

Research review

Pollination and seed predation by moths on *Silene* and allied Caryophyllaceae: evaluating a model system to study the evolution of mutualisms

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Summary

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Nursery pollinators, and the plants they use as hosts for offspring development, function as exemplary models of coevolutionary mutualism. The two pre-eminent examples – fig wasps and yucca moths – show little variation in the interaction: the primary pollinator is an obligate mutualist. By contrast, nursery pollination of certain Caryophyllaceae, including *Silene* spp., by two nocturnal moth genera, *Hadena* and *Perizoma*, ranges from antagonistic to potentially mutualistic, offering an opportunity to test hypotheses about the factors that promote or discourage the evolution of mutualism. Here, we review nursery pollination and host–plant interactions in over 30 caryophyllaceous plants, based on published studies and a survey of researchers investigating pollination, seed predation, and moth morphology and behavior. We detected little direct evidence of mutualism in these moth–plant interactions, but found traits and patterns in both that are nonetheless consistent with the evolution of mutualism and merit further attention.

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Introduction

Plant–pollinator relationships have figured prominently in our understanding of mutualism and floral trait evolution (Thomson, 2003; Fenster *et al.*, 2004). Moreover, the pattern of selection generated in the plant–pollinator interaction depends on a diverse web of organisms, which also exhibit spatio-temporal variation and inherent conflicts of interest (Herre *et al.*, 1999; Fenster & Dudash, 2001; Rutter & Rausher, 2004). The tightly evolved mutualisms of *Yucca-Tegeticula* moths and *Ficus-Agaonid*

wasps are considered paradigms for the importance of such interactions in driving trait evolution and speciation (Thompson & Cunningham, 2002; Datwyler & Weiblen, 2004). In these obligate mutualisms, pollinating species use developing seeds as resources for progeny (i.e. are nursery pollinators). Although advantageous as models with readily quantifiable fitness trade-offs, these partnerships are exceptional, as most nursery pollination systems are less specific, facultatively mutualistic, or antagonistic (Thompson & Pellmyr, 1992; Dufay & Anstett, 2003).

To quantify the processes underlying the evolution of nursery pollination, and contribute to a broader understanding of mutualisms, we need model systems that exhibit variation in their interactions. Well-studied mutualisms are often tightly coevolved, making it difficult to reconstruct the ecological conditions leading to one-to-one mutualisms. However, two nocturnal moth genera (*Hadena*, Noctuidae; *Perizoma*, Geometridae) interact with *Silene* and several allied genera (Caryophyllaceae) in diverse ways, which suggest that these systems are capable of shifting between antagonism and mutualism (Collin *et al.*, 2002; Dufay & Anstett, 2003; Westerbergh, 2004). In this system, the moths are simultaneously effective seed predators and pollinators, with wide variation in the abundances of interacting species, in the costs exacted by larval feeding and in the ecological contexts influencing selection (Pettersson, 1991a; Westerbergh, 2004). The Caryophyllaceae is a particularly rich and well-studied system for examining the evolution of mutualisms, yet important questions remain unanswered. For example, empirical data and modeling of the *Silene*–*Perizoma* interaction in Finland provide compelling evidence for potential mutualism (Westerbergh & Westerbergh, 2001; Westerberg, 2004), whereas *S. vulgaris*–*Hadena* interactions appear to be largely antagonistic (i.e. destructive to plants with little apparent benefit) (Pettersson, 1991a). In addition, very few families provide suitable candidates for the study of nursery pollination: among 13 families recently reviewed, the interactions in the Caryophyllaceae (i.e. *Silene*–*Hadena*) emerge as particularly variable, with relationships to pollinator–seed predators that imply a relatively unspecialized, ineffectively regulated ‘primitive state’ (Dufay & Anstett, 2003). Finally, over 600 species of *Silene* occur worldwide, in complexes including nursery pollinators, parasitoids and pathogens (Elzinga *et al.*, 2005; Biere & Honders, 2006; Giles *et al.*, 2006). Here, we investigate whether moth seed predators are effective pollinators, evaluating traits in both the moths and their host plants that affect the outcome, whether mutualistic or antagonistic.

This review integrates a scattered literature on plant–pollinator/seed predator interactions in *Silene* and related Caryophyllaceae with unpublished data from a meta-survey to evaluate the evolution of their close association with nocturnal moths. Using over 50 case studies for geographically diverse species, we ask:

- (1) Is there evidence for specialization of *Hadena* and *Perizoma* moths as either parasites or mutualists of caryophyllaceous hosts?
- (2) Do moths act as selective agents on floral traits associated with both pollination and seed predation?
- (3) Are specific behavioral, chemical, or morphological characteristics evident in *Hadena* or *Perizoma* that facilitate pollination?

Incorporating empirical data and theory spanning ≈ 30 yr (Brantjes, 1976a,b,c) to date, we seek to stimulate studies of

Caryophyllaceae–moth interactions that quantify the sign of the interaction and the ecological conditions that either inhibit or promote the evolution of mutualism.

Conceptual background for nursery pollination

Nursery pollination

Insects that rear offspring on the seeds of flowers they pollinate constitute ‘nursery’ pollination systems (*sensu* Dufay & Anstett, 2003) and potentially impose large fitness costs on their plant hosts. Inherent conflict over seeds as larval resources vs future progeny may stimulate trait evolution (Herre *et al.*, 1999), with efficient active pollination stabilizing obligate mutualisms by ensuring food for offspring while reducing overexploitation. Of at least 13 nursery pollinator systems (Dufay & Anstett, 2003), the most strongly mutualistic (*Yucca*–*Tegeticula* moths and *Ficus*–Agaonid wasps) show active pollination (i.e. trait adaptations in a coevolutionary context facilitating pollination) (Weiblen, 2002; Pellmyr, 2003). Here, mutualism is clear as removal of either partner leads to reproductive failure of both. In nonobligate systems, however, evolutionary conflicts are poorly resolved – the mutual benefit of the pollinating seed predator is less obvious because effective pollination by copollinators may shift the direction of the interaction. For example, in *S. dioica*, a positive benefit by *Perizoma* moths occurs only if copollinators service $\leq 60\%$ of flowers (Westerbergh, 2004). Otherwise, the ratio of seeds gained through pollination vs lost to predation may result in commensalism, at best.

Both the ecological context of pollination, and the frequency and relative effectiveness of nursery pollinators and copollinators, influence the net positive effect on a host. In senita cacti, where active pollination by the nursery pollinating moth mutualist is clear (Fleming & Holland, 1998), the role of bee copollinators in fruit-set is environmentally dependent, evident only in years of abundant precipitation and cool temperatures (Holland & Fleming, 2002). Similar uncertainty accompanies interactions between *Silene* and *Hadena* or *Perizoma* because the prevalence of important copollinators varies with site and year, potentially swamping any mutualism, and shifting the interaction towards parasitism (Pettersson, 1991b; Westerbergh, 2004).

