Limiting the costs of mutualism: multiple modes of interaction between yuccas and yucca moths

John F. Addicott and Tan Bao

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

In pollination–seed predation mutualisms between yuccas and yucca moths, conflicts of interest exist for yuccas, because benefits of increased pollination may be outweighed by increased seed consumption. These conflicts raise the problem of what limits seed consumption, and ultimately what limits or regulates moth populations. Although the current hypothesis is that yuccas should selectively abscise flowers with high numbers of yucca-moth eggs, within-inflorescence selective abscission occurs in only one out of the three moth–yucca systems that we studied. It occurs only when oviposition directly damages developing ovules, and does not, therefore, provide a general explanation for the resolution of moth–yucca conflicts. Within-locule egg mortality provides an alternative and stronger mechanism for limiting seed damage, and generating density-dependent mortality for yucca-moth populations. However, the most important feature of moth–yucca systems is that they are diverse, encompassing multiple modes of interaction, each with different consequences for limiting and regulating yucca moths.

Keywords: benefits; conflicts of interest; costs; pollination; seed predation; selective abscission

1. INTRODUCTION

One of the fundamental problems in the study of mutualism is to determine what processes affect the costs and benefits that hosts and visitors experience as a result of their interactions (Thompson 1982). Although mutualisms are interactions in which both hosts and visitors benefit, mutualists are not necessarily or even usually ‘cooperative’. Rather, conflicts of interest between hosts and visitors are inherent to many mutualistic interactions (Bronstein 1994) and affect whether a mutualism should arise in the first place (Axelrod & Hamilton 1981; Connor 1995; Roughgarden 1975) or what proportion of hosts or visitors should be mutualists or cheaters (Soberon & Martinez del Rio 1985).

Conflicts of interest between mutualists are most likely to occur where hosts invest in their visitors or visitors ‘purloin’ benefits from their hosts (Connor 1995), interactions in which there is a significant cost to hosts. With invested or purloined benefits, visitors should benefit from increased exploitation of their hosts, at least until visitors begin to compete for the host’s resources. Whether hosts would also benefit from increased exploitation by visitors depends upon the linkage between the costs and benefits of exploitation (Addicott & Tyre 1995). In pollination–seed predation mutualisms (Riley 1892; Bronstein 1992; Pellmyr 1989), increased visitation may quickly achieve complete fertilization of ovules, but exploitation of seeds may continue to rise, leading to decreased host fitness (Addicott & Tyre 1995; Herre & West 1997; but see Anstett *et al.* 1996). Given these conflicts of interests, can hosts prevent overexploitation? Do hosts ‘defect’ against visitors that overexploit them? Is it in visitors’ best short-term interests to limit how much they exploit their hosts? Are there other ecological processes that limit exploita-

tion or limit visitors to densities where overexploitation does not occur?

In this paper we address limits to the exploitation of hosts by visitors in pollination–seed predation mutualisms between yucca moths (*Tegeticula yuccasella* spp., *Incurvariidae*) and yuccas (*Yucca* spp., *Agavaceae*) (Riley 1892). Yuccas are obligately dependent on yucca moths for sexual reproduction (but see Dodd & Linhart 1994), with pollen collection and pollen transfer by female yucca moths being active rather than passive. Similarly, yucca moths are obligately dependent on yuccas, as yucca-moth larvae feed only on the reproductive tissues of yuccas (Riley 1892; Davis 1967). Female yucca moths may oviposit in and pollinate a single flower multiple times, and will visit tens of flowers on several inflorescences during their lifetimes (see Addicott & Tyre 1995).

