

A.K. Brody · S.I. Morita

A positive association between oviposition and fruit set: female choice or manipulation?

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Abstract The relationship between where a female chooses to oviposit and her larvae's performance at those sites is critical to both the ecology and evolution of plant-insect interactions. For predispersal seed predators that do not themselves pollinate their host and whose larvae are sessile, females must be able to predict which flowers will ultimately be pollinated and set fruit, or be able to manipulate flowers in some way to ensure they set fruit. Otherwise, their offspring will perish. Here we describe the results of an experiment in which we tested if female *Hylemya* (Diptera: Anthomyiidae) are choosing oviposition sites wisely, or if they are manipulating flowers of their host, *Ipomopsis aggregata* (Polemoniaceae), in some way to ensure fruit set. Previous work in this system established a positive correlation between oviposition and fruit set. By bagging females on flowers, we removed their ability to choose flowers on which to oviposit. We found that flowers females oviposited on, whether bagged ("no choice") or unbagged ("female choice"), had a significantly higher probability of setting fruit than "control" flowers that we bagged but did not cage females on. In addition, we tested if *Hylemya* prefer particular architectural locations of flowers and if those locations correspond with higher than average fruit set. Although flowers at the distal end of the plant, and those most proximal to the main stem, were more likely to set fruit overall, *Hylemya* was no more likely to oviposit on those flowers than others on the plant. Taken together, our results suggest that *Hylemya* is somehow able to manipulate its host to ensure fruit set and thus the provisioning of their larvae.

Key words Predispersal seed predators · Female choice · *Hylemya* · Plant-animal interactions · *Ipomopsis aggregata*

Introduction

The relationship between oviposition choices made by a female insect and her larvae's performance at those sites is critical to fitness and should experience strong selection (Thompson 1988). For sessile larvae in particular, the choices made by ovipositing females are important: progeny either prosper or perish depending on their mother's choice of an adequate site. But do females choose wisely? Sometimes they do (Ahman 1985; Forsberg 1987; Singer et al. 1988; Craig et al. 1989; Carr et al. 1998; Steinbauer et al. 1998), and sometimes they do not (Chew 1977; Karban and Courtney 1987; Courtney and Kibota 1990; Larsson and Strong 1992; Burstein and Wool 1993; Larsson et al. 1995). The mechanisms governing choices made by ovipositing insects are often unclear, but traits such as host chemistry, morphology and phenology may be important to female choice (reviewed by Bernays and Chapman 1994).

Interactions with conspecifics, or even among ovipositing females and other plant visitors such as pollinators or other herbivore species, may be equal to host plant characters in determining larval success (Luft and Paine 1997; Onyabe and Roitberg 1997; Schroeder 1997; Bronstein et al. 1998; McClure et al. 1998). Such indirect interactions are critical for pre-dispersal seed predators that do not pollinate their hosts: flowers on which females oviposit must be visited by pollinators to set seed and thereby provide larvae a food resource. Although many pre-dispersal seed predators lay eggs in or on seeds themselves (e.g., Mitchell 1975; Moegenburg 1996; Desouhant 1998; McClure et al. 1998), some lay eggs prior to the flower's being pollinated. Leaving aside those that effect pollination themselves, such as yucca moths and fig wasps (Aker and Udovic 1981; Addicott 1986; Addicott et al. 1990), ovipositing females that do

A.K. Brody (✉)
Department of Biology,
University of Vermont, Burlington, VT 05405, USA
e-mail: akbrody@zoo.uvm.edu

A.K. Brody · S.I. Morita
Rocky Mountain Biological Laboratory,
PO Box 519, Crested Butte, CO 81224, USA

S.I. Morita
Department of Biology, University of California,
Riverside, CA 92521, USA

not pollinate their hosts must be able to “predict” which flowers will subsequently attract pollinators and which will be most likely, if pollinated, to set seed. Alternatively, females could “bet hedge” that by ovipositing on several flowers on different plants, some will be visited and set seed; however such a strategy could potentially be quite wasteful.

