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Nectar and Pollen Feeding by Insect Herbivores and Implications for Multitrophic Interactions

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Key Words

plant-herbivore interactions, population structure, indirect interactions, apparent competition, floral resources

Abstract

Among herbivorous insects with a complete metamorphosis the larval and adult stages usually differ considerably in their nutritional requirements and food ecology. Often, feeding on plant structural tissue is restricted to the larval stage, whereas the adult stage feeds primarily or exclusively on plant-provided food supplements such as nectar and pollen. Research on herbivore nutritional ecology has largely been divided along these lines. Most studies focus on actual herbivory by larval stages, while nectar and pollen feeding by adult herbivores has been addressed mainly in the light of plant-pollinator interactions. Only recently have we started to realize that the two phenomena are closely interlinked and that nectar and pollen feeding by adult herbivores can have a strong impact on plant-herbivore interactions. Here we address this largely ignored aspect of multitrophic level interactions and discuss its wide-ranging implications.

FOOD SOURCES USED BY ADULT HERBIVORES

In addition to feeding on plant tissue, herbivorous arthropods may utilize a broad range of other food sources, including plant-provided food such as pollen, (extra) floral nectar, and (rotting) fruits, but also honeydew, dung, and bird droppings (13, 68, 101, 105). Females of some species receive additional nutrients during matings, called nuptial gifts. This applies to some herbivorous groups of the orders Lepidoptera, Diptera, and Coleoptera (14). Among Lepidoptera and Diptera some species depend primarily on larval reserves throughout their adult life and require little or no additional feeding (32, 67, 91).

In this paper we concentrate on plant-provided food sources because of their direct role in plant-herbivore interactions and because they are important for a broad range of adult herbivores. Nectar is primarily a sugar-rich plant secretion that may contain low levels of amino acids, proteins, lipids, vitamins, secondary plant compounds, as well as other organic compounds and minerals (8). Pollen, on the other hand, is mainly a source of nitrogenous compounds with protein levels ranging from 2.5% to 60% (107). In addition to proteins and amino acids, pollen usually also contains some sterols, lipids, and carbohydrates (mainly starch). The detailed chemical composition of pollen and nectar, their nutritional value, and suitability as insect food have been extensively covered elsewhere (8, 107, 135).

Herbivores can be grouped into three categories according to the stages during which they feed on plant tissue and/or other food items:

- Species whose diet is restricted to plant tissue during larval stages and that change this for a nectar or pollen diet in the adult stage. Examples include most Lepidoptera, as well as some Hymenoptera (sawflies, Tenthredinidae) (9, 105) and Diptera (Anthomyiidae).

- Species that combine tissue feeding with nectar/pollen feeding as adults, although they are strictly herbivorous during their larval stage. Examples of this category are found among Coleoptera (e.g., *Diabrotica* spp.) (85) and Diptera (e.g., *Liriomyza* spp.).
- Species that combine tissue feeding with nectar/pollen feeding during larval as well as adult stages. Examples of this category are found among Thysanoptera (93), Coleoptera (e.g., pollen beetles of the genus *Meligethes*) (23), Heteroptera (e.g., *Lygus* spp.) (28, 151), and certain Hymenoptera (Tenthredinidae) (9).

Adult Lepidoptera feed primarily on sugar sources. The ability to feed on pollen has been described for only a few species (13, 105). Among Diptera, many cyclorrhaphous flies including Tephritidae (fruit flies), Anthomyiidae (root maggot flies), and Psilidae (rust flies) feed on exposed fluids including floral and extrafloral nectar, but they may also consume pollen (105). Among Coleoptera floral feeding is especially prevalent within Chrysomelidae and Bruchidae (70, 109). Flower-visiting beetles frequently feed on pollen. Direct nectar feeding by beetles, on the other hand, seems rare (77, 109). Adult sawflies (Symphyta) feed on a range of sugar sources, including floral and extrafloral nectar, whereas pollen feeding has been reported for only a few species (e.g., from the families Xyelidae, Argidae, and Tenthredinidae) (9, 68). Adults of plant-feeding Heteroptera from a number of families (Miridae, Lygaeidae, Rhopalidae, and Thyreocoridae) can be found visiting flowers, apparently feeding on nectar (54, 140). There is indirect evidence that mirids exploit extrafloral nectar, since the tarnished plant bug, *Lygus lineolaris*, was found in significantly higher numbers in nectar-producing cotton than in nectariless cotton (113, 114). Pollen feeding has also been reported for mirids (28). Among thrips (Thysanoptera) many herbivorous species of

the families Thripidae and Phlaeothripidae feed on pollen and nectar (76), including the so-called flower thrips of the genera *Thrips*, *Haplothrips*, and *Frankliniella*, as well as foliar-feeding thrips (e.g., *Thrips tabaci*) (93).