Within-inflorescence selective abscission of flowers with high numbers of ovipositions is hypothesized to be a potent mechanism for limiting seed damage and therefore limiting conflicts of interest in pollination–seed predation mutualisms (Murray 1985; Bull & Rice 1991). The potential for within-inflorescence selective abscission is particularly strong in yuccas, because fruit production in most yuccas is resource limited (see, for example, Addicott 1985; Aker 1982). Many factors influence the fate of yucca flowers and the yucca-moth eggs contained therein. However, most discussions of limitation of seed damage and consequent regulation of yucca-moth populations focus on selective abscission of flowers with either inadequate pollination and/or high numbers of yucca-moth eggs (Fuller 1990; Pellmyr & Huth 1994; Richter 1995; Wilson & Addicott 1998).

In this paper we present a broader perspective on processes that might limit seed damage and limit or regulate yucca-moth populations. Specifically, we will

demonstrate the following. First, there are multiple modes of interaction between yuccas and yucca moths, depending upon the behaviour and morphology of moths and yuccas. Second, within-inflorescence selective abscission is associated with only some modes of interaction, and therefore cannot provide a general explanation for the limitation of seed damage. Third, within-locule egg mortality and differences among inflorescences in fruit morphology provide alternative or additional mechanisms for limiting seed damage. Fourth, unlike selective abscission, within-locule egg mortality is strongly density dependent and is, therefore, more likely to provide a mechanism for regulating populations of yucca moths.

2. METHODS

(a) Study systems

We studied interactions between two species of yucca (*Y. kanabensis* and *Y. baccata*) and three undescribed species of yucca moth in the *Tegeticula yuccasella* species complex (see Addicott 1996; Pellmyr *et al.* 1996). *Yucca kanabensis* has two species of pollinator, which we designate as being 'deep' and 'shallow' species (hereafter known as deeps and shallows), based on their morphology and oviposition behaviour (see Addicott 1996; Addicott & Tyre 1995; Wilson & Addicott 1998). Deepes have relatively long ovipositors and lay their eggs in the locular cavity. Shallows have relatively short ovipositors and lay their eggs in the surface of the carpel wall. The pollinators on *Y. baccata* belong to the deep group of species, but are morphologically distinct from the deeps of *Y. kanabensis* (Addicott 1996).

Our study sites for *Y. kanabensis* are in southern Utah, USA (for details see Addicott 1998; Addicott & Tyre 1995; Wilson & Addicott 1998). We studied *Y. baccata* at a site on the eastern edge of the Kaibab Plateau in northern Arizona (112°54'30" W, 36°53'30" N).

(b) Selective abscission

Abscission data for *Y. kanabensis* are based on detailed observations of all 1899 flowers from 24 inflorescences (see Addicott (1998) for details). For *Y. baccata* we observed all 1951 flowers from 33 inflorescences. For each abscised flower or developing fruit we counted numbers of oviposition marks. There is a 1:1 correspondence between oviposition marks and eggs (J. F. Addicott, unpublished data).

To test for population-level patterns of selective abscission, we conducted logistic regressions of flower fate (0=abscised, 1=retained) on numbers of ovipositions per flower. To allow for non-monotonic functions, we included both linear and inverse terms for the independent variable. We conducted these and all other analyses with SPSS 7.5 for Windows.

Small numbers of fruit per inflorescence preclude using logistic regressions to test for within-inflorescence selective abscission. Instead, we used *k* values (Varley *et al.* 1975) to estimate the mortality of yucca-moth eggs beyond that which would have occurred if abscission were completely random (see figure 2 for details). We used one-sample *t*-tests to determine whether *k* values were significantly different from zero.

(c) Egg and larval mortality

In 1997 we assessed egg and larval survivorship for deeps and shallows on *Y. kanabensis* by harvesting flowers 10 d after anthesis. We then counted oviposition marks and first-instar larvae