Silene and allied genera, an emerging model system

Moth pollinators that act as seed predators occur in multiple caryophyllaceous genera (e.g. *Dianthus sylvestris*, Collin *et al.*, 2002; *S. latifolia*; Wright & Meagher, 2003). *Silene*–*Hadena* interactions are of particular interest as a potentially less specialized, basal form of nursery pollination, lacking regulation of seed damage by moths (Dufay & Anstett, 2003). Diverse ‘pollination syndromes’ (e.g. bird, fly, moth, bee) and breeding systems (e.g. dioecy, gynomonecy, trioecy) also allow exploration of the contexts associated with these potentially mutualistic

to antagonistic interactions. *Hadena* moths are similarly diverse, with over 145 species in palearctic and nearctic regions (Troubridge & Crabo, 2002). Varying flight patterns and oviposition choices by these moths also affect hybrid formation between co-occurring silenes (Goulson & Jerrim, 1997). Nursery pollinators are both prey for parasitoids (Elzinga *et al.*, 2005) and vectors for spores of an anther-smut, *Microbotryum violaceum*, which reduces floral attractiveness and influences seed set (Shykoff & Bucheli, 1995; Carlsson-Graner *et al.*, 1998).

Natural history of the *Silene*–moth interaction

Accurate knowledge of the direction of interactions between seed predating moths and Caryophyllaceae hosts requires data on pollinator frequency and effectiveness, and on predation pressure from larval offspring, ideally from multiple species, years and populations. At least 20 insect genera develop on species of *Dianthus*, *Silene*, *Lychnis* and *Viscaria* (Seppänen, 1970; Robinson *et al.*, 2005), but most are not pollinators. For example, the anthomyid fly, *Delia flavifrons*, consumes ovules of *S. vulgaris*, yet has no effect on pollen deposition or seed set (Pettersson, 1992). Only *Hadena* and *Perizoma* are widely recognized as nursery pollinators of *Silene* and as specialist, or rarely, obligate seed predators (Brantjes, 1976a; Westerbergh, 2004). *Hadena* moths gather nectar, pollinate and oviposit on caryophyllaceous hosts (Fig. 1; Brantjes,

1976a) whereas *Perizoma* pollinates *Silene* but obtains nectar elsewhere (e.g. *Veronica*; Westerbergh, 2004).

Seed-eating behaviors are best known for *H. bicurris* and *H. confusa* on *S. latifolia* and *S. vulgaris*, respectively. Early instar larvae consume ovules in young capsules at the site of oviposition, and subsequently enter secondary capsules through the top or via holes chewed by these larvae (Brantjes, 1976a). The rewards to the predispersal seed predator, *Hadena*, include the ovules eaten by larvae, nectar consumed by adults (Brantjes, 1976a; Pettersson, 1991a), and protection within the calyx from parasitoids (Biere & Honders, 2006). The percentage of flowers and capsules damaged ranges from 0 to 100% (Wolfe, 2002); and larval cannibalism occurs in *H. bicurris* (Brantjes, 1976b) potentially limiting damage to plant progeny.

Antagonistic to potentially mutualistic relationships involving both moth genera appear to be context- and species-dependent. *H. compta* and *H. bicurris* are frequent, effective pollinators of *D. sylvestris* and *S. latifolia*, respectively (Collin *et al.*, 2002; Bopp & Gottsberger, 2004). In Swedish populations of *S. vulgaris*, however, *H. bicurris* is one of 26 visiting species and a relatively ineffective pollinator, suggesting that seed gain from pollination dwarfs its loss from predation (Pettersson, 1991a,b). Recent studies of *Silene* and *Hadena* highlight the cost of larval seed predation as a selective force favoring traits that limit exposure to the moth (e.g. flowering phenology) (Wright & Meagher, 2003) and plant mating system characters (Collin *et al.*, 2002).

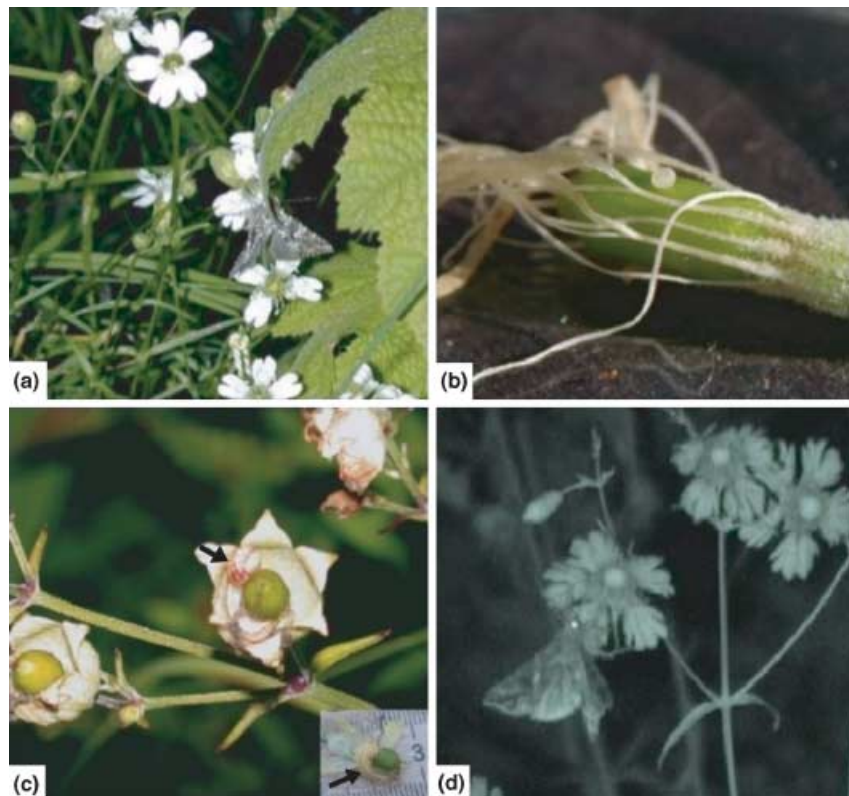


Fig. 1 (a,b) Nursery pollinator *Hadena variolata* gathers nectar at 22:00 hours before depositing an egg on an ovary of *Silene douglasii*. Photographs courtesy of S. Kephart and P. Swenson. (c,d) Larval seed predator, *Hadena ectypa*, wedged between the ovary and calyx of *S. stellata*, whose flowers are also visited by the copollinator *Autographa precatonensis*. Photographs courtesy of K. Barry, M. Dudash, C. Fenster and R. Reynolds.

Web survey analysis and key variables

To document the role and behavior of moths on specific caryophyllaceous plants, we invited researchers studying *Silene* and related genera to complete a web survey detailing the names of interacting taxa plus qualitative and quantitative data on: (1) pollination and seed predation, (2) floral traits and breeding systems, and (3) habitat, population and community characteristics. We limited the case study to two large lineages in the subfamily Silenoideae with nursery pollination: *Dianthus–Saponaria*, and the *Lychnis–Silene–Viscaria* complex, now circumscribed as distinct genera based on molecular data (Oxelman *et al.*, 2001).