For most hermaphroditic plants, not all flowers are likely to be pollinated and many flowers, even if pollinated, do not set seed (Stephenson 1981). Resource allocation may vary among modules of a given plant (reviewed by Watson and Casper 1984; Diggle 1995) thus affecting whether any particular flower sets seed. Given that there may be within-plant differences among flowers in their value to an ovipositing seed predator and her larvae, how do ovipositing females choose where to lay their eggs? Do they treat the inherently variable world as uniformly attractive, or choose “wisely” to enhance the success of their offspring? Alternatively, might females or their offspring manipulate the host plant so as to enhance the resources available for larval growth (Brody and Waser 1995)? Host manipulation to the insect’s benefit has received considerable attention for galling insects (reviewed by Abrahamson and Weis 1987 and Weis et al. 1988), but to our knowledge has not been examined for pre-dispersal seed predators outside of our study system (Brody and Waser 1995).

Here we explore the positive relationship between oviposition choices made by *Hylemya* and fruit set of one of its hosts, *Ipomopsis aggregata*, in the mountains of western Colorado. Previous work demonstrated that flowers chosen as oviposition sites were more likely to set seed than those on the same plant that flies did not oviposit on (Brody 1992b; Brody and Waser 1995). Females do not pollinate the flowers on which they lay eggs, and the larvae do not appear to manipulate the plant. Experimental removal of eggs (before the larvae hatched) had no effect on the correlation between oviposition and fruit set (Brody and Waser 1995). In the experiments reported on here, we address the remaining possibilities. We hypothesize that either female flies are good at choosing flowers that will ultimately be pollinated and set seed, or they are able to manipulate flowers in such a way as to ensure they set fruit. Because a flower’s fate may, in part, be due to its position within the plant (Diggle 1995), and plant architecture can affect resource allocation to particular parts of a plant (Larson and Whitham 1997), we also examined the hypothesis that a flower’s location governs fruit set, and by choosing flowers in particular locations that are most likely to set seed, *Hylemya* are able to maximize their offspring’s success.

Materials and methods

The study organisms

Hylemya sp. (Diptera: Anthomyiidae) preys upon the seeds of *I. aggregata*, and confamilial *Polemonium foliosissimum* near the Rocky Mountain Biological Laboratory (RMBL), Crested Butte,

Colorado. Females lay their eggs under the sepals of elongating buds and recently opened flowers of *I. aggregata*. Eggs are most often laid singly and hatch in approximately 10 days (S.I. Morita, unpublished data). The larva then enters the fruit through the carpel wall and usually consumes all of the developing seeds (Zimmerman 1980; Brody 1992a, 1992b; Brody and Waser 1995). If successful, the larva makes an exit hole and falls to the ground to overwinter as a pupa (Zimmerman 1979, 1980).

Hylemya’s most common host plant at the RMBL, *I. aggregata*, is a monocarpic perennial, that inhabits relatively xeric slopes, and produces numerous red, tubular flowers on a paniculate inflorescence (Waser 1978). The flowers are protandrous, remaining in male phase for 1 or more days, before the stigmas become receptive (Campbell 1991). Plants live for 2–7 years or more, flower once, and then die (Waser and Price 1989). *I. aggregata* is self-incompatible, and thus all seeds are the result of one or more pollination events. The primary pollinators of *I. aggregata* at and around the RMBL are broad-tailed (*Selasphorus platycercus*) and rufous (*S. rufus*) hummingbirds (Waser 1978). *Hylemya* do not pollinate *I. aggregata* flowers (A.K. Brody, personal observation). Therefore, females require pollinators to visit the flowers on which they have oviposited for their larvae to be provisioned with food – i.e., seeds.