IMPACT OF NECTAR AND POLLEN FEEDING ON HERBIVORE FITNESS

The level at which adult herbivores require nutrient or energy supplements depends on a number of factors, including a species' foraging range and egg production, with species laying egg clusters on common plants requiring less energy compared with species that distribute single eggs on rare plants (91). Sexes may also differ with regard to their nutrient requirements, with females generally having a higher nutrient demand than males (140). Lepidopteran species that emerge with a large proportion of mature eggs, on the other hand, are less dependent on adult food uptake or do not feed at all (67).

Nutrients ingested during the adult stage can affect various life-table parameters including longevity, (pre)oviposition period, and daily and lifetime fecundity (105). The positive impact on lifetime fecundity can be due to a prolonged oviposition period (e.g., *Ostrinia nubilalis*, *Lycæna hippothoe*), an increase in the daily fecundity (e.g., *Cnaphalocrocis medinalis*), or both (e.g., *Euxoa messoria*) (Table 1). Even when adult feeding increases the oviposition period, this does not need to translate into a fecundity increase. In the case of *Spodoptera exigua*, food-deprived females compensate for their reduction in life span by increasing daily fecundity (124).

The impact of feeding on herbivore fitness depends on the herbivore order/species as well as on the adult food source consumed (Table 1). Lepidoptera typically produce viable eggs in the absence of adult feeding (67). Nevertheless, sugar feeding may result in a 10-fold increase of lifetime fecundity in some species (Table 1). Only few lepi-

dopteran species, such as *Heliconius* spp., have evolved adaptations to allow pollen feeding (33). Even though the nitrogen-rich nature of pollen should make this a particular suitable food source to sustain oogenesis, the benefit of pollen feeding to *Heliconius charitonius* fecundity does not appear to exceed the benefit that a species such as *Helicoverpa zea* derives from nectar feeding (Table 1).

In contrast to Lepidoptera, most Diptera appear completely dependent on adult feeding for egg maturation. In the absence of adult food, females often fail to produce any eggs (Table 1).

Pollen feeding stimulates egg maturation in some Coleoptera (103). Other coleopteran species can produce eggs when fed carbohydrates only. Nevertheless, they still benefit from nutrients obtained through pollen feeding (38, 83) (Table 1).

The importance of nectar or pollen feeding among plant-feeding Heteroptera is largely unknown. The mirid *Lygocoris pabulinus* is reported to have an elevated egg maturation rate when potato leaves are supplemented with pollen (28) (Table 1).

Pollen has a large impact on adult survival and reproduction in many thrips species (Table 1). However, its discrete effect on fecundity is difficult to assess because pollen is always presented together with plants, which thrips use both as oviposition substrate and as adult food. The relative impact of pollen as food supplement depends largely on the chemical composition of the plant. Trichilo & Leigh (125) showed that the effect of pollen on thrips reproduction is much bigger on a resistant cotton cultivar than on a susceptible cotton cultivar (Table 1). The fitness effects may also differ between pollen species (56).

Little is known about the impact of adult food uptake on longevity and fecundity in hymenopteran sawflies (9, 68). However, it is likely that sawflies require adult food in order to reach their full reproductive potential as they are typically synovigenic and produce yolk-rich eggs (68).

Table 1 Effect of adult feeding on oviposition period and fecundity in herbivorous insects^a