Whether moths enhance plant fitness via seed production is dependent on the pollinator community. Thus, we asked investigators to identify major pollinators (i.e. those with the greatest overall positive effect on plant fitness) based on pollinator frequency, pollen load on insects and, when available, effectiveness in pollen transfer to stigmas (as in Inouye *et al.*, 1994; Dafni *et al.*, 2005). We gathered data on pollen or resource limitation, as it might affect the sign of the moth–plant interaction. We further explored whether a functional group of pollinators (*sensu* Fenster *et al.*, 2004) might exert similar selective pressures on floral design. We quantified associations between nocturnal moth pollination and floral traits predicted for this guild (e.g. related to time of anther dehiscence, flower color and fragrance). We included scent as a response variable in the metasurvey, as it may be an important distinguishing feature of nocturnally pollinated Caryophyllaceae (Jürgens *et al.*, 2002a, 2003). We also noted structures or behaviors that might signify active pollination, and whether plants exhibited traits that facilitate oviposition or minimize seed loss to larval predation. As moths must oviposit in flowers with female function for larvae to gain access to ovules, variation in breeding systems might partly reflect mechanisms to minimize seed loss.

We assessed moths as seed predators, using investigator-provided data for fruit damaged by larvae, and analyzed any potential relationship to ovule number, which could reflect selection to provide a reward to moths while simultaneously minimizing seed predation. We conducted a separate survey of host–plant interactions, using major websites recommended by noctuid moth experts, and cross-checked all sites against published data, our metasurvey and taxonomic synonyms. We also sought to compare data on seed predation and pollinator effectiveness across populations, variable habitats and community structures. However, most survey taxa inhabit similar open environments, and data on community composition were variable in quality, preventing full analysis.

We analyzed 36 taxa (nine *Dianthus*, 23 *Silene* and four others), augmenting survey data from published sources to supply missing variables before statistical analysis (SAS Institute, 2004). For multiple entries in widely studied taxa (e.g. *S. latifolia*), we used modal or mean values for categorical and

continuous data, respectively, restricting analysis to native populations for characters influenced by residency (e.g. flowering time, pollinators). We used Fisher's exact test to analyze associations between categorical variables (some cell-expected values were ≤ 5) and *t*-tests to determine whether categorical variables were significant sources of variation in continuous variables. Correlation analysis allowed the examination of linear relationships between continuous variables. To detect multivariate patterns in scent chemistry, we ran nonmetric multidimensional scaling (NMDS) ordination (PC-ORD 4.0) using Sorensen distance and slow, thorough, autopilot settings.

Caryophyllaceae–moth interactions as potential specialized mutualisms

The first goal was to evaluate evidence for specialization in the interaction of *Silene* and related genera with *Hadena* or *Perizoma*. If these are emerging as specialized mutualisms, we hypothesized that investigators would classify the moths as primary pollinators.

Two insect groups comprise over 75% of the animal taxa designated as major pollinators (Table 1): diurnal and nocturnal moths (48.1%; e.g. Noctuidae and Sphingidae); and bees (29.6%; Apidae, especially *Bombus*). By far, lepidopterans pollinated the majority (55.5%) of the 27 taxa with a known major pollinator or suite of pollinators, with diurnal moths and butterflies poorly represented (14.8%), relative to nocturnal moths (40.7%). Of plants with lepidopterans as primary visitors, 73.3% are nocturnally pollinated, either by noctuids (usually *Hadena*) or sphingids (e.g. hawkmoth *Deilephila porcellus*). Moreover, *Hadena* is a major or common pollinator for most moth-pollinated plants (67%, Table 1).

Hadena clearly emerges as an important pollinator, but clear evidence of specialization is critical to establishing whether *Hadena*–Caryophyllaceae interactions represent a pathway to obligate mutualism, as exemplified in *Yucca* and *Ficus*. Originating > 80 Ma (Datwyler & Weiblen, 2004), the highly evolved fig–wasp interactions provide stringent baseline criteria for an exclusive mutualism: (1) a moth species lays eggs on a single caryophyllaceous taxon; (2) a caryophyllaceous taxon has one moth taxon responsible for ovule and seed predation; and (3) this single moth species is a plant's sole or major pollinator. Specialization in nursery pollination can be inferred from various criteria, including a close, potentially 1 : 1, association of host and pollinator–seed predator and concordant geographical ranges or activity periods of the two partners.

We uncovered little evidence for the tight association manifested in figs or yuccas (Fig. 2a,b), but several types of data demonstrate the evolutionary potential for such interactions. First, our survey detected 14 *Hadena* species whose larvae use the flowers and seed capsules of 26 caryophyllaceous plants as larval hosts (Appendix 1). Second, *Hadena* caterpillars feed

Table 1 Primary mode of pollination, breeding system, and floral traits in Caryophyllaceae where *Hadena* is present (Y) and known to be a major pollinator (MP) or a common pollinator (CP)^a

Species	Sex	Flower colour	Flower shape	Time of pollination	Major pollinator(s)	Other pollinators	Hadena +	References
Moth pollination								
<i>Dianthus sylvestris</i>	g	pink	n	noc	<i>Hadena compta</i> (Noctuidae)	<i>Herse convolvuli</i> , <i>Macroglossum stellatarum</i> , bees, syrphids	Y-MP	Erhardt (1988); Collin <i>et al.</i> (2002)
<i>Dianthus superbus</i>	h	pink	n	noc	<i>Herse convolvuli</i> (Sphingidae)	<i>Celerio euphorbiae</i> , <i>Autographa bractea</i>	Y	Erhardt (1991)
<i>Saponaria officinalis</i>	h	wht/pink	n	noc	<i>Autographa gamma</i> (Noctuidae)	<i>Hadena bicruris</i>	Y-CP	Jürgens <i>et al.</i> (1996)
<i>Silene douglasii</i> vs <i>douglasii</i>	h	white	o	noc	<i>Hadena variolata</i> (Noctuidae)	Syrphids, halictids, sphingids	Y-MP	S. Kephart (unpublished)
<i>Silene douglasii</i> vs <i>rupinae</i>	h	white	o	noc	<i>Hadena variolata</i> (Noctuidae)	Halictids, <i>Bombus</i> , syrphids, <i>Autographa</i>	Y-MP	S. Kephart (unpublished)
<i>S. grayi</i>	h	pink	n	noc	Sphingidae	Syrphids		Showers (1987)
<i>S. latifolia</i>	d	white	o	noc	<i>Hadena bicruris</i>	<i>H. rivularis</i> , <i>Autographa gamma</i> , sphingids	Y-MP	Jürgens <i>et al.</i> (1996)
<i>S. nutans</i>	g	white	n	noc	<i>Diachrysia chrysitis</i> (Noctuidae)	<i>Autographa</i> , other noctuids, <i>Bombus</i>		Jürgens <i>et al.</i> (1996)
<i>S. stellata</i>	h	white	f	noc	<i>Hadena ectypa</i>	Noctuid moths, <i>Bombus</i> spp.	Y-MP	R. J. Reynolds <i>et al.</i> (unpublished)
<i>S. uniflora</i>	g	white	o	noc	<i>Hadena</i> , other noctuids, <i>Deilephila porcellus</i> (Sphingidae)	Noctuids, solitary bees (e.g. halictids), flies	Y-CP	Pettersson (1997); H. Prentice (unpublished)
<i>S. vulgaris</i>	g	white	o	noc	<i>Diachrysia chrysitis</i> and other noctuids	<i>Apamea furva</i> , <i>Autographa</i> spp., <i>Cucullia umbratica</i> , <i>Hadena</i> spp., sphingid moths	Y-CP	Pettersson (1991a,b); M. Glaettli (unpublished)
<i>D. glacialis</i>	h	red	n	di	Selfing or <i>Zygaena</i>	<i>Zygaena exulans</i> (diurnal moth)	N	Erhardt & Jaggi (1995)
<i>D. gratianopolitanus</i>	h	pink	n	di	<i>Macroglossum stellatarum</i> (Sphingidae)	<i>Papilio machaon</i> , <i>Autographa gamma</i> , <i>Euchalcia variabilis</i> (Noctuidae)	Y	Erhardt (1990)
Butterfly pollination								
<i>D. carthusianorum</i>	g	red	n	di	<i>Satyrus ferula</i> , <i>Melanargia galathea</i> (Satyridae)	<i>Ochlodes venatus</i> ; <i>Thymelicus</i> & other butterflies, zygaenid & sphingid moths	U	Müller (1873); A. Erhardt <i>et al.</i> (unpublished)
<i>D. deltoides</i>	h	red	n	di	<i>Ochlodes venatus</i> , <i>Thymelicus lineola</i> (Hesperiidae)	Dipterans (e.g. syrphids)	Y	Jennersten (1988b)
Bumblebee pollination								
<i>Lychnis flos-cuculi</i>	h	pink	n	di	<i>Bombus lapidarius</i> (Apidae)	<i>Rhingia campestris</i> , <i>Hadena bicruris</i>	Y	A. Biere (unpublished)
<i>S. acaulis</i> v. <i>subacaulescens</i>	g	pink	n	di	<i>B. sylvicola</i>	Moths, beetles, flies	N	Shykoff (1992); Delph & Caroll (2001)
<i>S. acaulis</i>	g	pink	n	di	<i>Bombus</i> sp.	Flies, butterflies	N	see Alatalo & Molau (2001)
<i>S. acutifolia</i>	h	pink	n	di	<i>B. pascuorum</i> , <i>hortorum</i> , <i>Bombylius</i>	<i>Anthophora</i> spp., sphingids	U	Buide & Guitián (2002)
<i>S. caroliniana</i>	h	pink	n	di	<i>Bombus</i> sp.	Bombyliids; <i>Bombus</i> , <i>Hemaris</i> spp.	N	M. Buide (unpublished)
<i>S. dioica</i>	d	pink	o	di	<i>Bombus terrestris</i> , <i>Bombus</i> spp. ^b	Muscid, syrphid flies; sphingid moths, pierid butterflies, <i>Apis</i>	Y	C. Fenster <i>et al.</i> (unpublished)
<i>S. spaldingii</i>	h	white	n	di	<i>B. fervidus</i>	Halictid bees	Y	Carlsson-Graner <i>et al.</i> (1998); Westerbergh (2004); Goulson & Jerrim (1997)
								Lesica & Heidel (1996)