Choice or manipulation experiment

To determine if female *Hylemya* choose flowers that have a high probability of setting seed, or somehow manipulate flowers to ensure they set fruit, we removed females’ choice of flowers by caging flies on flowers that we chose randomly. Our experimental design was as follows. We chose two, fully elongated *I. aggregata* buds without *Hylemya* eggs over which we placed individual cages. We chose buds that were within 1 day of opening and thus near the maximum stage of development acceptable to free-flying female *Hylemya* (A.K. Brody, unpublished data). Cages consisted of 3”x2” cylindrical mesh bags which were held open and away from the bud by a thin wire and sealed at both ends with Velcro tape. We randomly assigned the two buds to one of two treatments. In one bag, we placed a female *Hylemya* caught in the same area. The other served as the “bagging control”, in which the bud was bagged for the same period of time but no fly was placed in the bag. We allowed females to remain in the bags for 24 h and then censused the (now open) flower for a newly laid egg. We removed the bags from both flowers and marked the calyces with a small dot of non-toxic, acrylic paint to designate the treatment and whether or not an egg had been laid. In addition to marking flowers with eggs, we marked flowers that females had “rejected” (i.e., buds on which females had been bagged but did not lay an egg) with a distinctive color. Doing so allowed us to assess whether these same flowers became acceptable to other, free-flying females after the bags were removed. At the time of bag removal, we located a similarly staged, unbagged flower on the same plant that a female had freely chosen as an oviposition site and marked it as well. Thus we had flowers in three treatments on each plant: (1) “bagged, no choice”; (2) “bagged, control”; and (3) “no bag, female choice”.

Our hypothesis was that if females chose flowers that are ultimately likely to be pollinated and set fruit, by caging them on flowers and removing their ability to choose, we would eliminate the previously found correlation between egg presence and fruit set. Alternatively, if females are somehow able to manipulate flowers to ensure they set fruit, “forcing” them to lay on bagged flowers should have no effect and the correlation would be upheld. In that case, flowers that the fly chose freely should be no different than those we forced them to oviposit on.

A total of 237 flies were caged on flowers at 2 different sites. The sites were approximately 1 km apart, both in dense populations of *I. aggregata* where *Hylemya* is common (A.K. Brody, personal observation). Of the 237 caged flies, 55 laid eggs within the allotted 24-hour period. However, 19 of these were later excluded (along with the “bagged control” and “female choice” flower of

the triplet) because the “bagged control” flower in the triplet was oviposited on after the bag had been removed. In all cases, eggs were removed before they hatched so that we could quantify subsequent seed production of fruits (i.e., without their being destroyed by larval seed predators). We collected all fruits just before they dehisced, and examined each fruit to determine if it set seed and counted the number of seeds per fruit. We analyzed the fruit set data using a chi-square analysis since the response variable (whether or not a flower set fruit) is categorical (Sokal and Rohlf 1995). We analyzed the average number of seeds per fruit using a randomized block design with plants treated as blocks, and choice treatment tested over the error term (Sokal and Rohlf 1995).

Effects of architecture and oviposition on fruit set

We made a detailed map of each plant and recorded the locations of flowers used as oviposition sites and which flowers set fruit. We used these maps to investigate whether flies chose specific locations on the plant for oviposition, and whether those choices were coincident with architectural or position effects on fruit set. For this experiment, we chose five plants in close proximity. All elongated buds and flowers were marked with a different-colored paint pen every 3–4 days, representing a flowering time block. Within a block, all buds and flowers with an *Hylemya* egg were also marked with a black Sharpie dot on the underside of the calyx. The positions of flowers with eggs were recorded on the maps. We collected all marked calyces at the end of the season and recorded whether or not the flower had set fruit and counted all seeds.

We examined the importance of egg and flower location on fruit set by dividing inflorescences horizontally into four sections that we called ranks (Fig. 1). Rank number 1 separated the apical

