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Benefit and cost curves for typical pollination mutualisms

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Abstract. Mutualisms provide benefits to interacting species, but they also involve costs. If costs come to exceed benefits as population density or the frequency of encounters between species increases, the interaction will no longer be mutualistic. Thus curves that represent benefits and costs as functions of interaction frequency are important tools for predicting when a mutualism will tip over into antagonism. Currently, most of what we know about benefit and cost curves in pollination mutualisms comes from highly specialized pollinating seed–consumer mutualisms, such as the yucca moth–yucca interaction. There, benefits to female reproduction saturate as the number of visits to a flower increases (because the amount of pollen needed to fertilize all the flower's ovules is finite), but costs continue to increase (because pollinator offspring consume developing seeds), leading to a peak in seed production at an intermediate number of visits. But for most plant–pollinator mutualisms, costs to the plant are more subtle than consumption of seeds, and how such costs scale with interaction frequency remains largely unknown. Here, we present reasonable benefit and cost curves that are appropriate for typical pollinator–plant interactions, and we show how they can result in a wide diversity of relationships between net benefit (benefit minus cost) and interaction frequency. We then use maximum-likelihood methods to fit net-benefit curves to measures of female reproductive success for three typical pollination mutualisms from two continents, and for each system we chose the most parsimonious model using information-criterion statistics. We discuss the implications of the shape of the net-benefit curve for the ecology and evolution of plant–pollinator mutualisms, as well as the challenges that lie ahead for disentangling the underlying benefit and cost curves for typical pollination mutualisms.

Key words: benefits and costs of mutualism; density dependence; interaction frequency; nectar robbery; pollinating seed–consumer mutualism.

INTRODUCTION

"Mutualism" is, by one definition, an interaction between individuals of different species in which both individuals receive net benefits. As most so-called mutualisms are, in reality, balanced antagonisms that involve both benefits and costs to both interacting partners (Addicott 1986, Pierce et al. 1987, Cushman and Beattie 1991, Bronstein 2001, Holland 2002, Richardson 2004; but see Connor 1995), the interaction is mutually beneficial only if benefits exceed costs for both species. However, benefits and costs are not fixed, but instead vary with environmental conditions, with the density of other species in the community, and with the density of the interacting mutualists themselves (Cushman and Whitham 1989, Breton and Addicott 1992, Bronstein 1994, Herre and West 1997, Morales 2000, Holland et al. 2002, Ness et al. 2006, Chamberlain and Holland 2008). Dependence of benefits and costs upon the density of the mutualists is a potentially important mechanism that inhibits runaway population growth of the interacting species in the face of reciprocal benefits. In particular, if benefits to one partner decline or its costs increase as the density of the other partner increases, mutualism may disappear, or even tip over into a net antagonism, when the second partner becomes abundant.

From the perspective of benefits and costs, what is perhaps the best-studied pollination mutualism is the interaction between pollinating seed consumers and

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their host plants, such as the yucca moth–yucca interaction. At high moth densities yucca flowers likely receive more visits on average. In turn, both benefits and costs to yucca likely depend on the number of visits per flower. Female reproductive benefit will level off as visit number increases, once the flower has received sufficient pollen to fertilize all of its ovules. However, the cost will likely continue to increase, because more visits will result in more ovipositions by adult moths into the flower's ovary, and thus a greater fraction of seeds consumed by moth larvae. Consequently, Holland and DeAngelis (2001, 2002; also see Bronstein 2001) have argued that net benefit to yuccas will be maximal at an intermediate number of visits per flower, and therefore at an intermediate moth density. Increasing costs select for traits that prevent or retaliate against a high number of visits (e.g., selective abortion of yucca fruits that have received many ovipositions [Pellmyr and Huth 1994]; but see Addicott and Bao [1999] and Shapiro and Addicott [2004]).

Pollinating seed–consumer mutualisms have received so much attention in large part because the cost to the plant (seed consumption by larvae) is relatively easy to quantify. However, in the more widespread pollination mutualisms that do not involve seed consumption, which we label in this paper as "typical" pollination mutualisms, costs are both more difficult to observe and more varied in nature. In typical pollination mutualisms, costs to the plant that may vary with the number of visits (as distinct from floral construction costs that are "fixed" sensu Addicott 1984) include: (1) replenishment of rewards (typically nectar) collected by visitors (Pleasants and Chaplin 1983, Southwick 1984, Pyke 1991, Harder and Barrett 1992; but see McDade and Weeks 2004); (2) damage to floral structures made by visitors, or the plant's attempts to repair that damage (McDade and Kinsman 1980, Galen 1983, Traveset et al. 1998); (3) removal of pollen that was deposited on a flower's stigma by earlier visitors (Young 1988, Young and Young 1992, Gross and Mackay 1998); (4) greater competition among pollen tubes leading to a lower fraction of ovules fertilized (Young and Young 1992); (5) infection by pathogens that are transmitted by visitors (Alexander and Antonovics 1988, Shykoff et al. 1996); and (6) infection of nectaries by yeasts vectored by visitors that reduce nectar quality and thus the frequency or duration of subsequent visits (Herrera et al. 2008). We know very little about how these costs, or for that matter plant benefits, change with the abundance of visitors in typical pollination mutualisms. Consequently, we do not know at present whether well-studied pollinating seed–consumer mutualisms provide a good model for density-dependent benefits and costs in pollination mutualisms in general.