Figure 1. Retention (proportion of visited flowers retained as fruit) as a function of number of eggs per flower. (a) Deepes on *Y. kanabensis* from 1992 ($y = 1/(1 + e^{-(0.521 - 0.312x - 1.85/x)})$), for 1209 visited flowers and 66 fruit, $\chi^2 = 40.7$, d.f. = 2, $p < 0.001$). (b) Shallows on *Y. kanabensis* from 1992 ($y = 1/(1 + e^{-(2.76 + 0.0213x - 2.84/x)})$), for 827 visited flowers and 85 fruit, $\chi^2 = 20.7$, d.f. = 2, $p < 0.001$. (c) Deepes on *Y. baccata* from 1997 ($y = 1/(1 + e^{-(0.528 + 0.0142x - 7.31/x)})$), for 769 visited flowers and 200 fruit, $\chi^2 = 132.5$, d.f. = 2, $p < 0.001$. Symbol sizes are proportional to sample size. Lines represent logistic regressions of flower fate (0, abscised; 1, retained) on ovipositions per flower and the inverse of ovipositions per flower.

within each locule. We computed second-order nonlinear regressions of numbers of larvae on numbers of oviposition marks for both deeps and shallows. We do not consider egg and larval survivorship in *Y. baccata*, because most *Y. baccata* produce no larvae, regardless of the number of ovipositions (Addicott 1986; Bao & Addicott 1998).

3. RESULTS

(a) Limitation by yuccas: selective abscission

(i) Population patterns of selective abscission

At the population level, selective abscission of flowers with high numbers of yucca-moth eggs only occurs in one of the three interactions that we observed. Population patterns of selective abscission against flowers with high numbers of eggs occur for deeps on *Y. kanabensis* (figure

1a). For shallows on *Y. kanabensis* (figure 1b) and deeps on *Y. baccata*, flowers with high numbers of eggs per flower are less likely to abscise (figure 1c).

However, population patterns of selective abscission do not necessarily indicate that individual yuccas discriminate against flowers with high numbers of eggs. Population patterns of selective abscission can arise even in the absence of within-inflorescence selective abscission if proportions of flowers visited per plant: (i) vary among plants; (ii) are positively correlated with numbers of eggs per visited flower; and (iii) are negatively correlated with retention of visited flowers (J. F. Addicott, unpublished data).

(ii) Within-inflorescence selective abscission

Direct analysis of within-inflorescence selective abscission shows the same patterns observed at the population level. Within-inflorescence selective abscission occurs for deeps on *Y. kanabensis* ($k=0.62>0$, one-sample $t=5.38$, d.f.=20, $p<0.001$) with average selectivity reflecting retained fruit having just 0.24 times the number of eggs expected if abscission were completely random (figure 2). However, there is reverse selective abscission for both deeps on *Y. baccata* ($\bar{k}=-0.44<0$, one-sample $t=-8.81$, d.f.=31, $p<0.001$) and shallows on *Y. kanabensis* ($\bar{k}=-0.24<0$, one-sample $t=-2.32$, d.f.=20, $p=0.031$), with average selectivity values reflecting 2.78 times and 1.73 times the number of eggs in retained fruit that would be expected by chance. There are also obvious trends between k values and numbers of ovipositions for deeps on *Y. kanabensis* and *Y. baccata* (see figure 2). However, the most important pattern is that within-inflorescence selective abscission has the potential to either limit or exacerbate seed damage by yucca moths, depending on the mode of interaction between moth and yucca.

(b) Within-locule egg mortality

Egg and larval mortality within retained fruit could also limit seed consumption, assuming, of course, that larval mortality is not the direct result of overexploitation of seeds. On *Y. kanabensis* larval survivorship to the first instar is strongly density dependent within locules for both deeps ($y=0.249x-0.012x^2$, $F_{2,303}=127$, $p<0.001$) and shallows ($y=0.172x-0.0049x^2$, $F_{2,362}=117$, $p<0.001$) (figure 3). Regardless of numbers of eggs per locule, there is an effective and relatively low upper limit on the number of surviving first-instar larvae per locule. Since we examined survivorship at the first instar, this mortality is independent of any possible subsequent overexploitation of seeds. Moreover, because shallows feed in the carpel wall for their first two instars, there is absolutely no opportunity for mortality to be the result of the overexploitation of seeds.