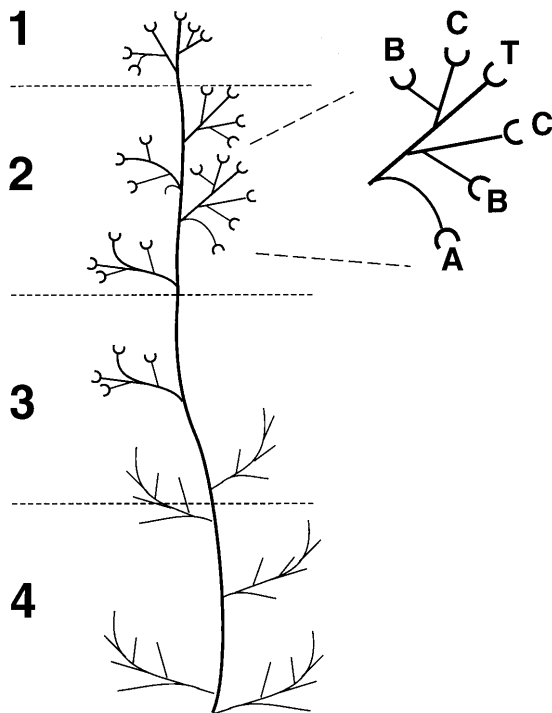


Fig. 1 A schematic, architectural map of *Ipomopsis aggregata*. The plants were divided into 4 horizontal ranks (1–4) and each cluster of flowers was divided based on the branching pattern from the main axis. Within a cluster of flowers, we designated the most proximal group A. After that, groups were labeled in alphabetical order up to C, with the most anatomically distal flower group labeled T for terminal

flowers from the rest of the plant, which were then divided into equal thirds and labeled ranks 2–4. The inflorescence is a panicle – that is, its main axis is terminated by a flower (Weberling 1989), and flowers are produced on numerous lateral cymes that flower over a period of ca. 5–7 weeks (Campbell and Halama 1993). In addition to examining the vertical position of flowers, we also labeled clusters of flowers based on their attachment to the main stem (Fig. 1). Within a cluster of flowers, or cyme, we labeled the most proximal group “A.” After that, groups were labeled in alphabetical order up to “C,” with the most anatomically distal flower group labeled “T” for terminal. However, only one plant had flowers in group “C” mature and set fruit; therefore we excluded this group from the final analyses and examined fruits from only groups “A,” “B,” and “T”.

We examined the effect of flowering phenology on: (1) the probability of being oviposited on, and (2) the probability of setting seed, using separate repeated measures analyses of variance with plants and time (the repeated, within-subject factor; see Winer 1971) as main effects. To do so, we only used the first five time blocks since not all plants produced flowers in blocks (weeks) 6–9. Percent of flowers with eggs and percent of flowers setting fruit were treated as separate response variables, and each was averaged over all flowers in a given time block within each plant. The resulting average percent fruit set or percentage of flowers with eggs was arcsin square-root transformed to improve normality. We examined if the architectural location affected the probability of being oviposited on or the probability of setting seed, using a randomized blocks ANOVA, with the percentage of flowers in each rank that were oviposited on and the percentage of flowers in each rank that set fruit as response variables (both were arcsin square-root transformed), and plant as the blocking factor, rank-tested over the block by rank interaction and cluster-tested over the error term. In addition, we tested if egg presence affected fruit set using a randomized blocks ANOVA, with the percentage of flowers setting fruit as the response variable, plant as blocks, rank, and egg presence or absence as an additional main effect that was tested over error term.

Results

Choice or manipulation experiment

There was no significant difference in fruit or seed set per-plant, or per-treatment, between the two sites, so data for each of the response variables were combined across the two sites. Bagging treatments (“no choice”, “female choice” and “bagged control”) on the same plant were considered replicates in the same block, for a final sample size of 28 plants each with a single set of 3 treatments. Eight plants had more than one set of treatments. Because flowers on the same plant are not independent, we excluded replicates of treatments on the same plant; however, those data are presented in Table 1 for completeness. The treatment effect was significant ($\chi^2=8.17$; $P=0.031$; Table 1). Flowers that we bagged females on, thus removing their choice (the “no choice” treatment), and flowers that were unbagged that females chose to oviposit on (the “female choice” treatment) were significantly more likely to set fruit than flowers not exposed to females and that were not used as oviposition sites (the “bagged control” flowers; Fisher’s protected LSD tests for post-hoc comparisons; $P=0.004$ and $P=0.038$, respectively). However, the “no choice” and “female choice” treatments were not different from each other ($P=0.368$). Given that both the highest and lowest fruit