In this paper we attempt to redress the mismatch between the wealth of information we have about benefits and costs in a relatively uncommon type of mutualism (pollinating seed–consumer mutualisms) and our lack of knowledge about density-dependent benefits and costs in more widespread, typical pollination mutualisms. First, we present simple curves that show how gross benefit, gross cost, and net benefit (the difference between gross benefit and gross cost) may change with the number of visits per flower, and therefore with the abundance of floral visitors, and we show how underlying mechanisms of benefit and cost can change the shapes of these curves. We emphasize that we do not see our use of such curves as novel; indeed, they underpin much of our conceptual understanding of density dependence in mutualism (Bronstein 2001, Holland and DeAngelis 2001, Holland et al. 2002). Rather, we seek to identify curves that are appropriate for typical pollination mutualisms by giving them a mechanistic basis. We focus on female reproduction because of its importance for population dynamics, but we note that curves with shapes similar to those we present may also apply to male reproduction, and thus the curves may be useful tools for understanding selection on floral traits mediated through both male and female fitness. Second, we present net-benefit curves for components of female reproduction that we have measured for three plants in typical pollination mutualisms. Finally, we discuss the implications of these curves for the ecological and evolutionary dynamics of typical pollination mutualisms, and whether those dynamics are likely to be similar to or different than those of better-studied pollinating seed–consumer mutualisms.

THEORY: MECHANISMS AND FUNCTIONAL FORMS OF BENEFIT AND COST IN "TYPICAL" POLLINATION MUTUALISMS

To consider how the net benefit that a plant in a typical pollination mutualism receives might depend on the number of interactions it has with visitors, we begin with two premises. First, we assume that benefits and costs are additive, so that net benefit is simply the benefit minus the cost (cf. Roughgarden 1975, Keeler 1981, 1985, Bronstein 2001, Holland et al. 2002, 2004; but see Holland and DeAngelis [2001] for a multiplicative model). Second, we assume that both cumulative benefit and cumulative cost reach an asymptote as the number or frequency of interactions becomes large.

Our second premise warrants justification. In pollination mutualisms the plant benefits by pollen delivery. Because ovule number or available resources must eventually limit reproduction when delivery is high, cumulative benefit must reach an asymptote as the number of interactions increases. Although costs are more diverse, we claim that they, too, must plateau, regardless of their nature. The rates of reward production and of damage-repair processes must eventually be limited by physiological constraints, so such costs cannot increase indefinitely. Pollen removal from stigmas cannot exceed pollen previously deposited, which is limited by stigma area. Seeds lost to pollen

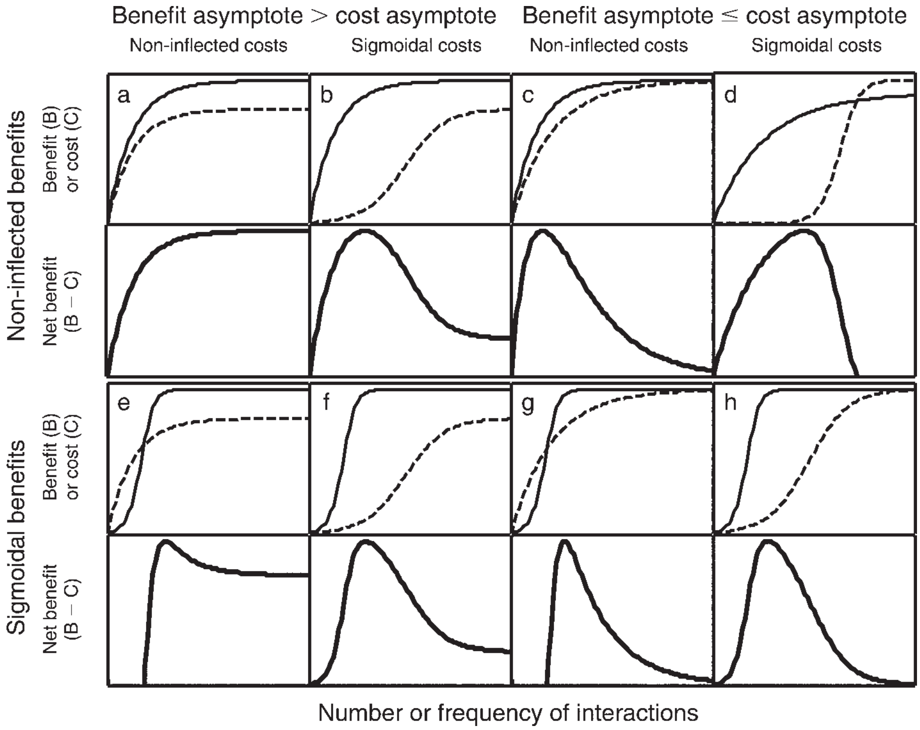

FIG. 1. A wide variety of net-benefit curves can result from combinations of saturating benefit and cost curves. Solid lines are benefit curves; dashed lines are cost curves.

competition cannot exceed the maximum number of seeds per flower. Finally, cumulative probability of infection by pathogens or yeasts cannot exceed 1. Thus the premise that both benefits and costs eventually saturate is reasonable.