4. DISCUSSION

Given conflicts of interest between yuccas and moths, individual yuccas would increase their fitness by defecting against yucca moths. Opportunities for defection exist because of the asynchrony between pollination and seed consumption. Individual yuccas can increase their short-term fitness by accepting the pollination services of yucca moths and subsequently facilitating the mortality of

Figure 2. Estimated k values for selective abscission per inflorescence as a function of the mean numbers of ovipositions per moth species per flower for deeps on *Y. kanabensis* in 1992 (filled squares), shallows on *Y. kanabensis* in 1992 (filled circles), and deeps on *Y. baccata* in 1997 (open squares). The k values provide a scaled estimate of the mortality between one life-history stage and another, and are computed as $\log_{10}(N_i/N_{i+x})$, where N_i is the number of individuals surviving to life-history stage i , and N_{i+x} is the number of individuals still alive x stages later. Here we computed k values for the estimated number of ovipositions expected in flowers if abscission were non-selective relative to the number of ovipositions observed in fruit: $\log_{10}(\text{eggs in flowers} \times \text{mean retention of visited flowers/eggs in fruit})$; k values would be positive or negative if there were the selective abscission of flowers with high or low numbers of ovipositions, respectively. In the absence of selective abscission or with selection for flowers with intermediate numbers of ovipositions, k values should be zero.

yucca-moth eggs and larvae. The opportunity for yuccas to defect stands in contrast to the limited opportunities for figs to defect against fig wasps (Addicott *et al.* 1990). A fig that decreases fig-wasp survival in the developing syconium would produce more seeds, thereby increasing its female reproductive success. However, it would simultaneously decrease its male reproductive success, because the adult female fig wasps emerging from a syconium are the vectors of pollen for that syconium.

Because fruit production in yuccas is usually resource limited (Addicott 1985), yuccas could increase their fitness by retaining those flowers that would produce the greatest number or quality of intact seeds. In addition, because each yucca-moth larva consumes approximately 5% of the ovules in a flower (Addicott 1986), yuccas would increase their fitness by selectively abscising flowers that would produce many yucca-moth larvae (Murray 1985; Bull & Rice 1991). Although most discussions of limits to seed damage in yuccas focus on selective abscission (Fuller 1990; Richter 1995; Pellmyr & Huth 1994; Wilson & Addicott 1998), selective abscission occurs in only one of our three systems.

Figure 3. Larvae per locule as a function of ovipositions per locule for *Y. kanabensis* in 1997: (a) deeps; (b) shallows. Symbol sizes are proportional to sample size. Solid lines are least-squares second-order regressions through the origin; the dotted lines represent the 1:1 relationship between larvae and ovipositions.

We now address two problems raised by our results. First, how general is within-inflorescence selective abscission as a mechanism limiting seed damage? We consider this problem in the context of why selective abscission occurs in some interactions but not others. Second, what are the consequences of within-inflorescence selective abscission and within-fruit egg mortality with respect to limiting seed consumption and regulating yucca-moth populations?

(a) Occurrence of selective abscission

Essential to understanding the limitation and regulation of the moth–yucca mutualism is the fact that there are multiple modes of interaction, which depend on morphological and behavioural variation among yucca moths and morphological variation among yuccas. Some yucca moths have relatively long ovipositors and oviposit within the intralocular cavity, whereas others have relatively short ovipositors and oviposit superficially in various floral tissues (Addicott 1996; Davis 1967). In addition, egg placement varies from the typical medial position in the ovary (Riley 1892), to the boundary between the ovary and style (Bao & Addicott 1998), to the style for some moths on *Y. elata* (J. F. Addicott, unpublished data), to the sepals for *Parategeticula pollenifera* on *Y. schottii* (Davis 1967). In turn, yuccas vary in carpel-wall thickness, and in whether the apex of the ovary contains viable or inviable ovules (Bao & Addicott 1998).