Species (Family)	Mean daily fecundity ^b		Oviposition period (days)		Lifetime fecundity		Conditions		Reference	Remarks	
	Control	+Food	AFFT ^c	Control	+Food	Control	+Food	Control			AFFT ^c
LEPIDOPTERA											
<i>Enasa messaria</i> (Noctuidae)	49.3	123	2.5	5.3	10.6	261.3	1303.8	5	Water	24	19
<i>Hyalocampa zea</i> (Noctuidae)						46	465	10.1	Water		86
<i>Pieris brassicae</i> (Pieridae)	18	27	1.5	7.5	14.4	135	389	2.9	Water	20	106
<i>Epiphyas postvittana</i> (Tortricidae)	51.8	38.6	0.7	8	11.6	414.1	448.3	1.1	Water	23	48
<i>Spodoptera exigua</i> (Hübner)	325.3	163.8	0.5	3.8	9.2	123.6	1507	1.2	Water	30	124
<i>Ostrinia nubilalis</i> (Crambidae)	59.3	61.3	1	5.1	9.2	302.2	563.5	1.9	Water	27:20 (day/night)	82
<i>Cnaphalocyes medinalis</i> (Pyralidae)	1.5	7.8	5.2			5	40	8	Water	30:24 (day/night)	138
<i>Lycena hippothoe</i> (Lycaenidae)	16.2	17.9	1.1	4	28	64.9	500.1	7.7	Water	25	44
<i>Heliconius charitonius</i> (Nymphalidae)	~8.6	~10.5	1.2	<23	>74	~172	~742	~4.3	Sucrose solution (20%)		33
DIPTERA											
<i>Delia radicum</i> (Anthomyiidae)						1	41	41	Water	15-21	42
<i>Bactrocera (Dacus) oleae</i> (Tephritidae)	0	2.6	d _∞						Water	25	12.6
<i>Rhagoletis pomonella</i> (Tephritidae)	0	0.3	d _∞						Water	24	53
	0	6.5	d _∞						Water	24	53
<i>Lampyris eques</i> (Syrphidae)						7.6	83.4	11	Water		31
COLEOPTERA											
<i>Phoradendron semipunctata</i> (Cerambycidae)						7.7	188.7	24.5	Water	18-24	51
<i>Bruchidius obtectus</i> (Bruchidae)						21	47.2	2.2	Water	30	36
<i>Bruchidius quadrimaculatus</i> (Bruchidae)						114.9	132.2	1.2	Water		79
<i>Acanthoscelides obtectus</i> (Bruchidae)						26.9	44	1.6	Water	27	83
<i>Callosobruchius chinensis</i> (Bruchidae)				6.8	33.1	26.9	43	1.6	Water	27	83
<i>Lasiorhynchus komaritsis</i> (Curculionidae)						~22	~65	~3	Water	20	38

HETEROPTERA													
<i>Lygocoris publinus</i> (Miridae)						6.6	12.9	2.0	Potato leaf	Bee-collected pollen	20	28	1
THYSANOPTERA													
<i>Koeleripis pisicorus</i> (Thripidae)	0.1	1.0	15.0						Sucrose solution (10%)	<i>Vicia faba</i> (= host) pollen	20-25	74	m
<i>Thrips fascipennis</i> (Thripidae)	0.3	2.3	6.8						Sucrose solution (10%)	<i>Brassica napus</i> pollen	20-25	74	m
<i>Thrips imaginis</i> (Thripidae)	0.3	4.0	14.7	72.6 ^c	52.1 ^c	19.8	209	10.6	Stamen of snapdragon	Snapdragon anthers (<i>Antirrhinum majus</i>)	24	4	c
<i>Thrips obscuratus</i> (Thripidae)	1.2	6.4	5.3						Peach fruit	Rose pollen	20	121	n
<i>Frankliniella occidentalis</i> (Thripidae)	1.7	5.1	3.1	30	38	50	195	3.9	Susceptible cotton leaf	Cotton (<i>Gossypium barbadense</i>) pollen	27	125	
	0.2	3.6	21.7	24	36	4	130	32.5	Resistant cotton leaf	Cotton (<i>Gossypium barbadense</i>) pollen	27	125	
	2.8	10.4	4.5	21	24	59	250	4.2	Cucumber leaf	Pine (<i>Pinus sylvestris</i>) pollen	25	56	o
<i>Trialeurodes vaporariorum</i> (Thripidae)	0.23	0.61	2.7	6.9	9.3	1.6	6.7	4.1	Sugar maple leaf	Sugar maple (<i>Acer saccharum</i>) pollen	12	84	

^aFor the more extensively studied Lepidoptera and Thysanoptera a representative selection among well-documented studies is presented.

^bDaily fecundity calculated as total eggs divided by oviposition period.

^cAdult food fecundity index (AFI), fecundity with food divided by fecundity of control individuals.

^d∞ indicates that the AFI could not be calculated owing to control fecundity being zero.

^eLarvae had been reared on cotton squares. Data for larvae reared on corn or artificial diet are also given.

^fA range of other adult food sources were also tested.

^gMoths were kept in groups in test cages (four females and four males per cage). Daily fecundity is calculated per female day, lifetime fecundity is based on the initial female number.

^hFecundity data calculated from graphical data. Pollen-feeding treatment was terminated after 74 days.