Table 1 continued

Species	Sex	Flower colour	Flower shape	Time of pollination	Major pollinator(s)	Other pollinators	Hadena +	References
<i>Viscaria vulgaris</i>	h	red	n	di	<i>B. hortorum</i>	<i>Apis</i> , <i>Bombus</i> , butterflies, syrphids, <i>Deilephila</i>	Y	Jennersten (1988a); Jennersten & Nilsson (1993)
Fly pollination								
<i>S. integripetala</i>	h	pink	f	di	<i>Bombylius</i> sp.	Apoidea, Diptera, butterflies, beetles		B. Oxelman (unpublished)
<i>S. stockenii</i>	g	red	n	di	<i>Acanthogeton</i> sp.	<i>Bombylius discolor</i>	Y	Jürgens <i>et al.</i> (1996); Talavera <i>et al.</i> (1996)
Hummingbird pollination								
<i>S. regia</i>	h	red	n	di	<i>Archilochus colubris</i>	Papilionid butterflies	Y	Menges (1995)
<i>S. virginica</i>	h	red	n	di	<i>Archilochus colubris</i>	<i>Bombus</i> spp., syrphid flies, solitary bees	Y	Fenster & Dudash (2001)
Other								
<i>S. douglasii</i> v. <i>oraria</i>	h	white	o	di, noc	selfing	Syrphid flies; halictid bees, <i>Bombus</i> (rare)	N	Kephart <i>et al.</i> (1999); Brown & Kephart (1999)
<i>S. noctiflora</i>	h	white	o	di, noc	selfing	<i>Bombus</i> (rare)	N	Jürgens <i>et al.</i> (1996)

^ad, dioecy; g, gynodioecy or gynomonecy; h, hermaphroditic for diurnal (di) or nocturnal (noc) pollination in flowers with funnellform (f), narrow (n), or ovoid (o) floral tubes.

^bIn some populations of *S. dioica*, the moth *Perizoma affinitata* (Geometridae) is probably the main effective pollinator (see Westerbergh 2004 and the text for details).

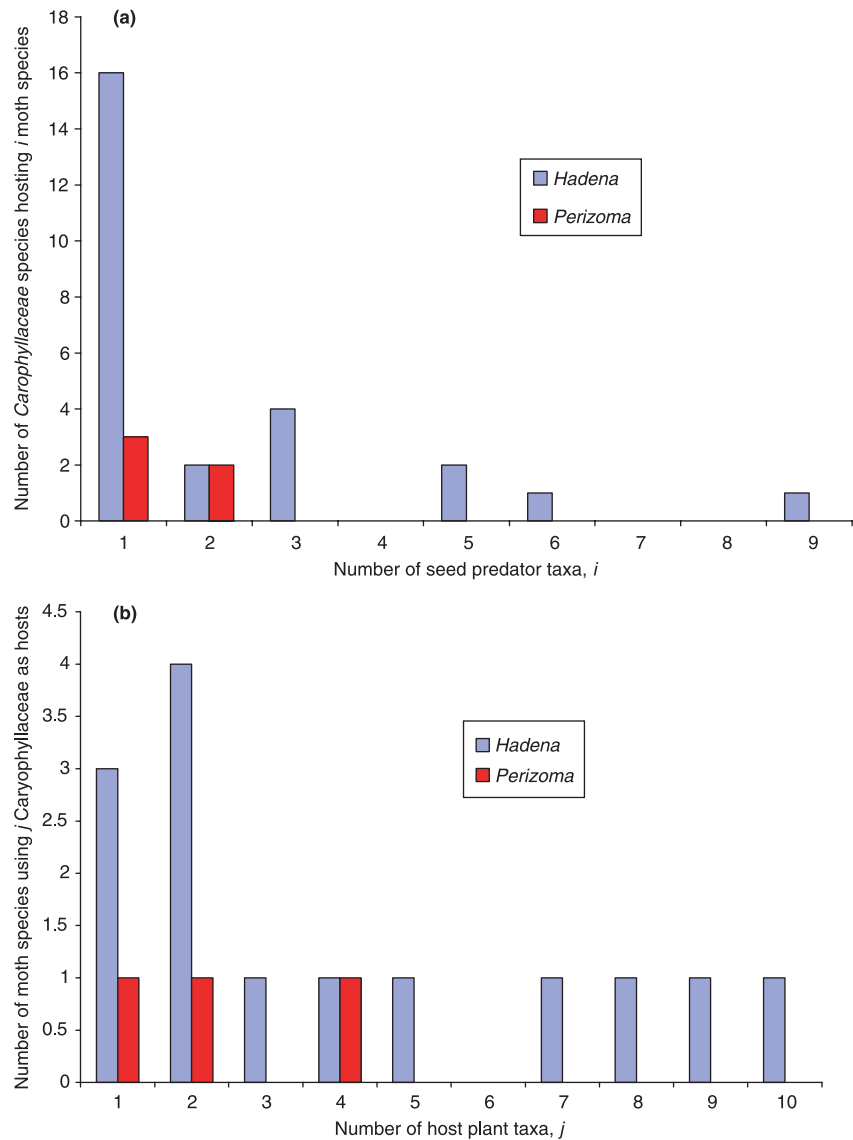


Fig. 2 (a) Specificity in moth–plant interactions. (a) Number of caryophyllaceous plants hosting *i* taxa of moth seed-predators *Hadena* or *Perizoma*. (b) Number of moth species using *j* caryophyllaceous plants as hosts.