While our two premises necessarily narrow the possible ways that net benefits may change as visits increase, the range of possibilities is still large due to variation in the shapes, asymptotes, and intercepts of the saturating benefit and cost curves. These curves may be noninflected functions (i.e., with second derivative always ≤ 0) that resemble a type II functional response of a predator to an increasing density of its prey, or they may be sigmoidal functions that resemble a type III predator functional response. In addition, the asymptote of the cost curve may lie below that of the benefit curve, or it may equal or exceed it. Finally, the y-intercept of the benefit or cost curve may be 0 or greater. In Figs. 1 and 2 we illustrate a range of possible net-benefit curves that variation in these three aspects of the benefit and cost curves can produce, and in the next paragraph we discuss possible mechanisms producing that variation.

Simple saturation of benefits and costs will produce noninflected curves. However, if costs are due to damage by floral visitors, the cost curve may be sigmoidal if each successive increment of damage has greater effects than the preceding increment, perhaps because the plant's ability to repair damage is overwhelmed, until eventually the asymptotic cost is reached. A sigmoidal cost curve could also result if each unit of reward becomes more costly to produce as the amount previously produced increases, as we show in Appendix A. A sigmoidal benefit curve could result if per flower reproductive success is an accelerating function of the number of pollen grains deposited on the stigma, but the maximum number of pollen grains that can contact the stigma is limited (see Appendix A).

If the cost curve's asymptote is less than that of the benefit curve, the net benefit will approach a positive asymptote as the number of visits increases, whereas if the benefit and cost asymptotes are equal, the asymptotic net benefit is 0, and the net-benefit curve will peak at an intermediate number of visits (cf. Fig. 1a, c; also see Bronstein 2001, Holland and DeAngelis 2001, 2002, Holland et al. 2002, 2004). A peak can also result when the benefit asymptote is greater than the cost asymptote, but the benefit curve, the cost curve, or both are sigmoidal (Fig. 1b, e, f). In principle, costs may exceed benefits at a high or a low number of interactions, resulting in a negative net benefit (cf. Holland et al. 2002: Fig. 1A), yet it may not be possible to observe negative net benefits in a particular experiment. For example, if net benefits are measured as the probability that single flowers set fruit as a function of the number of visits they receive, the observed net benefit obviously cannot be negative. Nonetheless, the true net benefit can still be negative if an excess of costs over benefits in one flower reduces the reproductive success of other flowers on the plant or if it reduces growth or survival.

The *y*-intercept of the benefit curve will be greater than 0 if flowers can produce fruits without receiving any visits (e.g., by autogamy). If the benefit curve is sigmoidal and its *y* intercept is positive, the net-benefit curve can be highly nonlinear, and may initially decline as the number of visits increases (Fig. 2). Thus two simple shapes of the benefit and cost curves (non-inflected and sigmoidal), when their positions are allowed to vary, can generate wide diversity in aspects of the net-benefit curve, including its intercept, its asymptote, and, importantly, whether it exhibits a peak at an intermediate number of interactions.

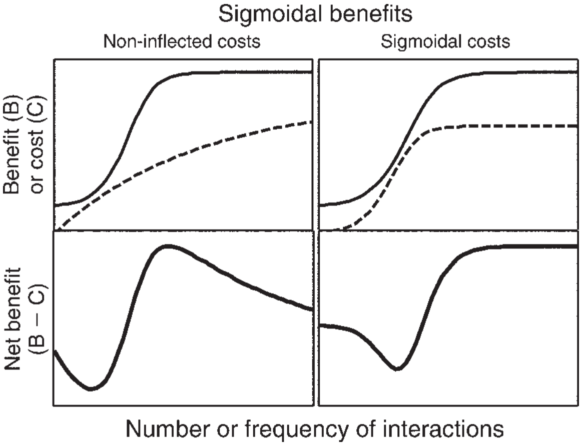

FIG. 2. If the benefit curve (solid line) is sigmoidal and has an intercept higher than that of the cost curve (dashed line) (upper panels), net benefits (lower panels) may initially decrease with the number of visits, whether the cost curve is noninflected (left panels) or sigmoidal (right panels).

EMPIRICAL APPLICATION: ESTIMATING THE NET-BENEFIT CURVES FOR THREE INSECT-POLLINATED PLANTS

Although we cannot separate the underlying benefit and cost curves without measuring costs, and the nature of those costs is not known in many typical pollination systems, we can nevertheless quantify the shape of the net-benefit curve, and ask in particular if it shows a saturating vs. a unimodal pattern. We measured net-benefit curves for three typical pollination systems by allowing different numbers of insects to visit individual flowers, measuring components of those flowers' female reproductive success, and fitting functions to the data. Because they describe the female success of individual flowers, the net-benefit curves we measured are one component of an entire plant's reproductive success; we place the female success curves in the context of whole-plant success in *Discussion: Evolutionary implications of net-benefit curves*, below.

