was a statistically and biologically significant source of density-dependent mortality for the moth population (Fig. 2).

Even though fruit abortion asymptotes at $1 - G$, moth recruitment decreases with moth density because eggs per aborted fruit continue to increase with moth density due to moth host specialization on *Yucca*. This is supported by the empirical observation that pre-adult moth mortality, as measured by eggs per aborted fruit, increases with fruit abortion (Fig. 3). It is important to note, however, that the exact magnitude of mortality resulting from fruit abortion may vary with the distribution of ovipositions among flowers (Holland et al. 2002, Shapiro and Addicott 2004). The only way that per-capita pre-adult mortality cannot continue to increase beyond $1 - G$ is if moths preferentially clump their eggs on flowers that set fruit rather than abort. If moths distribute their eggs randomly or evenly among flowers, as appears to be the case for yucca and senita moths (Huth and Pellmyr 1999, Holland et al. 2004a), then moth recruitment resulting from fruit abortion will decrease with moth density beyond $1 - G$.

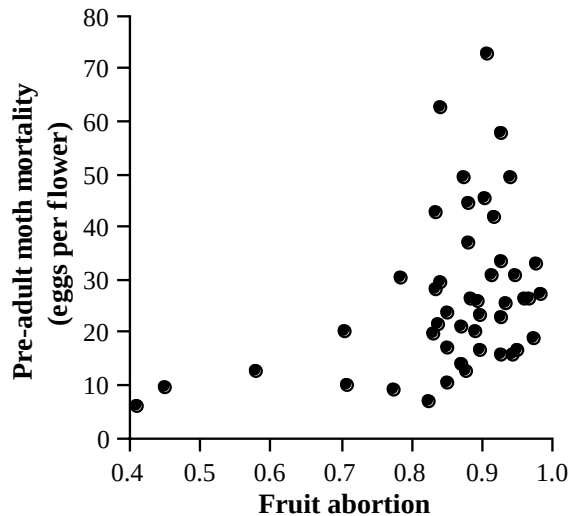


Fig. 3. Moth mortality (eggs per flower) resulting from fruit abortion (fraction of flowers visited minus fruit set). Regression of mortality on fruit abortion was significant ($F_{1,44} = 15$, $p < 0.0003$, $r^2 = 0.26$; $b = 0.81$, $t = 3.9$, $p < 0.0003$; [$\log_{10}(\text{eggs/flower}) = 0.40 + 0.81 \times \text{asin}(\sqrt{\text{fruit abortion}})$]).

Fruit abortion and population regulation vs population limitation

In the preceding sections, we demonstrated that fruit set and fruit abortion are dependent on moth density. If moth density is low, then fruit set is pollen limited and no fruit abortions occur, whereas if moths are abundant, then fruit set is resource limited and fruit abortions occur (Fig. 1). We also showed that fruit abortion in turn results in density-dependent deaths of pre-adult life stages of moth populations (Fig. 1,2,3). Here, we examine whether fruit abortion and resource-limited fruit set can regulate and/or limit the population density of moths. There is much discussion in the ecological literature over regulation versus limitation of populations. Our intention is not to rehash or delve into such issues, but rather to examine whether population regulation and/or limitation may result from resource-limited fruit set and fruit abortion.

A differential equation for the population dynamics of moths obligately associated with *Yucca* or senita plants is

$$dM/dt = \alpha FF_s(D/P) - \delta M \quad (2)$$

(for other similar equations examining moth dynamics, see Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004b). In Eq. 2, $P = 1 - e^{-\gamma_1 \bar{r}(M,F)}$ is the fraction of flowers pollinated and $D = 1 - e^{-\gamma_2 \bar{r}(M,F)}$ is the fraction of flowers oviposited by moths, where γ_1 and γ_2 are pollination and oviposition rates of moths, respectively. The factor α is the maximum number of moth larvae that can survive per set fruit. In the senita system, for