Table 1 The number of flowers that set fruit as a function of treatment with multiple replicates on the same plant excluded, and with multiple replicates on the same plant included. Fruit set as a function of treatment. Data were analyzed using a log likelihood model with the likelihood ratio compared to a chi-square ($\chi^2=6.95$; $P=0.031$)

Fruit set	Female choice	Bagged, no choice	Bagged, control	Totals
Excluding replicates on same plant				
0	5	3	11	19
1	23	25	17	65
Totals	28	28	28	84
Including replicates on same plant				
0	7	4	14	25
1	29	32	22	83
Totals	36	36	36	108

Table 2 Repeated measures ANOVA of percent fruit set and eggs/flower as a function of the timing of flowering

Source	SS	MS	df	F	P
Average fruit set per plant per time block					
Plant	0.4895	0.1224	4	3.41	0.034
Time block	3.4731	0.8683	4	24.20	0.000
Error	0.5741	0.0359	16		
Average percent of flowers oviposited on in each time block					
Plant	0.4945	0.1236	4	4.60	0.015
Time block	0.8517	0.2129	4	7.93	0.001
Error	0.4296	0.0268	16		

set occurred in caged flowers, there was no indication that caging itself affected fruit set. For those flowers that set fruit, the number of seeds produced was not affected by treatment ($F_{2,56}=0.48$; $P=0.620$). The mean seed set for those fruits that set seed in the “female choice”, “no choice”, and “bagged control” treatments were 6.07, 6.07, and 6.60, respectively.

Effects of phenology and architecture on oviposition and fruit set

The timing of flower production had a significant effect on the percentage of flowers that set fruit within that time block ($F_{4,16}=24.20$; $P<0.0005$, Table 2). Flowers produced early in the season had a 68.9% (± 5.1 ; $N=231$) chance of setting fruit, while none of those ($N=107$) beyond time block 4 set fruit (Fig. 2). Flowers produced early in the season were also more likely to be oviposited on ($F_{4,16}=7.93$; $P=0.001$, Table 2), but the trend was not linear as it was for fruit set (Fig. 2). A flower’s position also affected fruit set. There were significant differences in the percentage of flowers that set fruit along the vertical axis of the plant (i.e., among different ranks; $F_{3,12}=8.08$; $P<0.025$; Table 3, Fig. 3) and among flowers’ position along the horizontal axes of branches off

Table 3 ANOVA of percent fruit set and percentage of flowers oviposited on by *Hylemya* as a function of the architectural location of flowers within plants. Plants were treated as random blocks, rank and cluster as fixed effects. Rank is tested over the plant by rank interaction, and cluster is tested over the error term. Percentage data were arcsin square-root transformed to improve normality

Source	SS	MS	df	F	P
Percent fruit set					
Plant	2.1438	0.5360	4	2.7759	0.037
Rank	7.0581	2.3527	3	8.0794	0.000
Cluster	2.3128	1.1564	2	5.9893	0.005
Rank*Plant	3.4943	0.2912	12	1.5082	0.154
Error	9.2678	0.1931	48		
Percent of flowers oviposited on					
Plant	0.5398	0.1350	4	1.0738	0.380
Rank	0.1655	0.0552	3	0.3324	0.726
Cluster	0.1196	0.0598	2	0.4757	0.624
Rank*Plant	1.9917	0.1660	12	1.3206	0.238
Error	6.0328	0.1257	48		