Study species and sites

Citrus paradisi (Rutaceae; "grapefruit" or "pomelo") is an economically important crop in northern Argentina, where it is pollinated primarily by honey bees (*Apis mellifera*), which was the only visitor in the results presented here. Each flower is receptive for 1–4 days. Here, we reanalyze data of Chacoff et al. (2008) that were collected in 2003 in the Upper Bermejo River Basin in the province of Salta, Argentina.

Capparis atamisquea (Capparaceae; "atamisque") is a shrub characteristic of the Monte desert in Argentina. We conducted our field study in December 2007 at the Villavicencio Natural Reserve located 28 km north of the city of Mendoza (32°31′22″ S, 68°56′28″ W), where atamisque flowering peaks in December after most other plants have finished flowering. Because the flowers have an open form, they are accessible to a wide array of visitors. In our study, we observed 18 insect taxa visiting the flowers (some of these taxa may include >1 species). Each flower stays open for ≥1 week, and so may receive many visits over its lifetime.

Bagged flowers that were not pollinated and those pollinated with self pollen had low (and equal) fruit set relative to those pollinated with outcross pollen, suggesting that atamisque is largely self-incompatible (D. Vázquez, *unpublished data*).

Mertensia paniculata (Boraginaceae; "bluebells") is an herbaceous perennial native to alpine and taiga biomes in North America. We measured the net-benefit curve for bluebells in June and July 2008 at the field site in Alaska used by Morris (1996). The corolla of bluebell flowers has a tube and a bell-shaped limb. The filaments are stiff and form a net-like barrier where they insert at the junction between the corolla tube and limb, making it difficult for short-tongued insects to reach the two nectaries located at the base of the ovary (see Morris 1996: Fig. 1). As a result, bluebell flowers are frequently visited by nectar-robbing bumble bees, which chew a hole at the base of the corolla tube to reach the nectaries. During such "robbing" visits, bees contact neither the anthers nor the stigma. The same species of bumble bees also make "legitimate" visits by entering the mouth of the corolla to collect nectar or pollen, and thus may contact the anthers and stigma. Thus robbing visits provide no benefit to bluebells and only impose costs, whereas legitimate visits both provide benefits and impose costs (although those costs may differ from the costs of robbing visits). Other bees, wasps, and syrphid and muscoid flies also visited bluebell flowers legitimately during our experiments. Each flower remains open for 3–5 days (Morris 1996), and plants are self-compatible (W. Morris, *unpublished data*).

Experimental methods

We used similar methods to measure the net-benefit curves for our study species. We enclosed branches with flower buds in mesh bags, after removing all open flowers. When new flowers had opened, we opened the bag and attached a numbered tag with string or a piece of colored tape to the pedicel of each open (and unvisited) flower. We then allowed insects to visit, recording the number of visits each flower received. We only included visits in which the insect contacted the stigma, anthers, or nectaries. For bluebells, we recorded robbing and legitimate visits separately. Although it would have been impractical to assign a number of visits at random to each flower (because the inflorescence structure of all three study species makes it cumbersome to bag individual flowers), we achieved a range of visit numbers by varying the time branches were exposed before re-closing the bag. In some cases, we exposed flowers on >1 day. Later, we measured aspects of reproductive success for each flower. For grapefruit, we use stigmatic pollen load as the measure of net benefit; honey bees deposit pollen on stigmas (a benefit) but may also remove it (a potential cost). For atamisque, each fruit contains a single seed, so we use the fraction of flowers setting fruit to measure net benefit. Bluebells (like all borages) can mature ≤ 4 seeds per flower, so we use the number of seeds per flower to measure net benefit. We obtained data for 190, 157, and 670 flowers from 8, 5, and 9 individual plants of grapefruit, atamisque, and bluebells, respectively. Because of limited sample size, we combined flowers across plants in our analysis, even though plants may differ in average per flower success.

Fitting net-benefit curves to the experimental data

We compared the fit of 10 net-benefit models to the data (Appendix C). Eight models consist of all possible combinations of noninflected or sigmoidal benefit and cost curves with the asymptotes of the two curves constrained or not constrained to be equal. Noninflected benefit curves have the form $B = p_1 + (p_2 - p_1)(1 - e^{-p_3 V})$ and sigmoidal curves have the form $B = p_2/(1 + (p_2/p_1 - 1)e^{-p_3 V})$, where B is benefit, V is the number of visits by all taxa combined, p_1 is the y-intercept (i.e., reproductive success for unvisited [$V = 0$] flowers), p_2 is the asymptote (i.e., B when $V = \infty$), and p_3 governs the rate of approach to the asymptote. Cost curves are similar three-parameter functions. For each of these models, the net-benefit curve is simply the difference between the benefit and cost curves. Thus the first eight models have either five or six parameters, depending on whether the benefit and cost asymptotes are equal. Although we can devise functions with fewer parameters that allow for a unimodal shape, a y intercept, and a nonzero asymptote, we chose to use net-benefit functions that are explicitly the difference between benefit and cost curves, to connect with our preceding discussion. Depending on the parameter values, these models can produce saturating, unimodal, or highly nonlinear net-benefit curves (Figs. 1 and 2). Models 9 and 10 were a simple three-parameter saturating net-benefit curve $N = p_1 + (p_2 - p_1)(1 - e^{-p_3 V})$ with y-intercept p_1 and asymptote p_2, and a simple unimodal net-benefit curve $N = p_1 + p_2 V e^{-p_3 V}$, also with three parameters (in both cases, N is net benefit). We asked if a simpler saturating or unimodal net-benefit model fit the data as well as models with the same shape but more parameters.