example, only one larva survives per fruit, such that $\alpha = 1$, whereas in the *Yucca*/moth mutualism, multiple larvae can survive per fruit that, such that $\alpha > 1$. The term δM represents the death rate of moths independent of resource-limited fruit set and fruit abortion. In the first term, F is the number of flowers, and D/P represents the fact that oviposition occurs on pollinated flowers. The term $\alpha FF_s(D/P)$ is the recruitment rate of moths, where F_s is given by Eq. 1. It is this recruitment rate that is affected by fruit abortion. When fruit set is pollen limited, Eq. 2 becomes $dM/dt = \alpha FD - \delta M$, such that there is no effect of resource-limited fruit set and fruit abortion on the recruitment rate of moths. When fruit set is resource limited, Eq. 2 becomes $dM/dt = \alpha FG(D/P) - \delta M$, for which moth recruitment is reduced by resource-limited fruit set (G) and fruit abortion. In Eq. 2, the density-dependent effect of resource-limited fruit set and fruit abortion on moth mortality is represented as a reduction in moth recruitment. Equation 2 explicitly incorporates the biological mechanism by which resource-limited fruit set and fruit abortion can influence moth population dynamics. However, Eq. 2 does not explicitly include some of the other factors that may influence moth dynamics. Prior studies have incorporated many of these other factors that could influence the effectiveness of fruit abortion to control moth populations; such factors included third-party predators, variation in egg-larval mortality, moth oviposition patterns, demographic stochasticity, migration, intraspecific cheating, hermaphroditic sex allocation, ratio- and predator-dependent functional responses, and seasonality in flower production (Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004b). Here, we are specifically interested in examining the effects of resource-limited fruit set and fruit abortion on the regulation and limitation of moth populations.

We examined the effect of fruit abortion on moth density by considering the steady-state equilibria of Eq. 2 for different numbers of flowers, F . Suppose that there are resources for only a limited number of fruit, $FF_s = FG = \text{Fruit}_{\max}$, per plant. Plants can produce more flowers, F , but only $\text{Fruit}_{\max}$ fruit can be produced. Thus, the maximum possible fraction of flowers that can set fruit, G , varies inversely with flower production, F . (We ignore the cost of flower production here, which would further subtract from the energy available for $\text{Fruit}_{\max}$, though that is included in the more general analysis of Holland et al. 2004b). As a consequence, the larger the number of flowers produced, the greater the potential number of fruit abortions. Hence, fruit abortion's effect on moth density can be evaluated by examining how steady-state equilibria of moths vary with flower number, F . For concreteness, assume the function $f(M, F)$ takes the form M/F , so that a larger number of flowers requires a proportionally larger

number of moths to pollinate or oviposit the same fraction of flowers. This assumption is justified in Holland et al. (2004b) and it assumes that a moth requires a handling time for both pollination and oviposition. The steady-state equilibria for the adult moths can be found by plotting both moth recruitment $[\alpha FF_s(D/P)]$, as influenced by fruit abortion, and moth death rate (δM) of Eq. 2 as functions of moth density, M (Fig. 4). Note that the four different moth recruitment curves plotted in Fig. 4, each with a different value of F , all asymptote to the same value. Equilibrium moth densities are determined by the intersections of the moth recruitment and moth mortality curves. The larger the number of flowers is, and hence the larger the number of fruit abortions, the smaller is the equilibrium moth density. These equilibria are stable to perturbations in moth density.

Fruit abortion ensuing from excess flower production and resource-limited fruit set can control moth population density. It is important to note that plant allocation of available resources between flower production (F) and resource-limited fruit set (G) is an evolutionary variable. Nevertheless, fruit abortion has ecological consequences for moth abundance and the stability of both *Yucca*/moth and senita/moth mutualisms. Fruit abortion resulting from excess flower production and resource-limited fruit set can maintain the moth population at low