Given multiple modes of interaction, we hypothesize that selective abscission will occur only when oviposition

by yucca moths directly damages developing ovules. Deep ovipositions in the medial zone of the ovary damage 10–15% of the viable ovules per affected locule (Addicott 1986), leading to the constricted fruit that are characteristic of many yuccas (Addicott 1986; McKelvey 1938, 1947; Riley 1892; Ziv & Bronstein 1996). It is this pattern of oviposition that is associated with selective abscission in *Y. kanabensis* (figures 1a and 2), and *Y. filamentosa* (Pellmyr & Huth 1994). In contrast, oviposition by shallows never directly damages developing ovules or leads to constricted fruit, and on *Y. kanabensis* does not elicit selective abscission (figures 1b and 2).

The failure of deeps to elicit selective abscission on *Y. baccata* may at first appear to contradict our hypothesis. However, as first observed by McKelvey (1938) for *Y. faxoniana*, moths associated with some yuccas in the subgenus *Sarcocarpa* oviposit at the base of the style rather than in the medial portion of the ovary. Moreover, in these yuccas the apical-most ovules are not viable (Bao & Addicott 1998). Consequently, when these moths oviposit into *Y. baccata* flowers, they do not damage developing ovules (Bao & Addicott 1998), they do not cause constricted fruit (McKelvey 1938), and they do not induce selective abscission (see figures 1c and 2).

Two predictions follow from our hypothesis. First, the absence of selective abscission should not be restricted to the two systems that we studied. Rather, the absence of selective abscission should be widespread among moth–yucca interactions. We know of three other yuccas in which deeps do not damage ovules (*Y. arizonica*, *Y. carnerosana* and *Y. faxoniana*), and four other yuccas that interact with shallows (*Y. utahensis*, *Y. baileyi*, *Y. angustissima* and *Y. elata*). We also suspect that oviposition in long-styled yuccas in the subgenus *Chaenocarpa* (e.g. *Y. rostrata*) may not damage ovules. We predict that selective abscission should not occur in any of these interactions. Furthermore, among the 26 species of yucca recognized by McKelvey (1938, 1947), eight had ‘tapered’ fruit, two had symmetrical fruit and 11 had mostly symmetrical fruit. Only five typically had the asymmetrical (constricted) fruit that result from oviposition-induced damage to ovules. Therefore, the absence of selective abscission as a process limiting seed consumption may be very widespread among the yuccas.

Second, if our hypothesis is correct, then yuccas are making retention–abscission decisions based on proximate cues that, for shallows in *Y. kanabensis* and deeps in *Y. baccata*, are poor predictors of the probable number of mature, undamaged seeds per fruit. For *Y. kanabensis*, flowers with equivalent numbers of deep and shallow eggs should produce equivalent numbers of mature, viable seeds. Deeps produce slightly fewer larvae than shallows (see figure 3), but balancing this is the fact that deep oviposition damages some ovules directly and shallows feed in the carpel wall for two instars. However, even though deeps and shallows should cause approximately equivalent levels of damage, *Y. kanabensis* selectively abscises deeps but not shallows (see figures 1 and 2). In addition, when both yucca moths are present, *Y. kanabensis* discriminates against deeps in favour of shallows (Wilson & Addicott 1998; J. Csotonyi and J. F. Addicott, unpublished data). This suggests that in the absence of damage to developing ovules from the act of oviposition,

Table 1. Summary of the efficacy of different mechanisms for limiting seed damage for different modes of interaction in moth–yucca mutualisms

(For each mode of interaction and source of mortality, ‘yes’ and ‘no’ indicate that the source of mortality does or does not operate. DD, DI and IDD indicate that mortality is density dependent, density independent, and inverse density dependent, respectively.)

mode of interaction			mechanisms limiting seed damage				
egg placement	damage to ovules	inviabile ovules in apex of ovary	modified moth oviposition behaviour	within-locule egg mortality	within-inflorescence selective abscission	between-inflorescence differences in visitation	between-inflorescence differences in fruit morphology
(a) deep-medial	yes	no	no (or weak)	yes (DD)	yes (DD)	yes (weak)	no
(b) shallow	no	no	no (or weak)	yes (DD)	yes (but IDD)	yes (weak)	no
(c) deep-apical	no	yes	no (?)	yes (but DI?)	yes (but IDD)	yes (weak)	yes (but DI)

yuccas do not obtain reliable information on the probable production of viable seeds per fruit.