We fit all models to the data by the method of maximum likelihood using R (R Development Core Team 2005; details are in Appendix B), and then used Akaike's information criterion (AIC) to identify the most parsimonious models for each data set. AIC is simply the negative log-likelihood of a model, $-L$, "penalized" by the number of parameters in the model, k ($\mathrm{AIC} = -2L + 2k$); models with low AIC values provide the most parsimonious fit to the data (Burnham and Anderson 2002). In computing likelihoods, we used both standard and overdispersed probability distributions (Bolker 2008, Richards 2008). Specifically, for grapefruit we fit models assuming the number of stigmatic pollen grains followed Poisson and negative binomial distributions. For atamisque and bluebells, we assumed that the number of flowers setting fruit and the number of seeds per flower, respectively, were binomially and beta-binomially distributed. For grapefruit and bluebells, overdispersed distributions produced substantially lower AIC values, so we used them for all results presented here. For atamisque, the maximum-likelihood estimate of the overdispersion parameter indicated the absence of overdispersion; therefore we present results based on a binomial distribution. We give maximum-likelihood parameter estimates, AIC values, and ΔAIC values for all models in Appendix C: Table C2 (but we report key AIC results in the text), and we illustrate net-benefit curves for all models with a difference from the lowest AIC model (ΔAIC) of ≤ 2. Richards (2005, 2008) showed, by simulating models with complexity and distributions similar to ours, that this rule of thumb included the true model among those selected ~80% of the time.

RESULTS

For grapefruit, the average number of pollen grains on stigmas increased and then either saturated or decreased slightly as the number of honey bee visits to flowers increased (Fig. 3). Because the sample size of flowers with high visit numbers is small, the data cannot differentiate between two models with the same, lowest AIC values, a simple saturating model and a simple unimodal model with a very slight decline in predicted pollen load above $V = 1/p_3 = 7.8$ visits. Similarly, the best-fit versions of the more complex models were divided between saturating and unimodal net-benefit patterns (Appendix C: Table C2).

For atamisque, the probability that a flower set fruit showed a clear unimodal pattern, with a low probability for 0–1 visits, a maximum at 8 visits, and a sharp decrease to zero after 10 visits (Fig. 3). The two most parsimonious net-benefit models had logistic underlying benefit and cost functions, but differed in whether the benefit and cost asymptotes were equal or different. Despite having more parameters, the most parsimonious model had a decidedly lower AIC value than did both