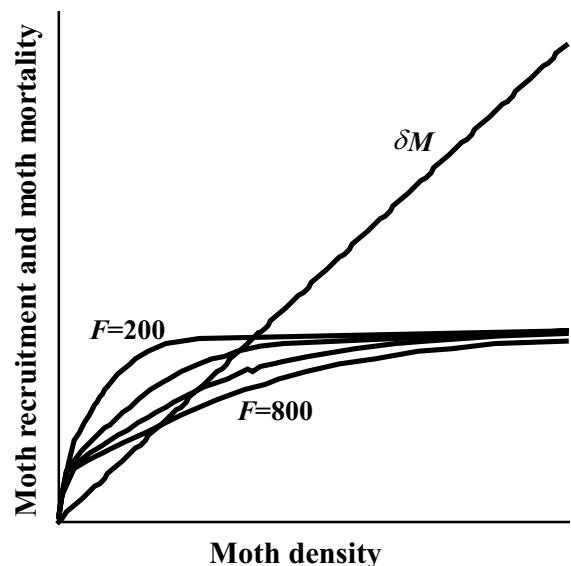


Fig. 4. Equilibrium densities of moths decrease with increasing fruit abortion. Moth mortality, δM , is plotted for $\delta = 0.75$. Moth recruitment, $\alpha FF_s(D/P)$, is plotted for four values of flower number, F ; 200, 400, 600, and 800 (from top to bottom). It is assumed that resources are available for only 150 fruit. Therefore, the values of fractional fruit set are, respectively, $G = 0.75, 0.375, 0.25$, and 0.185 . Other parameters were $\alpha = 10$, $\gamma_1 = 2.0$, $\gamma_2 = 0.5$. The intersections of $\alpha FF_s(D/P)$ and δM represent equilibrium densities of moths (on the x-axis).

enough numbers that the moth population will not saturate the flowers with their eggs and larvae.

We additionally evaluated the influence of fruit set and fruit abortion on population regulation versus population limitation through numerical solutions of Eq. 2. We used descriptions of population regulation and limitation of Case (2000) as the basis for our analyses of moth dynamics. Population limitation occurs when environmental factors, whether they be abiotic (e.g. catastrophic events) or biotic (e.g. predators, parasites), act to check or restrain population size. Such environmental factors can be either enhancers of population size, when addition of the factor leads to increases in population size, or they can be suppressors of population size, when reduction of the factor leads to increases in population size. Population limitation does not necessarily involve density-dependent feedback on abundance. If resource-limited fruit set and fruit abortion limit moth density, then increasing G in Eq. 1 and 2 should lead to greater equilibrium densities of moth populations. Indeed, increasing G from 0.2 to 1.0 leads to greater densities of moths (Fig. 5A), supporting the conclusion of S&A that resource-limited fruit set and fruit abortion can limit moth population size. Essentially, moth population size is limited from the bottom-up via flowers available for oviposition and fruit food resources available for larvae. Increasing fruit set and reducing fruit abortion produces greater equilibrium densities of moths (Fig. 5A).

Population regulation, unlike limitation alone, necessarily involves density-dependent feedbacks on population size. In particular, regulated populations have a propensity to decrease in size or density when above a certain level or to increase in size or density when below that level. Furthermore, per-capita population growth rate (dN/Ndt) decreases with population size (N) due to density-dependent feedback on births, deaths, immigration, or emigration. Factors that regulate a population can also limit them, but limiting factors do not necessarily regulate population size. Furthermore, factors that regulate population size are density dependent, but not all density-dependent factors regulate population size. If resource-limited fruit set and fruit abortion have the potential to regulate moth density, then moths should decrease in density when above an equilibrium abundance associated with a particular value of G , or they should increase in density when below that equilibrium. Fig. 5B depicts changes in moth (pollinator) density for eight different initial population sizes, four greater than and four less than the equilibrium density for $G = 0.4$. For initial population densities greater than the equilibrium density, moths decreased in density due to negative density-dependent feedback on moth abundance (Fig. 5B). When moths are abundant enough that resource-limited fruit set and fruit abortion occur, then density-dependent mortality causes the moth population