(b) Other mechanisms for limiting seed consumption

If selective abscission is not general to moth–yucca mutualisms, then what other processes could limit seed consumption? Moths could restrict oviposition in flowers that already have eggs in them so as to avoid intraspecific larval competition for seeds (Aker & Udovic 1981; James *et al.* 1994). However, yucca moths show little, if any, tendency to modify their oviposition behaviour in response to previous ovipositions (Wilson & Addicott 1998; Addicott & Tyre 1995), and the number of eggs per flower can be very high (see figure 1). This observation suggests that, in contrast to insects that adjust their behaviour to previous ovipositions (see, for example, Roitberg & Prokopy 1987), the sequence of oviposition is relatively unimportant for yucca moths.

Another possible limiting mechanism is egg and/or larval mortality within flowers. Both yucca moths associated with *Y. kanabensis* show strong density-dependent egg and larval mortality within locules (see figure 3), mortality that very effectively limits seed consumption. On average, fewer than one deep or fewer than two shallow larvae feed in any locule regardless of the number eggs per locule (see figure 3). Although it would still be in the short-term interests of yuccas to have no larvae consuming their seeds, this number of larvae per locule would leave 56–82% of seeds intact (Addicott 1986). It is unlikely that yuccas generate this egg and larval mortality. We suspect that deeps suffer inadvertent cannibalism within locules. In addition, caging individual fruit significantly increases the egg survivorship of shallows (T. Bao, unpublished data). This result suggests that moth–plant interactions are not the primary determinants of within-flower mortality.

Limitation of seed damage in *Y. baccata* is associated primarily with variation between inflorescences in flower and fruit morphology, and egg mortality is clearly plant-driven (Bao & Addicott 1998). Over 70% of *Y. baccata* individuals have fruit from which no larvae emerge, regardless of the number of ovipositions. These individuals have reduced ovaries, in which the apical-most 50% or more of ovules are inviable. Eggs laid in these reduced ovaries almost invariably perish and seed

damage is essentially nil. In the remainder of the population, reduction of the ovary is much less pronounced, and some larvae survive (Bao & Addicott 1998).

Finally, limits to seed damage in the population as a whole can arise from differences among inflorescences in proportions of flowers visited, numbers of ovipositions per flower, and retention of visited flowers (see above).

Therefore, at least five different processes could limit seed damage within inflorescences or limit seed consumption in the population as a whole (see table 1). However, no single mechanism operates consistently and strongly among the three interactions we studied. In particular, in shallows on *Y. kanabensis* and deeps on *Y. baccata* within-inflorescence selective abscission would increase rather than decrease seed predation.

(c) Consequences of different modes of interaction

If densities of moths relative to flowers change from year to year (see, for example, Addicott 1998), will the intensity of mortality imposed by these processes change in a density-dependent manner, thereby facilitating the regulation of yucca-moth populations? To address this question, one must appreciate the distributed nature of interactions among yuccas and moths. Interactions occur at the levels of locules, flowers–fruit, and inflorescences, but density-limiting processes at any particular level need not necessarily translate into population-level density dependence.