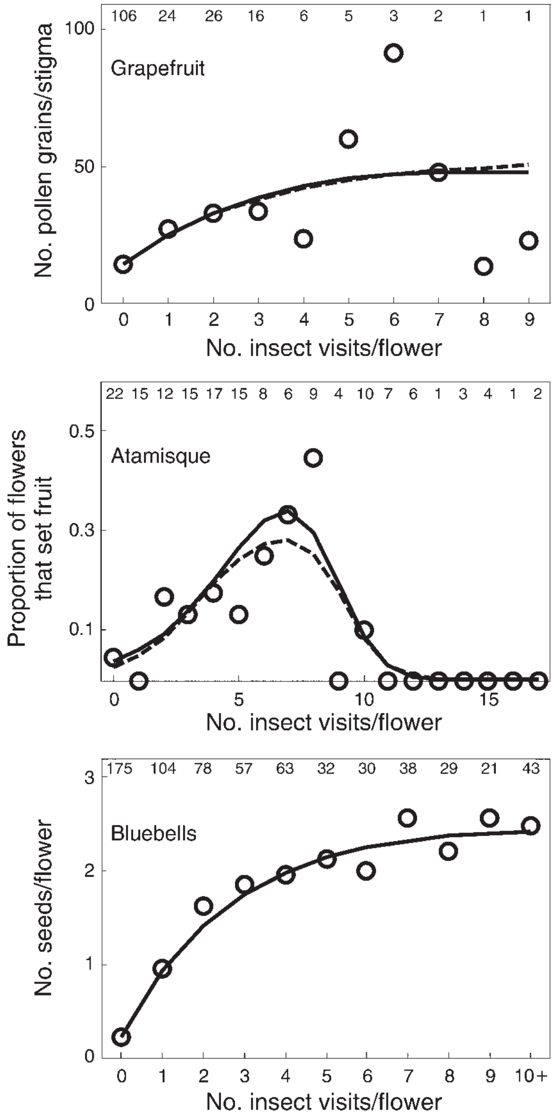

FIG. 3. Net-benefit curves for female reproductive success of three plants in typical pollination mutualisms. Circles represent the data (among-flower means are shown for grapefruit and bluebells). Numbers at the top of each panel indicate the number of flowers that received each number of insect visits. Curves represent the predictions of all models with ΔAIC $\leq$ 2. For grapefruit, the simple saturating (solid line) and unimodal (dashed line) models shared the lowest AIC. For atamisque, a model with sigmoidal benefit and cost curves with the same asymptote (solid line) had the lowest AIC, followed by the model with sigmoidal cost and benefits curves with different asymptotes (dashed line, ΔAIC = 1.97). For bluebells, the simple saturating model outperformed all others. AIC values and parameter estimates for all models are in Appendix C: Table C2.

the simple unimodal model (ΔAIC = 4.07) and the simple saturating net-benefits model (ΔAIC = 7.41). The best-fit versions of all models (except the simple saturating net-benefit model) showed peak fruit set at intermediate visit numbers (Appendix C: Table C2).

For bluebells, seeds per flower strictly increased over the observed range of visit numbers (Fig. 3), and the model with the lowest AIC was the simple saturating net-benefits model (indeed, all best-fit model versions, except the simple unimodal model, showed a saturating pattern; Appendix C: Table C2,). No other model had ΔAIC $\leq$2. Unlike for grapefruit and atamisque, for bluebells we could easily distinguish visits that could have benefits and costs ("legitimate" visits) from visits that could only have costs and no benefits ("robbing" visits). To look for a cost of robbing visits (which we reiterate is not necessarily the same as the cost of legitimate visits), we asked if a flower that received a given number of *legitimate* visits produced fewer seeds if it had also received robbing visits. We did so by fitting two models with saturating net benefits (and a beta-binomial probability distribution), one of which assumed all flowers had the same expected seed production whether robbed or not (four parameters, including the overdispersion parameter) and the other of which allowed unrobbed and robbed flowers to follow different curves (seven parameters; see details in Appendix C: Table C3). The best-fit net-benefit curve for robbed flowers lay mostly below the curve for unrobbed flowers (Fig. 4). Despite having more parameters, the model in which robbed and unrobbed flowers differed was clearly favored over the simpler model (which had ΔAIC = 15.35). The maximum-likelihood estimate of the *y* intercept was higher for robbed than unrobbed flowers, but the estimated asymptote was higher for unrobbed flowers (Fig. 4; Appendix 3: Table C3).

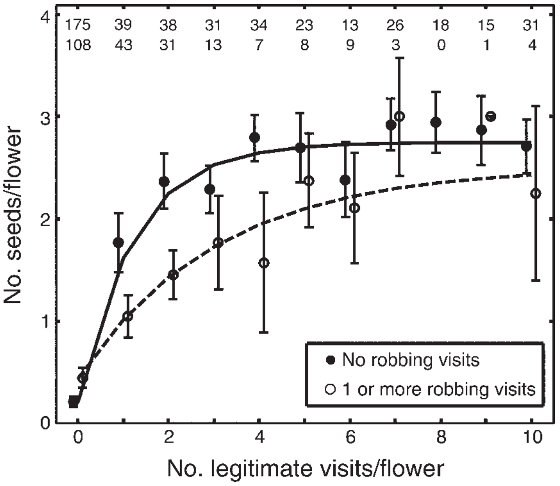

FIG. 4. For a given number of legitimate visits, bluebell flowers that also received robbing visits produced fewer seeds than did flowers that were only visited legitimately. Data are means ± SE. Curves are the best-fit simple saturating net-benefit model in which robbed and unrobbed flowers have different parameters (see maximum-likelihood parameter estimates and AIC values in Appendix C: Table C3). The numbers at the top are numbers of unrobbed (first row) and robbed (second row) flowers that received each number of visits.

DISCUSSION

For atamisque, we found that a flower's contribution to the plant's female reproduction was clearly highest at an intermediate number of insect visits, for bluebells net benefits were clearly saturating, and for grapefruit the results were inconclusive. For bluebells, we also found evidence of a cost of one type of interaction, robbing visits (Fig. 4). At the least, these results indicate that the relationship between net benefit and interaction frequency may often be highly nonlinear, not linear as has often been assumed in previous work, including some of our own (Vázquez et al. 2005). We close by discussing the implications of these results for the nature of costs in typical pollination mutualisms, for the ecological and evolutionary dynamics of typical pollination mutualisms, and for how those dynamics may compare with those of better-studied pollinating seed–consumer mutualisms.