almost exclusively on a small subset of genera in the Caryophyllaceae (i.e. *Dianthus*, *Silene–Lychnis–Viscaria*, and rarely others). Only *H. caesia* appears to also rear progeny on plants outside the carnation family (i.e. *Fragaria*, *Primula*; Seppänen, 1970). Third, host-plant records of the Natural History Museum of London (Robinson *et al.*, 2005), and our survey data, show that 16 of 26 plant taxa probably host only a single species of *Hadena* (Fig. 2a; mean 2.0 ± 0.38 *Hadena* species per plant). In a more limited data set of five species of *Silene–Lychnis* with *Perizoma* associations, three host a single *Perizoma* species.

A plant species might host diverse moth taxa, but specificity must also be viewed from the perspective of the moth's ability to use one or many hosts. *Perizoma* may have a broad range of hosts, but our survey revealed only four *Perizoma* species with Caryophyllaceae hosts, whereas many noncaryophylla-

ceous plants are known to host *Perizoma* moths, implying low overall specialization in *Perizoma–Caryophyllaceae* lineages. Similarly, London's Natural History Museum lists 16 *Perizoma* species on 29 angiosperm host genera, and 15 species of *Hadena* on 14 genera: for *Hadena*, 95% of the records with names are caryophyllaceous plants, compared with 23% for *Perizoma* (Robinson *et al.*, 2005). In Northern Europe, *P. affinitata* has an obligate dependence on *S. dioica* for rearing its young, and both moth and plant have the same distribution, flowering and flight periods in Finland (Westerbergh, 2004). However, three other *Hadena* moths and *P. flavofasciata* also occur on this *Silene* (Appendix 1), and bumblebees predominate in most *S. dioica* populations (Table 1), potentially swamping any mutualistic effect, except in isolated, serpentine populations where plants appear to be dependent on their nursery pollinator (Westerbergh, 2004).

Of 14 *Hadena* species using carnation family hosts, seven occur on one or two plant hosts (Fig. 2b). Moreover, in three instances involving two hosts, the plants used by the moth are close relatives (e.g. *H. ectypa* on *S. virginica* and *S. stellata*); in two cases, they have been treated historically within a single species (i.e. *H. filograna* on *S. vulgaris* and *S. uniflora* var. *petraea*; *H. variolata* on varieties *douglasii* and *rupinae* of *S. douglasii*). Three *Hadena*–*Silene* interactions show a 1 : 1 correspondence between the moth seed predator and its plant host (i.e. *H. circumvadis*–*S. spaldingii*, *H. irregularis*–*S. otites* and *H. sancta*–*S. stockenii*; Appendix 1). Most have diurnal pollination, so the moth seed-predators are probably not mutualistic, and they are not major pollinators, with the caveat of limited night observations (Lesica & Heide, 1996; Talavera *et al.*, 1996).

Ample evidence of generalization also exists among Caryophyllaceae–*Hadena* interactions. *V. vulgaris*, *S. nutans*, and *S. vulgaris* each host five to nine different species of *Hadena*, as well as the larvae of one or two *Perizoma* species (Appendix 1). All five *Silene* species known as hosts for *Perizoma* also support at least one *Hadena* species, highlighting again the absence of tight 1 : 1 associations between moth and caryophyllaceous species. These groups might also reflect a diffuse coevolution (Strauss *et al.*, 2005), with the unrelated moth species acting as a single functional group of nursery pollinators (*sensu* Fenster *et al.*, 2004). Not only do the relative roles of moths as pollinators–seed predators merit more study, but quantifying the ancestral and derived character states would allow us to determine the direction of evolution of the moth–Caryophyllaceae interactions (Pellmyr, 2003).

Despite the 1 : 1 correspondence among several interactions, in only four survey species did one *Hadena* species act as a seed predator and major pollinator, indicating the potential for mutualism to evolve. In the three nocturnally pollinated species (*H. compta*–*D. sylvestris*, *H. ectypa*–*S. stellata* and *H. variolata*–*S. douglasii*), moths consumed or damaged \approx 18–51% of capsules. Because we lack estimates of the total seed production attributable to *Hadena*, the interactions could be mutualistic or antagonistic. Clearly, future studies need to quantify the *Hadena* contribution to population-level seed set in these species relative to seed loss through larval predation. In *S. vulgaris*, Pettersson (1991a,b) quantified similar variables for a guild of *Hadena* species delivering \approx 7% of the pollen on stigmas, but consuming \approx 5–68% of capsules, indicating that this interaction is probably antagonistic. Presently, *H. ectypa* may account for up to \approx 45% of nocturnal visitors in populations of *S. stellata* and \approx 35% seed loss (R. J. Reynolds *et al.*, unpublished). Although other moth copollinators exist, *S. stellata* could have a mutualistic relationship with *H. ectypa* if it contributes more to seed production than loss. These preliminary data emphasize the need to quantify the abundances and effects of copollinator and nursery moths across populations and years, with respect to pollination and larval herbivory.

Trait evolution in plants and moths

Floral evolution in response to moths as pollinators

Another survey goal was to identify traits that might reflect the evolution of a specific moth–plant interaction, whether mutualistic or not. In an evolving nursery mutualism, we expect floral traits associated with pollination (e.g. in attraction or efficient pollen transfer) to reflect a response to *Hadena* or *Perizoma*.

Our analysis suggests that indeed some floral traits, commonly associated with attracting nocturnal lepidopterans, may have evolved in response to moths as selective agents. Fisher's exact test demonstrates a significant association between nocturnal pollination and white flower color ($P < 0.004$), the presence of scent ($P = 0.004$), and crepuscular or nocturnal anther dehiscence ($P < 0.001$). Only three nocturnally visited plants had nonwhite corollas, and all but *D. sylvestris* are pollinated by hawkmoths (Table 1). We detected a weak association between nocturnal pollination and plants with fringed petals ($P = 0.11$).