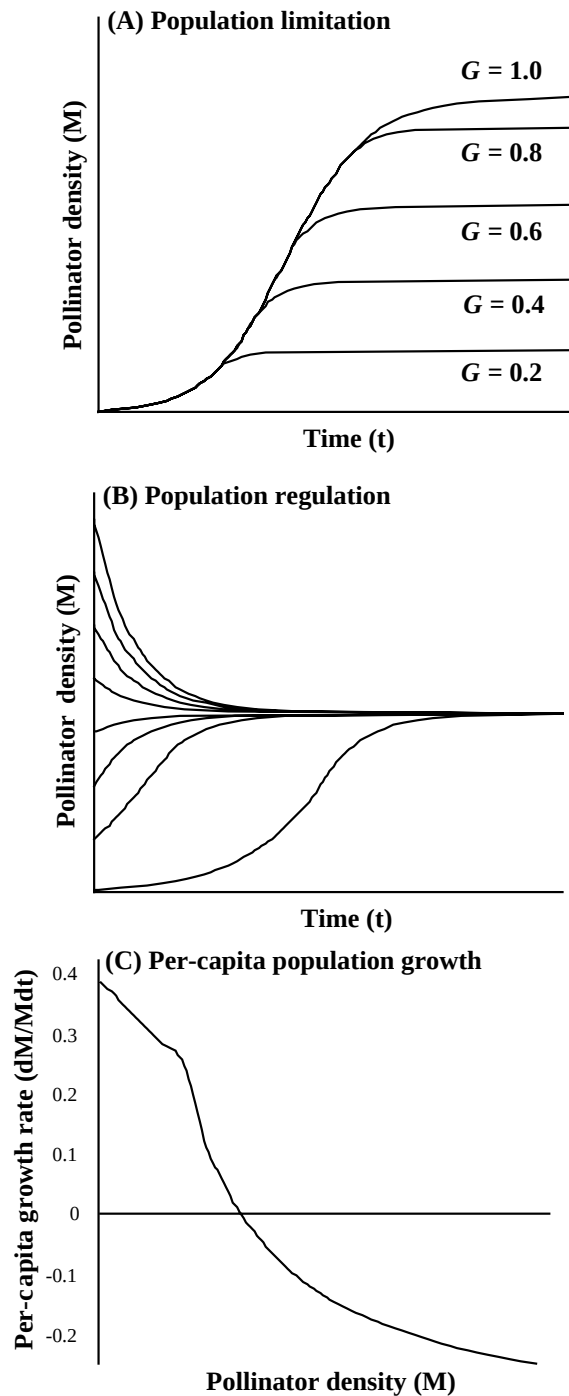


Fig. 5. Population limitation, population regulation, and per-capita population growth rates of moth pollinators (M) resulting from fruit abortion and resource-limited fruit set. In (A), levels of resource-limited fruit set increase from $G = 0.20 - 1.0$, corresponding to reducing the effect of resource-limited fruit set and fruit abortion on limiting moth density. In (B), eight trajectories of pollinator density are shown, 4 < and 4 > the equilibrium pollinator density for $G = 0.4$. In (C), per-capita population growth rate (dM/Mdt) is shown as a function of pollinator density. Parameter values were $\gamma_1 = 1.3$, $\gamma_2 = 1.0$, $G = 0.4$ (unless otherwise noted), $\delta = 0.5$, and $F = 100$.

growth rate to decline. Similarly, for initial population densities less than the equilibrium density for $G=0.4$, moths increased in density (Fig. 5B). When moth density is low, then fruit set is pollen limited, fruit abortions do not occur, and populations grow to the equilibrium density for the particular level of resource-limited fruit set, G . In sum, fruit abortion and resource-limited fruit set can both regulate and limit moth populations.

Once the fraction of flowers pollinated approaches unity, however, fruit abortions asymptote with moth density at $1-G$ (Fig. 1B); further increases in moth density do not lead to greater numbers of fruit abortion. This suggested to S&A that resource-limited fruit set and fruit abortion may not lead to further per-capita density-dependent mortality necessary for population regulation. To demonstrate their assertion, S&A (p. 450) outlined a scenario in which there was 10% fruit set and 90% fruit abortion. In their scenario, per-capita density-dependent mortality could not occur for the moth population, no matter how large the moth population became. This 10%/90% scenario assumes that an unlimited number of larvae can survive per fruit, such that, with further increases in moth density, and hence egg numbers per set fruit, the percentage of eggs and larvae surviving and dying remain constant. However, the food resources of individual fruit cannot support the growth of an unlimited number of larvae. If those flowers setting fruit support only a limited number of larvae, then per-capita larval mortality increases with moth density. This logic concerning negative density-dependent mortality of moths holds more generally as long as there is an upper limit on the number of larvae that can survive per set fruit.