The nature of plant costs in typical pollination mutualisms

Although we have not measured costs explicitly, our results suggest that costs in typical pollination mutualisms are likely to be diverse. Grapefruit flowers with 8–9 visits had lower average stigmatic pollen loads than did flowers with 5–7 visits, suggesting that removal of previously deposited pollen may be a cost of visitation in this system, but sample sizes are small and more data are needed to distinguish whether the pattern is saturating or unimodal. Even if it does occur, a decline in stigmatic pollen load at high visit numbers will not necessarily result in reduced female reproduction, as flowers may still receive enough pollen of sufficiently high quality to achieve full seed set. Removal of stigmatic pollen may also contribute to declining fruit set in atamisque (although this seems unlikely given that the amount of pollen needed to fertilize the single ovule in each atamisque flower may be small), but it cannot explain the cost of nectar robbing seen in Fig. 4, because bumble bees do not contact the stigma while robbing bluebell flowers.

Rather, the most likely costs of robbing visits to bluebells, and perhaps for visits to atamisque as well, are the cost of damage inflicted by visitors and the cost of replenishing nectar. In bluebell flowers the proximity of the ovary to the location where bumble bees chew holes in the corolla and to the nectaries that robbers probe vigorously with their tongues may make the ovary susceptible to robbing damage (cf. Traveset et al. 1998), and the atamisque ovary is elevated on a stalk, potentially exposing it to damage by visitors foraging for rewards. At present, we do not know how the cost of nectar production in bluebells or atamisque compares to that measured for other plants (see references in *Introduction*, above). Alternatively, removal of nectar by robbers may cause subsequent legitimate visits to the same flower to be shorter (because there is less reward to be removed), thus reducing the quality of those legitimate visits (cf. Irwin and Brody 1999). We also cannot rule out a greater risk of infection by pathogens or nectar-inhabiting yeasts or greater pollen competition as a possible negative consequence of a high number of visits to atamisque or bluebell flowers. In a preliminary study, we have found that nectar in atamisque flowers exposed to insect visits is more likely to contain yeast than is nectar from unvisited, bagged flowers (Mariana Combina and Cecilia Rojo, *personal observation*).

Evidence for a significant cost of nectar robbing to bluebells presented here conflicts with the lack of a difference in seed production between robbed and unrobbed flowers in an experiment reported by Morris (1996). In that earlier experiment, floral tubes were covered with plastic collars that prevented robbing or with sham collars that allowed bumble bees to rob, and the collars were left in place for each flower's lifetime. These two results might be reconciled if the cost of robbing declines with the number of legitimate visits, as the convergence of the two curves in Fig. 4 suggests. Because collared flowers in the earlier experiment were exposed to visitors for longer than were flowers in the current experiment, a high number of legitimate visits may have reduced the cost of robbing. Nevertheless, the current results suggest that in years when legitimate visits are scarce, nectar robbing may impose significant costs to bluebells.

Note that several of the likely costs in typical pollination systems that we have discussed differ in nature from the cost to plants that have co-evolved with pollinating seed parasites. Most of the latter species, including yuccas and figs, do not produce floral nectar (but see Holland and Fleming 1999), so costs of nectar production and infection by nectar-fermenting yeasts are at present irrelevant to these plants, although Pellmyr and Leebens-Mack (2000) have argued that the water-saving advantage of not having to produce nectar in an arid environment may have favored the initial association of yuccas with pollinating seed consumers, which need not be attracted by nectar. It is also unlikely that pollen removal from stigmas is a significant cost in obligate pollinating seed–consumer mutualisms, because it is in the interest of the insect to actively pollinate flowers to ensure the availability of seeds for their offspring to consume. In turn, the principal cost to plants such as yuccas and figs (i.e., reduced seed production due to consumption by pollinator larvae) is irrelevant to most pollination mutualisms.

A future challenge is to better identify and quantify costs in typical pollination mutualisms. Costs of reward production and infection by pathogens have been measured for some systems (see *Introduction*, above). Interestingly, one type of cost—damage to floral structures—has been measured successfully for visits by nectar robbers (McDade and Kinsman 1980, Galen 1983, Traveset et al. 1998), but we have not found examples where this has been attempted for legitimate visitors. Because costs may be more subtle than consumption of yucca or fig seeds by pollinator larvae, a valuable task is to develop methods to disentangle the underlying benefit and cost curves without measuring costs directly. For example, we might first hand-pollinate flowers in such a way as to ensure full reproductive success (which we realize is easier said than done; Young and Young 1992, Aizen and Harder 2007) and then expose them to different numbers of visits (cf. Anstett et al. 1996). Because these flowers would have received full benefits via hand pollination, visits would only impose costs. Thus the absolute difference between the maximum net benefit estimated from flowers that were hand pollinated only and the net-benefit curve estimated from flowers that were both hand pollinated and visited would provide a measure of the cost curve.

Ecological implications of net-benefit curves

At a fixed plant density the mean number of visits per flower will likely increase as pollinator density increases. Saturating patterns of female reproduction vs. visit number suggest that, all else being equal, plant recruitment will be positively related to pollinator density when that density is low but density independent thereafter, thus limiting the degree to which plant density is augmented by pollination mutualism (cf. Holland et al. 2002: Fig. 2). In contrast, unimodal patterns of female reproduction, driven by visitation costs that come to equal or exceed its benefits, may cause plant recruitment, and consequently plant density, to decline from a peak as pollinator abundance increases, which could then generate negative feedback to pollinator populations. Our case studies provide one example (atamisque) of a unimodal pattern, previously discussed mainly in the context of pollinating seed–consumer mutualisms, in a typical pollination mutualism.