Within-inflorescence selective abscission could generate density dependence at the population level, particularly if there is a fixed upper threshold for numbers of eggs per flower that yuccas will retain. Not only would seed consumption be limited within inflorescences, but as moth densities increased the number of emerging larvae would not increase. However, if retention of flowers with a given number of ovipositions is contingent on the distribution of numbers of ovipositions on all other flowers within an inflorescence, then within-inflorescence selective abscission could occur but the number of eggs per retained flower could increase with moth density. Our studies of *Y. kanabensis* show that retention is highly contingent. Under field conditions, there is an apparent threshold of ten deep eggs per flower above which abscission is essentially certain (see, for example, figure 1a). However, under experimental conditions, this ‘threshold’ shifts to more than 20 eggs per flower (Wilson & Addicott

1998) and with very high oviposition levels, *T. kanabensis* can retain flowers with 30–50 deep eggs. Therefore, if there is an upper threshold for retention, it is very high, and selective abscission is unlikely to induce strong, population-level density dependence.

In contrast, within-locule egg mortality does not appear to be contingent on the number of eggs in other locules or other fruit. As moth densities increase and numbers of eggs per visited flower increase, numbers of surviving larvae per fruit should remain essentially constant (see figure 3). Therefore, density-dependent within-locule egg mortality is likely to induce strong density dependence at the population level.

(d) **Conclusions**

We believe that the key to understanding the ecology and evolution of moth–yucca interactions will be in appreciating their diversity and complexity. The multiple modes of interaction among moths and yuccas generate different sources of mortality, with different consequences for limiting seed damage and regulating moth populations (see table 1). There are, in addition, major variations around the fundamental theme of pollination service in exchange for seed predation (Addicott 1996; Addicott & Tyre 1995; Aker & Udovic 1981; Bao & Addicott 1998; Dodd & Linhart 1994; Pellmyr *et al.* 1996). Such variation provides a wealth of opportunities for exploring both the evolutionary and the ecological dynamics of moth–yucca interactions.

This paper is dedicated to Fredrick T. Addicott for his long-standing interest in both the physiology and natural history of abscission. Drew Tyre and James Davies provided assistance in the field. We appreciate the helpful comments of Stuart West and two anonymous reviews on earlier versions of this paper. The work was partially supported by a grant from Natural Sciences and Engineering Research Council of Canada.