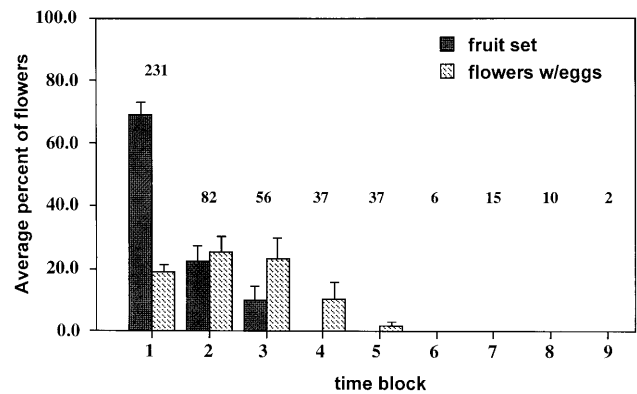


Fig. 2 The average percent of *Ipomopsis aggregata* flowers that set fruit across nine time blocks, and the average percent of the same flowers that were oviposited on by *Hylemya*. Both fruit set and the probability of receiving an *Hylemya* egg varied significantly across time due primarily to none of the flowers beyond block 3 setting fruit and none beyond block 5 being laid on

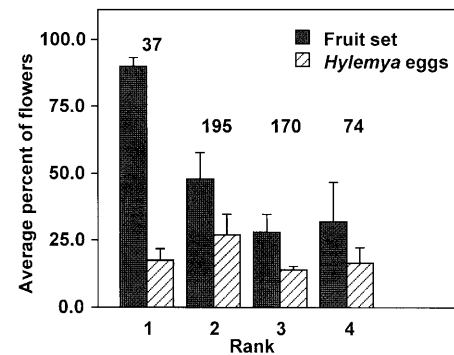


Fig. 3 The average percentage of *Ipomopsis aggregata* flowers that set fruit, and the average percentage of the same flowers that were oviposited on by *Hylemya* across the four sections, or ranks on each plant. The most distal flowers (rank 1) were significantly more likely to set fruit than those more proximal (ranks 2–4). There were no differences in the percentage of flowers oviposited on across ranks

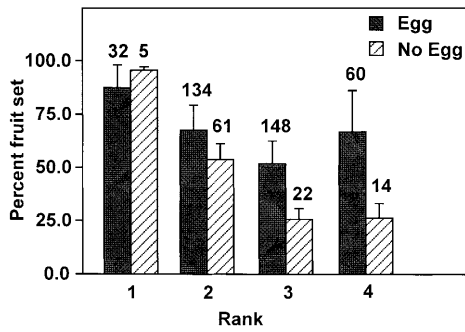


Fig. 4 The average percentage of *Ipomopsis aggregata* flowers with and without *Hylemya* eggs that set fruit across the four ranks. Except in rank 1, flowers with eggs were more likely to set fruit than those without eggs

Table 4 ANOVA of the percentage of flowers setting fruit as a function of plant, rank, and presence or absence of *Hylemya* eggs. The data were arcsin square-root transformed. Egg presence versus absence was treated as a fixed effect and tested over the error term

Source	SS	MS	df	F	P
Plant	3.0120	0.7530	4	3.0731	0.021
Rank	9.2964	3.0988	3	12.6467	0.000
Egg or No egg	0.9609	0.9609	1	3.9215	0.051
Error	19.1121	0.2450	78		

the main stem (i.e., among clusters; $F_{2,48}=5.99$; $P=0.005$, Table 3). However, neither rank nor cluster position significantly affected the probability of a flower's being oviposited on ($F_{3,12}=0.332$ and $F_{2,48}=0.476$; $P>0.05$, for rank and cluster, respectively, Table 3). But with the exception of flowers at the most distal end of the plant (rank 1), flowers within ranks that flies oviposited on had a higher probability of setting fruit than those not laid on ($F_{1,78}=3.92$; $P=0.05$; Table 4, Fig. 4).

Discussion

Results of our caging experiment suggest that ovipositing *Hylemya* are somehow able to manipulate flowers to ensure they set fruit, or to manipulate fruits to ensure they acquire enough resources to set seed. Flowers with caged flies were chosen randomly. Thus, the initial suitability of the flowers and the potential effect of their position on the plant did not contribute to the results we obtained. If a correspondence between oviposition and fruit set was strictly due to females making "wise choices" in laying their eggs, removing their choices by caging them on flowers should have eliminated the correlation. In that case, the fruit set of "no choice" flowers should have been statistically indistinguishable from that of control flowers. Instead, fruit set of the "no choice" flowers and the "female choice" flowers were both significantly higher than the control flowers, and not significantly different from each other. Thus it appears that females are somehow manipulating flowers.