An important outstanding question is how often plants in typical pollination mutualisms exhibit saturating, unimodal, or other, net-benefit patterns. Surprisingly few studies have manipulated visit numbers to flowers and measured their reproductive success, although other studies have varied the time of floral exposure rather than number of visits per se. In Appendix D: Table D1 we list all studies of both types that we have found. For typical pollination mutualisms, the most common outcome appears to be a saturating pattern of reproductive success vs. number of visits or time of exposure, followed by a linear increase over the range of visits or time observed. However, Young (1988) did find in one of two years that seed production by *Dieffenbachia longispatha* reached a maximum when flowers received an intermediate number of beetle visits. In contrast, the two studies (both of figs) that presented net-benefit curves for pollinating seed–consumer mutualisms found a unimodal pattern. Thus the studies in Table D1 suggest that unimodal patterns can occur in both typical and pollinating seed–consumer mutualisms, but that they may be more common in the latter. Clearly, more such studies are needed before this hypothesis can be better assessed.

Evolutionary implications of net-benefit curves

Declining plant reproduction at high visit numbers will generate selection for plant traits (e.g., short floral lifespan or selective abortion of damaged or infected flowers) that prevent or limit the impact of excess visits. However, as has been emphasized in the floral longevity literature (Ashman and Schoen 1994), for perfect flowers the optimum number of visits will be determined by both female and male fitness, which may not accrue at the same rate with the number of visits (Mitchell and Waser 1992, Wilson 1995*a*, *b*). In their model, Ashman and Schoen (1994) assumed that both male and female fitness are saturating functions of floral life span, but that maintenance costs increasing linearly with life span produce an optimum floral longevity. Unimodal female fitness curves (Fig. 3; Young 1988) should select for shorter floral life spans than would saturating curves (also see Shykoff et al. 1996), unless male fitness continues to increase substantially after female fitness peaks.

Here, we have considered benefits and costs to be functions of the number of interactions, rather than time of flower exposure. Visit number and exposure time are likely to be correlated, but not necessarily perfectly, and visitor-imposed benefits and costs to both female and male reproductive success are more likely to be related to the number of visits than to exposure time per se (although the value of a visit may depend on when in a flower's lifetime it occurs should stigma receptivity or pollen viability change as flowers age). Moreover, when the number of visits varies among flowers and the success curve has a negative second derivative over the range of visits, the realized average per flower success will be lower than the height of the curve at the average number of visits (via Jensen's inequality; Richards et al. 2009). Thus variation in visit number among a plant's flowers, even if all flowers remain open for the same length of time, can influence whole-plant reproductive success. Quantifying visit number is more tedious than simply varying exposure time, but the ability to distinguish the effects of visitor-imposed costs from time-based (e.g., maintenance or aging) costs may justify the extra effort.

In our studies and nearly all of those in Appendix D: Table D1, fitness components were measured for single flowers on multi-flowered plants, yet selection on floral traits will operate at the level of whole-plant fitness. In principle, we could compute whole-plant fitness by integrating per flower net-benefit curves for female and male fitness over the distribution of visit numbers per flower. But in practice the fitness contribution of a flower that receives a given number of visits may depend in complex ways on the number and spatial distribution of visits to other flowers on the plant, as a flower's female fitness may be influenced by the plant's allocation of resources among flowers and its male fitness may depend on where its pollen is deposited. Thus a remaining challenge is to measure whole-plant net-benefit curves (and underlying benefit and cost curves) in terms of the distribution of visits across all flowers on a plant.

Three other challenges also remain. First, although we have presented net-benefit curves as a function of the total number of visits, our study species are visited by multiple species, some of which may provide greater benefits or inflict greater costs than others. With more data, it may be possible to distinguish these visitor-specific effects by fitting models that allow the benefit and cost curves to differ among visitor taxa or functional groups (but at the cost of many more parameters to be estimated). Second, the same number of visits distributed over a short vs. a long interval of time, or in an early vs. late period in a flower's lifetime, may have different effects on net benefits (cf. Morris 1996, Castro et al. 2008). Finally, floral visitors will also experience benefits and costs of interacting with plants, and they may influence the optimum number of visits from pollinator's perspective. Thus benefit and cost curves for both plants and their floral visitors can provide a mechanism to link the consequences of individual interactions to the population and evolutionary dynamics of the interacting partners in typical pollination mutualisms.

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APPENDIX A

Underlying models that produce noninflected vs. sigmoidal benefit and cost curves (*Ecological Archives* E091-089-A1).

APPENDIX B

Likelihood methods to fit net-benefit curves (*Ecological Archives* E091-089-A2).

APPENDIX C

Ten net-benefit models, their AIC values, and maximum-likelihood parameter estimates (*Ecological Archives* E091-089-A3).

APPENDIX D

Studies of flower reproductive success vs. number of pollinator visits or exposure time (*Ecological Archives* E091-089-A4).