Scent is a key attractant for nocturnally visited Caryophyllaceae: its emission coincides with crepuscular opening of *S. latifolia* flowers (Dötterl *et al.*, 2005) and it both initiates seeking behavior in *Hadena* and guides its landing at close range (Brantjes, 1976a,c). For 13 plant species, our survey allowed us to associate the role of *Hadena* or other visitors as main pollinators with specific scent profiles (Jürgens *et al.*, 2002a, 2003; Jürgens, 2004). For these plants, NMDS generated a three-dimensional solution with clear separation of nocturnal and diurnal patterns (Fig. 3), for which axes 1 and 2 explain 20% and 69% of the variation. Diurnally pollinated species that serve as host plants for *Perizoma* and/or *Hadena* emit primarily fatty acid derivatives (mean 42.3%) and secondarily benzenoids (30%). In contrast, benzenoids (mean 51.9%) and isoprenoids (32.7%) are the main floral volatiles for nocturnally pollinated species. Only the four species with *Hadena* as a common/major pollinator emitted lilac aldehydes or methyl benzoate as dominant compounds (this survey; Jürgens *et al.*, 2002a, 2003). In *S. latifolia*–*H. bicruris*, dose-dependent tests of electrophysiologically active lilac aldehydes also demonstrate their role in attracting *Hadena* (Dötterl *et al.*, 2006). However, these compounds also attract other nocturnal visitors (Jürgens *et al.*, 2002a; 2003), obscuring the relationship between these special compounds and *Hadena*.

The combined survey data on floral traits, including scent, provide strong evidence of a nocturnal pollination syndrome for many *Silene* species. However, we know little about the exact role of *Hadena* and *Perizoma* moths as selective agents for the evolution of these floral traits. We detected no clearly documented case where a moth species is the sole pollinator of *Silene* or related genera, and these nursery systems have noctuid, sphingid and bumblebee copollinators that may also influence floral characters (Table 1). We need more complete

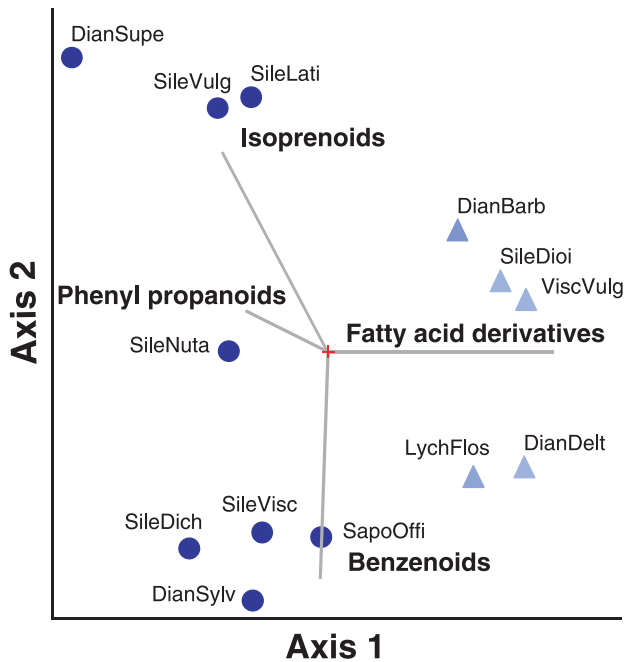


Fig. 3 Nonmetric multidimensional scaling (NMDS) ordination of volatiles emitted from flowers that are pollinated nocturnally (circles) and diurnally (triangles) for survey species with data on moth use as hosts. The figure compresses a three-dimensional solution along two axes, representing the components that explain the greatest variation in the data. Vector directions reflect correlations of percentage scent emissions with the ordination axis; vector lengths denote summed r -squared values. See Appendix 1 for full species names. Computed from survey data and with permission from Jürgens *et al.* (2002a; 2003) and Jürgens (2004).

data on *Hadena* and *Perizoma* species as pollinators and selective agents, including visitation rates, pollination effectiveness, effect on seed-set and, ultimately, the selection intensities and direction exerted by these moths.

Floral evolution in response to moths as seed predators

If present, a mutualism of *Silene* and sister groups with seed-eating moths should reflect the evolution of traits in response to both pollination and seed loss. So, is there evidence that seed predation also influences floral traits? First, our survey detected significantly higher rates of fruit predation with nocturnal pollination (30.6 ± 6.1 ; $P = 0.01$, $t = 2.79$) and nonhermaphroditic breeding systems (28.1 ± 7.0 ; $P = 0.04$, $t = 2.21$) compared with diurnal pollination (10.3 ± 3.5) and hermaphrodites (11.2 ± 3.5). These results implicate moths as potential selective agents for traits minimizing predation, in conjunction with effective pollination. Because diurnally pollinated plants experience significantly less predation than nocturnal species, diurnal pollination could represent a mechanism that avoids seed predation or, alternatively, an 'escape route' from nocturnal pollination. A complication is that diurnal pollination can be linked to environments

outside the moth's range (e.g. *S. caroliniana* is an early spring ephemeral; *S. acaulis* occurs at high latitudes and elevations). Second, if selection favors the evolution of a mutualism, we expect floral traits that minimize seed predation after pollination and egg-laying by moths. In dioecious *S. latifolia*, the rapid, 24 h decline of scent emission in pollinated vs unpollinated flowers is consistent with a response by plants to reduce seed predation over the life span of female flowers (Dötterl *et al.*, 2005) and to limit costs in nonhermaphrodite systems. The high predation in nonhermaphrodites in our survey also suggests that moths can specialize on female flowers. Thus, another promising avenue for study is that avoidance of seed loss may drive the evolution of breeding systems towards hermaphroditism.

We predicted initially that pollen limitation or pollinator scarcity might create opportunities for the evolution of mutualism if plants attain more pollination and fruit-set in the presence of seed predators than is possible in their absence. In nocturnally pollinated systems, the survey shows no inherent predation cost when these moths are major pollinators [i.e. investigator-estimated damage to fruits is similar regardless of whether *Hadena* is a major pollinator (35%) or not (30%)]. Thus, selection to increase the role of these moths as pollinators vs seed predators is possible. Pure seed predation and a minor role for moths as pollinators may be antecedents to evolution of a larger pollination role by these moths, but testing this hypothesis requires a more resolved phylogeny. Of species surveyed to date, nearly all are pollen-limited, implying that moth pollination might be important to overall plant reproductive success (Dudash & Fenster, 1997; Brown & Kephart, 1999; Alatalo & Molau, 2001).

If oviposition delivers pollen to stigmas, floral morphology may have evolved to facilitate and regulate egg-laying behavior by *Hadena* within accessible flowers. The survey provides some support for this: among lepidopteran-pollinated plants, those with *Hadena* as a main or common pollinator are almost exclusively ovoid or funnel form ($P = 0.02$, Fisher's Exact Test), including 75% of nocturnally visited plants (Table 1). However, we do not as yet know whether oviposition is associated with high pollen transfer, or if broad calyces (Fig. 1c) enhance egg-laying or larval survival (e.g. larvae may gain shelter from parasitoids, *sensu* Biere & Honders, 2006, if they can develop within a few large flowers). Morphological differences in stigma height and curvature may be regulatory in *S. dioica*: short-styled stigmas, presented at same level as the corolla tube opening, create difficult access for *Perizoma* females, thwarting oviposition despite successful pollination (Westerbergh, 2004). This trait variability in *Hadena*- or *Perizoma*-visited flowers might ensure that some flowers escape oviposition, thus reducing reproductive failure and stabilizing the mutualism.