Another possibility exists. The majority of flies we placed in cages did not lay eggs. Perhaps those individuals were *choosing* not to lay on the flowers presented to them. If such is the case, female preference must be strong enough that a female would rather forfeit oviposition than accept our random and presumably inferior flower; in such a case, the "no choice" flowers would be the same as those in the "female choice" treatment (since they were actually choosing). Our results only partially corroborate this explanation. Fruit set of the "no choice" and "female choice" flowers was equivalent. However, over half (58%) of the flowers not laid on by captive flies in the experiment were later oviposited on by free-flying *Hylemya*. Therefore, those same flowers were chosen and found suitable by another female. It is parsimonious to assume that all members of the population use the same criteria in making oviposition decisions, and thus it was not the case that females were actively choosing not to lay on those flowers in the cages. Again, these results suggest that females are manipulating their host – perhaps by manipulating resource allocation to fruits they have oviposited on – to ensure their larvae are provisioned with seeds.

Regardless of *Hylemya*'s potential ability to alter within-plant resource allocation, flowers must be pollinated to set fruit. *I. aggregata* is self-incompatible (Waser 1978; Waser and Price 1991) and fruit set is both pollen- and resource-limited (Campbell and Halama 1993). Although *Hylemya* do not pollinate *I. aggregata* flowers, they may be able to manipulate pollinated flowers to ensure they set fruit when plants are predominately resource- rather than pollen-limited. Fruits that abort due to unsuccessful pollination are indistinguishable from those that abort due to poor resource allocation for *Ipomopsis* (A.K. Brody, personal observation), and for most other plants as well (Diggle 1995). If a plant is resource-limited, it should allocate resources to maturing the highest quality fruits, i.e., those that will produce the greatest number or largest seeds. Competition for resources among fruits may be governed in part by the position of fruits within a plant (Watson and Casper 1984; Guitian 1994; Diggle 1995; Huth and Pellmyr 1997).

Thus, another possibility is that *Hylemya* chooses flowers at particular locations that are most likely to accrue resources and produce seeds. In fact, fruit set was non-random with respect to the architecture of *I. aggregata* inflorescences. Flowers produced in the most distal part of the plant were more likely to set fruit than those more proximal. However, architectural location did not explain where *Hylemya* chose to lay its eggs. Therefore, *Hylemya* is not simply choosing flowers at positions along the main axis of the plant that are likely to set fruit. Within location or ranks, flowers with *Hylemya* eggs had a higher probability of setting fruit than those without eggs. Except at the very distal end of the plant, where flowers overall had the highest probability of setting fruit, flowers with eggs had almost twice the probability of setting fruit (65.7%) than those without eggs (35.6%). Our results thus show that flowers *Hylemya*

oviposited on had a higher probability of setting seed than those females did not choose, in both the caging and architecture experiment and regardless of their position.

Because *Hylemya* does not pollinate the flowers on which it lays eggs, it must rely on those flowers being visited by pollinators. Pollinator visitation rate has been linked to flowering phenology for *I. aggregata* (Waser 1978; Waser and Real 1979; Brody 1997), and here flowering phenology was important both to fruit set and risk of predation. Only those flowers in bloom during the first four time blocks set seed. In addition, only those flowers open during the first four time blocks were oviposited on by *Hylemya*. It is also interesting that of 36 flowers in block 4, only 2 had eggs, and 1 of those was the only flower of the 36 to set fruit. The main message from these results is that the timing of flower production resulting in the highest fruit set and that of *Hylemya* oviposition are tightly linked. In a previous experiment, plants introduced to the area around RMBL early in the season were rarely oviposited on until members of the local population came into bloom, again demonstrating the link in flowering phenology and oviposition (A.K. Brody, unpublished data). However, these results do not necessarily imply that females are choosing early flowers, although other studies (A.K. Brody and M. Zimmerman, unpublished data) suggest they might. There may simply be a phenological correspondence between *Hylemya* and its host plants. In any case, by coordinating the timing between oviposition and pollinator activity, predispersal seed predators stand to gain a fitness advantage by ovipositing on those flowers most likely to set fruit (also see Pettersson 1991). Whatever the cause, fruit destruction by *Hylemya* may represent an important source of phenotypic selection favoring delayed flowering in *I. aggregata*. However, because selection favors early flowering through pollination (Campbell 1991), *I. aggregata* may experience a trade-off in attracting seed predators as well as pollinators early in the season.