Consistent with this verbal description is the decline in per-capita population growth rate with moth density in our quantitative analyses (Fig. 5C). Note, in particular, that in Fig. 5C the steepness of the negative slope increases at $dM/Mdt \approx 0.26$ because this is the point at which fruit set shifts from pollen to resource limitation, and fruit abortions begin to occur. While the effect of resource-limited fruit set and fruit abortion on per-capita mortality increases with moth density, it does so at a diminishing rate, as indicated by the decreasing slope in Fig. 5C at very high densities. Even after fruit abortion saturates at $1-G$ (Fig. 1B), the per-capita growth rate of moths does continue to decrease with moth density for two biological reasons. First, the number of ovipositions per flower continues to increase with moth density beyond $1-G$, as moths oviposit on no other host species, leading to greater mortality per aborted fruit. Second, resource-limited fruit set is a finite food resource for larvae. As moths increase in abundance, density-dependent larval mortality increases, as only a limited number of larvae can survive per flower that sets fruit. Thus, for very high moth densities, it is a combination of both larval mortality resulting from

intraspecific competition for resource-limited fruit set and egg/larval mortality resulting from fruit abortion that produces the negative density-dependent recruitment of moth populations. At most population densities, mortality resulting from fruit abortion is key to the process of population regulation, though at exceptionally high population densities larval competition for resource-limited fruit set dominates. In either case, resource-limited fruit set and fruit abortion do collectively impose ever greater negative density-dependent mortality upon moths necessary for population regulation and limitation.

Conclusion

Interplay between theory and empiricism can be instrumental in advancing our basic knowledge of the ecological sciences (preface of Fretwell 1972). Here, we have attempted to resolve conflicting results of theoretical and empirical research on the stability and dynamics of mutualistic populations by integrating theoretical and empirical analyses. Our investigation into moth population dynamics was motivated in part by the differences in conclusions of S&A and Holland and DeAngelis (2001, 2002) with regards to whether resource-limited fruit set and fruit abortion are density dependent, and whether resource-limited fruit set and fruit abortion may regulate and/or limit moth populations involved in pollinating seed-eating mutualisms. Here, we have shown both theoretically and empirically that resource-limited fruit set and fruit abortion can indeed produce density-dependent recruitment, and can both limit and regulate moth density, thereby preventing overexploitation and unbounded population growth of mutualistic species. After any perturbation that increases or decreases moth density, the population will return to the steady-state equilibrium value associated with particular values of resource-limited fruit set. The moth population cannot exceed the density supported by the number of flowers setting fruit, as those fruit determine the quantity of larval food resources available for moth populations. However, when the dynamics of the entire system are considered, including flower production, resource-limited fruit set, and fruit abortion, then moth populations can also be regulated around that density associated with particular levels of resource-limited fruit set. Resource allocation between flower and fruit production (i.e. sex allocation) in hermaphroditic plants is an evolutionary variable, although proximally influenced by resources available for flower and fruit production (Holland et al. 2004b). Moth density is regulated by resource-limited fruit set and fruit abortion, even though on an ecological time scale (i.e. within a flowering season) plants do not appear to adjust fruit set to moth density. Although resource-limited fruit set and

fruit abortion can limit and regulate moth density, it may well be that other processes (e.g. larval mortality induced by locule-ovule damage in *Yucca*, Shapiro and Addicott 2003, 2004) act in concert with or supersede resource-limited fruit set and fruit abortion in determining moth densities. While other such mechanisms may occur in the *Yucca*/moth mutualism, none appear to occur in the senita/moth mutualism, such that population regulation and limitation may depend solely on density-dependent mortality associated with resource-limited fruit set and fruit abortion.

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