This survey also revealed a weakly positive association between ovule number per flower and larval herbivory ($P = 0.06$, $F = 4.6$; correlation = 0.56, $r^2 = 0.32$), which is consistent with trait

changes expected in response to high seed predation. High ovule number might either compensate for seed predation or act as a reward to seed predators. Data from additional species will be critical for understanding this pattern, as the relationship garnered from our survey is dominated by a high value in *S. latifolia* (> 500 ovules per flower). The ovule number is also large in *S. dioica* (> 250 ovules per flower), the sole host for the obligate nursery pollinator *P. affinitata* (Carlsson-Graner *et al.*, 1998; Jürgens *et al.*, 2002b; Westerbergh, 2004). In contrast, of closely related *S. caroliniana*, *S. stellata* and *S. virginica*, *S. stellata* has the highest seed loss to *Hadena*, yet fewer ovules dispersed into greater per-plant flower production, a potential strategy to reduce overall seed predation by moths in this pollen-limited plant (R. J. Reynolds *et al.*, unpublished).

At an intraspecific level, some tantalizing evidence exists for plant response to limit seed predation by moths. Capsule wall thickness is significantly greater in native European populations of *S. latifolia* receiving higher predation by *Hadena* than in their introduced North American counterparts (Wolfe, 2002; Blair & Wolfe, 2004), but confirmation that capsule thickness actually impairs damage by *Hadena* larvae is needed. For example, during primary attack, the soft wall of a young ovary seems unlikely to impede initial larval penetration. In a secondary attack, mobile larvae typically gain access to ovules or seeds by chewing into the top of developing fruits (Elzinga *et al.*, 2005).

Evolution of moth behavior and morphology

If selection for mutualism favors the provision of benefits by the moth, adaptations by nursery pollinators should include specific behavioral, biochemical, or morphological characteristics that not only enhance their performance as seed predators, but facilitate effective pollination. *Yucca* moths use maxillary tentacles to collect and compact pollen, storing it in a cavity under the head (Pellmyr, 2003). In *Hadena*, no morphological structures seem to be specifically adapted for pollination. The calyx tube in *D. sylvestris*, and the proboscis in *H. compta*, are both \approx 23 mm, and *Dianthus* pollen is most abundant on the proboscis and labial palps of *H. compta* and *H. caesia* (Erhardt, 1988, 1990), but few specimens have been studied.

The survey reveals much diversity and some selectivity in *Hadena* behavior, which has been studied in detail in European *S. latifolia* (Brantjes, 1976a,b,c). *H. bicruris* selectively oviposits in its flowers over co-occurring *Dianthus*, *S. dioica*, *S. nutans*, *S. vulgaris* and *Saponaria* (Erhardt, 1988; Goulson & Jerrim, 1997; Bopp & Gottsberger, 2004). As in cases known among the caryophyllaceous plants we surveyed, typically *Hadena* imbibes nectar before successful oviposition (71%), and flowers receive only one egg (all survey taxa; Brantjes, 1976b). During nectar feeding on *S. latifolia*, the initial floral contact with the proboscis precedes contact with

the head as moths repeatedly and more vigorously pump flowers for nectar (Brantjes, 1976a). During oviposition, the legs, abdomen and ovipositor also contact floral parts (Brantjes, 1976a). Similarly, in close congeners *S. uniflora* var. *petraea* and *S. vulgaris*, *Hadena* brushes stamens and pistils, then bends its body while ovipositing, vigorously inserting its abdomen (M. W. Pettersson, unpublished; H. Prentice, unpublished). *Hadena* also contacts anthers and stigmas on North American *S. douglasii* and *S. stellata*, gathering nectar first, then ovipositing in a subset of these flowers (S. Kephart, unpublished; R. J. Reynolds *et al.*, unpublished). Nectar collection typically precedes oviposition on a different flower (71% of survey cases), but can also occur simultaneously with it in *Silene* and *Dianthus*; either behavior can result in pollination (this survey; Brantjes, 1976b), but definitive tests of the relative effectiveness of these behaviors in securing pollination and fruit set are sorely needed.

The behavior of geometrid *P. affinitata* on *S. dioica* reveals both commonalities and distinct differences from *Hadena* (Westerbergh, 2004). *Hadena* and *Perizoma* typically lay one egg per flower, have cannibalistic larvae that leave seeds in some capsules, and show stereotypical oviposition behaviors (Brantjes, 1976a,b; this survey). *Perizoma* alone exhibits a dense brush of hair on the ovipositor that retains pollen, exclusive development of larvae within one fruit and the absence of nectar feeding because the proboscis is too short to reach *S. dioica* nectar (Westerbergh, 2004). *Perizoma* females differ in behavior and visit length during probes of male and female flowers of dioecious *S. dioica* (one per plant in 94% of visits); both the abdomen and ovipositor enter the floral tube making contact with anthers and/or stigmas (Westerbergh, 2004). In both *Perizoma* and *Hadena* interactions with Caryophyllaceae, however, we need fuller exploration of moth behavior in relation to pollination and seed loss, within and among populations.

Conclusions and future directions

Although our survey of over 30 plant taxa spans only a fraction of the diversity in *Silene* and allied genera, the review identifies promising avenues of future research. Moth seed predators can be major pollinators, and evidence exists that floral traits have probably evolved in response to the selection pressures they exert. Nocturnal moth pollination is associated with floral traits classically assigned to moth pollination, including white color, fragrance and nocturnal anthesis (Faegri & van der Pijl, 1979); all are consistent with a response to selection exerted by *Hadena* and *Perizoma*, especially when they serve as major pollinators. In some nocturnally pollinated *Silene*, the petals also close (i.e. roll towards the center) during the day, either blocking (*S. latifolia*) or reducing (*S. douglasii*, *S. nutans*) access to nectar; for two of these species, *Hadena* moths are important pollinators (Table 1). Flowers of *D. deltooides*, a diurnal species found in open habitats, act in reverse, closing

at night (Jennersten, 1988b), suggesting that the phenomenon is not simply a mechanism of water conservation.

Mutualisms may evolve from an ancestral state where only one of the species in the interaction benefits (Dale *et al.*, 2001) but currently, of the moth–plant associations surveyed, no strict one-to-one interaction involving both pollination and seed predation exists throughout the geographical range of a given species. To assess the generality of this finding, however, we need more field observations documenting the taxonomic identity of pollinators and seed predators of caryophyllaceous plants. We have observed cases of parasitism by moths without benefit to plants, and cases suggesting mutualism. To discriminate between antagonistic relationships and the presence of nursery mutualisms, we encourage field studies comparing the relative cost-benefits of these pollination systems among related plant species. Studies should incorporate detailed measurements of both reductions in seed production as a result of predation and gains in plant fitness arising from moth pollination, particularly in pollen-limited populations. Spatio-temporal components would help us to evaluate whether the evolving interactions form a ‘coevolutionary mosaic’, a perspective that has been fruitful thus far for nursery pollination systems (Thompson & Cunningham, 2002).

In the *Silene–Hadena* systems, the stereotyped behaviors and retention of the hairs on the ovipositor of *P. affinitata* are potential precursors to effective active pollination. Study of additional species will reveal the commonality of such characteristics within *Perizoma*, as the presence of active pollination could shift the interaction towards mutualism. To determine if evolved mutualisms characterize these interactions, however, more detailed morphological measurements are needed, along with the pollen distribution on moths, amounts of pollen transferred to stigmas during nectar feeding and oviposition, and the extent to which these behaviors augment seed-set. Presently, for species that have been studied intensively, the evidence that *Hadena* moths are more effective than other nocturnal moths in pollen transfer is equivocal (Pettersson, 1991b; Collin *et al.*, 2002; R. J. Reynolds *et al.*, unpublished). Identifying the pollinator’s sex is important, because nonovipositing male pollinators may only contribute to positive components of the interaction while gathering nectar, unlike female moths that feed and oviposit, becoming potential parasites. Focal species in which seed-predating moths are the major pollinators deserve special attention.