Although we are unaware of other studies demonstrating that predispersal seed predators are capable of manipulating resource-sink relationships in their hosts, gall-forming insects are known to alter resource allocation in their host plants. Manipulation of host tissues and resource allocation thereto appears to be under hormonal control (Weis et al. 1988). One such hormone, auxin, is implicated to be the stimulus for gall formation (Miles 1968a, 1968b; Dieleman 1969) and has been found in significantly higher concentrations in needles galled by cecidomyiid midges than in needles without galls (Byers et al. 1976). Auxin has also been noted for delaying flower abscission (van Doorn and Stead 1997). One intriguing possibility is that *Hylemya* deposits an auxin-like compound at the time of oviposition, and by so doing females inhibit the abscission of the corolla. Even a short delay in corolla abscission would, in turn, increase the chance of that flower being subsequently visited by pollinators and fertilized. Alternatively, the deposition of auxin or auxin-like substances might enhance localized resource allocation to developing fruits, and thus in-

crease the chances of a flower setting fruit. Auxin is known to enhance plant cell growth at a very localized scale and in very small concentrations (Audus 1972; Hori 1992), and it is present in the saliva of several gall-inducing insects (Hori 1992). Although we can now only speculate on these as potential mechanisms, the association between oviposition and fruit set appears to be robust and highly repeatable (both experiments here; Brody 1992b; Brody and Waser 1995).

The relationship between oviposition preference and larval performance has been viewed as the kingpin of herbivore-plant interactions (Thompson 1988). If females oviposit on host species, host individuals, or plant parts unsuitable for larval growth and development, their larvae perish. Thus the ability to make wise oviposition choices will ultimately determine individual fitness, and could have population-level consequences as well. In some cases, ovipositing females are provided cues that correlate positively with offspring performance. For example, young or fast-growing leaf tissue correlates positively with larval growth and performance for gall-forming insects and leaf-feeders (Craig et al. 1989; de Kogel et al. 1997). However, for *Hylemya*, the situation is more complex. *Hylemya* offspring will perish if the flowers on which they hatch have not been visited by pollinators and fertilized, or for other reasons fail to set seed. Many predispersal seed predators such as tephritid flies, seed-feeding weevils and bruchid beetles circumvent this problem by ovipositing on the developing flower heads or seeds themselves (e.g., Solbreck and Sillén-Tullberg 1986; Moegenburg 1996; Desouhant 1998; McClure et al. 1998; Pilon 2000). Others, such as *Hylemya* sp. and *Delia flavifrons* (Pettersson 1992) employ a strategy that is inherently riskier by ovipositing on flowers before they are pollinated. Although our knowledge of the mechanism is still incomplete, both of these flies appear to oviposit on flowers that have a high probability of setting seed. In the case of *Hylemya*, it appears that if the flower is pollinated, then somehow the fly is ensuring that the flower sets fruit.

The evolution of plant-insect interactions has often been likened to an arms race; an idea first championed by Whittaker and Feeny (1971) and later by Berenbaum and Feeny (1981). Whatever the underlying mechanism for a positive relationship between oviposition by *Hylemya* and fruit set in its host, *I. aggregata*, it appears that in this interaction the insect has the upper hand. The possibility that host manipulation may not be limited to gall-forming insects sheds new and important light on the ecological and evolutionary relationships among plants and their seed-eating predators. We will conduct further investigations to elucidate how *Hylemya* manipulates its host and the potential for *I. aggregata* to respond.

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