REFERENCES

- Addicott, J. F. 1985 Competition in mutualistic systems. In *The biology of mutualism: ecology and evolution* (ed. D. H. Boucher), pp. 217–247. London: Croom Helm.
- Addicott, J. F. 1986 Variation in the costs and benefits of mutualism: The interaction between yuccas and yucca moths. *Oecologia* **70**, 486–494.
- Addicott, J. F. 1996 Cheaters in yucca/moth mutualism. *Nature* **380**, 114–115.
- Addicott, J. F. 1998 Regulation of mutualism between yuccas and yucca moths: population level processes. *Oikos* **81**, 119–129.
- Addicott, J. F. & Tyre, A. J. 1995 Cheating in an obligate mutualism: how often do yucca moths benefit yuccas. *Oikos* **72**, 382–394.
- Addicott, J. F., Bronstein, J. & Kjellberg, F. 1990 Evolution of mutualistic life-cycles: yucca moths and fig wasps. In *Insect life cycles: genetics, evolution and co-ordination* (ed. F. Gilbert), pp. 143–161. London: Springer-Verlag.
- Aker, C. L. 1982 Spatial and temporal dispersion patterns of pollinators and their relationship to the flowering strategy of *Yucca whipplei* (Agavaceae). *Oecologia* **54**, 243–252.
- Aker, C. L. & 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.
- Anstett, M.-C., Bronstein, J. L. & Hossaert-McKey, M. 1996 Resource allocation: A conflict in the fig/fig wasp mutualism? *J. Evol. Biol.* **9**, 417–428.
- Axelrod, R. & Hamilton, W. D. 1981 The evolution of co-operation. *Science* **211**, 1390–1396.
- Bao, T. & Addicott, J. F. 1998 Cheating in mutualism: Defection of *Yucca baccata* against its yucca moths. *Ecol. Lett.* **1**, 155–159.
- Bronstein, J. L. 1992 Seed predators as mutualists: Ecology and evolution of the fig/pollinator interaction. In *Insect–plant interactions* (ed. E. B. Bernays), pp. 1–43. Boca Raton, FL: CRC Press.
- Bronstein, J. L. 1994 Our current understanding of mutualism. *Q. Rev. Biol.* **69**, 31–51.
- Bull, J. J. & Rice, W. R. 1991 Distinguishing mechanisms for the evolution of co-operation. *J. Theor. Biol.* **149**, 63–74.
- Connor, R. C. 1995 The benefits of mutualism: a conceptual framework. *Biol. Rev.* **70**, 427–457.
- Davis, D. R. 1967 *A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae)*. United States National Museum Bulletin no. 255, pp. 1–170.
- Dodd, R. J. & Linhart, Y. B. 1994 Reproductive consequences of interactions between *Yucca glauca* (Agavaceae) and *Tegeticula yuccasella* (Lepidoptera) in Colorado. *Am. J. Bot.* **81**, 815–825.
- Fuller, O. S. 1990 *Factors affecting the balance of co-operation and conflict between the yucca moth, Tegeticula yuccasella and its mutualist, Yucca glauca*. PhD thesis, University of New Mexico.
- Herre, E. A. & West, S. A. 1997 Conflict of interest in a mutualism: documenting the elusive fig wasp-seed trade-off. *Proc. R. Soc. Lond. B* **264**, 1501–1507.
- James, C. D., Hoffman, M. T., Lightfoot, D. C., Forbes, G. S. & Whitford, W. G. 1994 Fruit abortion in *Yucca elata* and its implications for the mutualistic association with yucca moths. *Oikos* **69**, 207–216.
- McKelvey, S. D. 1938 *Yuccas of the Southwestern United States*. 1. Jamaica Plain, Massachusetts: The Arnold Arboretum of Harvard University.
- McKelvey, S. D. 1947 *Yuccas of the Southwestern United States*. 2. Jamaica Plain, Massachusetts: The Arnold Arboretum of Harvard University.
- Murray, M. G. 1985 Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol. J. Linn. Soc.* **26**, 65–81.
- Pellmyr, O. 1989 The cost of mutualism: interactions between *Trollius europaeus* and its pollinating parasites. *Oecologia* **78**, 53–59.
- Pellmyr, O. & Huth, C. J. 1994 Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**, 257–260.
- Pellmyr, O., Leebensmack, J. & Huth, C. J. 1996 Non mutualistic yucca moths and their evolutionary consequences. *Nature* **380**, 155–156.
- Richter, K. S. 1995 *The pollination of Yucca whipplei by Tegeticula maculata: the benefits and costs of an obligate mutualism*. PhD thesis, University of California, Irvine.
- Riley, C. V. 1892 The yucca moth and yucca pollination. *A. Rep. Missouri Bot. Gard.* **3**, 99–159.
- Roitberg, B. D. & Prokopy, R. J. 1987 Insects that mark host plants. *BioScience* **37**, 400–406.
- Roughgarden, J. 1975 Evolution of marine symbiosis—a simple cost-benefit model. *Ecology* **56**, 1201–1208.
- Soberon, J. & Martinez del Rio, C. 1985 Cheating and taking advantage in mutualistic associations. In *The biology of mutualism* (ed. D. H. Boucher), pp. 192–216. London: Croom Helm.
- Thompson, J. N. 1982 *Interaction and coevolution*. New York: John Wiley & Sons.
- Varley, G. C., Gradwell, G. R. & Hassell, M. P. 1975 *Insect population ecology: an analytical approach*. Oxford: Blackwell.
- Wilson, R. D. & Addicott, J. F. 1998 Regulation of mutualism between yuccas and yucca moths: is oviposition behavior responsive to selective abscission of flowers? *Oikos* **81**, 109–118.
- Ziv Y. & Bronstein, J. L. 1996 Infertile seeds of *Yucca schottii*: a beneficial role for the plant in the yucca yucca moth mutualism. *Evol. Ecol.* **10**, 63–76.