While relatively few questions are definitively answered by our survey, this review demonstrates how richly variable this system is for future study of species interactions. For lesser-known nursery pollination systems, we must define the ecological conditions that might ultimately foster the evolution of an exclusive mutualism without copollinators. Just as importantly, embedding the results of pollination and predation studies within a well-supported phylogenies of both moth and plant species will permit major advances in our understanding of the direction and frequency of evolutionary change for

traits underlying nursery pollination, and of the factors shaping the form and timing of transitional stages in the evolution of mutualisms.

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Appendix 1

Plant host–moth relationships in 26 species of *Silene* and related Caryophyllaceae based on our survey and two comprehensive websites (1 and 2)

Plant host	Moth seed predator(s)	Reference
1. <i>Dianthus barbatus</i> L.	<i>Hadena bicurris</i> Hufn. (1), <i>Hadena compta</i> Schiff. (2)	Robinson <i>et al.</i> (2005) ('1' hereafter); Sakela (2005) ('2' hereafter)
2. <i>Dianthus caryophyllus</i> L.	<i>Hadena bicurris</i> , <i>Hadena compta</i> , <i>Hadena rivularis</i> F. ^a (3)	1, 2, Seppänen (1970) ('3' hereafter)
3. <i>Dianthus carthusianorum</i> L.	<i>Hadena compta</i>	B. Jaggi & A. Erhardt (unpublished)
4. <i>Dianthus deltooides</i> L.	<i>Hadena compta</i>	1–3
5. <i>Dianthus gratianopolitanus</i> Vill.	<i>Hadena caesia</i> Schiff. (4)	Erhardt (1990); A. Erhardt (unpublished)
6. <i>Dianthus plumarius</i> L.	<i>Hadena compta</i>	1–3
7. <i>Dianthus sylvestris</i> Wulf	<i>Hadena compta</i>	Erhardt (1991); Collin <i>et al.</i> (2002)
8. <i>Dianthus superbus</i> L.	<i>Hadena rivularis</i>	1–3; A. Erhardt (unpublished)
9. <i>Lychnis chalcedonica</i> L.	<i>Hadena rivularis</i>	1–3
10. <i>Lychnis flos-cuculi</i> L.	<i>Hadena bicurris</i> , <i>Hadena confusa</i> Hufn. (5) <i>Hadena rivularis</i>	1–3; Biere (1995)
11. <i>Saponaria officinalis</i> L.	<i>Hadena caesia</i>	1
12. <i>Silene dichotoma</i> Ehrh.	<i>Hadena bicurris</i> , <i>Hadena rivularis</i>	1–3
13. <i>S. dioica</i> (L.) Clairv (also as <i>Melandrium rubrum</i>)	<i>Hadena bicurris</i> , <i>Hadena perplexa</i> D. & S (6), <i>Hadena rivularis</i> <i>Perizoma affinitata</i> Steph. (7), <i>Perizoma flavofasciata</i> Thun. (8)	1–3; Goulson & Jerrim (1997); Bopp & Gottsberger (2004) 1–3; Westerbergh (2004)
14. <i>S. douglasii</i> Hook. var. <i>douglasii</i>	<i>Hadena variolata</i> Smith (9)	S. Kephart & P. Hammond (unpublished)
15. <i>S. douglasii</i> var. <i>rupinae</i> Keph. & Sturg.	<i>Hadena variolata</i>	S. Kephart & P. Hammond (unpublished)
16. <i>S. latifolia</i> Poir. ssp. <i>alba</i> (Mill.) Greut & Burdet (also as <i>Melandrium album</i> , <i>S. pratense</i>)	<i>Hadena bicurris</i> , <i>Hadena perplexa</i> , <i>Hadena rivularis</i> <i>Perizoma hydrata</i> Treitschke (10), <i>Perizoma flavofasciata</i>	1–3; Goulson & Jerrim (1997); Elzinga <i>et al.</i> (2005) 1–3
17. <i>S. nutans</i> L.	<i>Hadena albimacula</i> Bork (11), <i>Hadena bicurris</i> , <i>Hadena compta</i> , <i>Hadena confusa</i> , <i>Hadena luteago</i> D. and S. ^b (12), <i>Hadena perplexa</i> <i>Perizoma hydrata</i>	1–3; Jürgens <i>et al.</i> (1996) 1–3
18. <i>S. otites</i> (L.) Wibel.	<i>Hadena irregularis</i> (13)	1
19. <i>S. spaldingii</i> Wats.	<i>Hadena circumvadis</i> Smith (14)	P. Lesica <i>et al.</i> (unpublished)
20. <i>S. stellata</i> (L.) Ait.	<i>Hadena ectypa</i> Morrison (15)	1,2; R. J. Reynolds <i>et al.</i> (unpublished)
21. <i>S. stockenii</i> Chater	<i>H. sancta</i> Staud. (16)	Talavera <i>et al.</i> (1996)
22. <i>S. uniflora</i> Roth ssp. <i>petraea</i> (also as <i>Silene maritima</i>)	<i>Hadena albimacula</i> , <i>Hadena confusa</i> , <i>Hadena filograna</i> Esper (17), <i>Hadena perplexa</i> , <i>Hadena rivularis</i>	1–3; Pettersson (1992); M. Pettersson (unpublished)
23. <i>S. virginica</i> L.	<i>Hadena ectypa</i>	R. J. Reynolds <i>et al.</i> (unpublished)
24. <i>S. viscosa</i> (L.) Pers.	<i>Hadena perplexa</i>	1–3
25. <i>S. vulgaris</i> (Moench) Garcke (also as <i>Silene cucubalus</i>)	<i>Hadena albimacula</i> , <i>Hadena bicurris</i> , <i>Hadena caesia</i> , <i>Hadena compta</i> , <i>Hadena confusa</i> , <i>Hadena luteago</i> , <i>Hadena filograna</i> , <i>Hadena perplexa</i> , <i>Hadena rivularis</i> <i>Perizoma hydrata</i>	1–3; Pettersson (1991b); M. Pettersson (unpublished) 1–3
26. <i>Viscaria vulgaris</i> Röhl (also as <i>Lychnis viscaria</i>)	<i>Hadena albimacula</i> , <i>Hadena bicurris</i> , <i>H. confusa</i> , <i>Hadena perplexa</i> , <i>Hadena rivularis</i> <i>Perizoma hydrata</i>	2,3; Jennersten (1988a); Jennersten & Nilsson (1993) 2,3; Jennersten (1988a); Jennersten & Nilsson (1993)

Numbered moth taxa in *Hadena* and *Perizoma* ($n = 17$ species in combined genera) are shown in parentheses. Bold type indicates moth species known to visit only a single species of *Silene* in its native geographical area, to our best knowledge.

^aSometimes treated as *Sideridis rivularis*.

^bSometimes treated as *Conisania luteago*; also uses *Spergularia rupicola* as a host, although not included in this survey. Similarly, *Stellaria media* is listed by Seppänen (1970) as a host for *Perizoma taeniata*.