ⁱOnly median fecundity (at 50% deaths) is given.

^jTotal potential fecundity (eggs laid plus unaid eggs counted after female death).

^kAge at start of the experiment; is unknown as adults were field collected. Experiment was terminated after 280 days when no further oviposition occurred.

^lData refer to mature eggs in dissected females.

^mDaily fecundity calculated per female per day based on 48-h observation.

ⁿDay 3-9 of experiment; females of unknown age.

^oHighest value of six pollen species tested.

The data presented in **Table 1** may underestimate the effect of food on herbivore life-table parameters under natural conditions. Most experiments are conducted with caged individuals that are restricted in their mobility and are presented ad libitum oviposition sites and food. Under natural conditions, mobile herbivores may cover long distances searching for oviposition and foraging sites. As a result they likely use considerably more energy, which would increase the need for adult feeding and enhance its impact on longevity and fecundity (146).

IMPLICATIONS FOR POPULATION STRUCTURE AND POPULATION DYNAMICS OF ADULT HERBIVORES

Population Structure

For those herbivore species that feed on floral resources as adults, the spatial distribution of flowering plants can be an important factor in shaping their (meta-) population structure. When nectar or pollen resources have a fragmented distribution, adult herbivores often show some level of aggregation around their feeding sites. This phenomenon has been described for Lepidoptera (13, 16, 35, 46, 65, 69, 91, 94, 95, 97, 142), Coleoptera (21), Diptera (6, 54, 88), and Thysanoptera (71, 73, 132). Ehrlich & Gilbert (35) showed that the home range of the tropical butterfly *Heliconius ethilla* is more constrained by the presence of pollen plants than by larval food resources. Similarly, Gilbert & Singer (46) showed that the population structure of the nectar-feeding butterfly *Euphydryas editha* was shaped primarily by adult resources rather than by larval resources. In a study by Ohsaki (97) *Pieris rapae* and *Pieris melete* were found mainly at sites where nectar and oviposition plants coexisted, whereas numbers were considerably lower at sites featuring only one of the two resources.

Such herbivore aggregation may be the result of a range of (nonexclusive) mechanisms. Clustering may be due to long-range attrac-

tion to feeding sites, especially when adult food sources are advertised by distinctive floral odors and visual displays (32a, 39, 70). Alternatively, herbivores may be arrested following feeding, or change to a more area-restricted search pattern (6, 12). Spatial learning may enhance herbivore aggregation, as it enables herbivores to return to rewarding food sites (35, 37). Aggregation around food sites can be enhanced further when herbivores use their foraging sites for additional functions, such as roosting or mating (97). Independent from these behavioral mechanisms, a clustered distribution near food resources may be purely a reflection of the longevity and fecundity bonus obtained from food consumption, as an increase in herbivore life span and reproductive success can translate into locally elevated herbivore numbers. Whereas the first three mechanisms require some degree of herbivore mobility, the last mechanism likely has the largest impact on relatively immobile herbivores. The various reports of adult herbivores clustering around food sites may be attributable to one or a combination of these mechanisms.

Evidence for herbivore aggregation around adult feeding sites is not ubiquitous. Wiklund (141) describes that foraging and oviposition habitats of the butterfly *Leptidea sinapis* are spatially separated. Sharp et al. (115) compared data from Lepidoptera surveys with those of nectar surveys. Depending on butterfly species and site, they found both (suggestive) positive and (suggestive) negative correlations, showing that food responses can be idiosyncratic. Williams (144) suggested that interference by males might actually drive ovipositing female *Euphydryas chalcedona* away from nectar habitats. However, Murphy et al. (95) found no evidence for male harassment in *E. chalcedona*.

Whereas the issue of whether and how mate interactions affect feeding patterns remains to be resolved, there is unambiguous evidence that adult foraging can have an effect on mate interactions (73). In those species in which sexes differ in their adult food

requirements (90) and/or foraging behavior (97, 142), the separation of female and male food sites can result in mate segregation (120). Ohsaki (97) showed that the sex ratio of *P. rapae* was strongly male-biased in sites featuring nectar plants only and that it was skewed toward females on sites with only oviposition plants. When food sites occur in isolated patches, this might furthermore result in reproductive isolation of herbivore populations (35).

Population Dynamics

Nectar and pollen feeding not only shapes the spatial distribution of herbivore populations, it can also affect their temporal dynamics. The impact of adult feeding on the longevity and fecundity of individual herbivores (Table 1) can be amplified over generations at the population level. Herbivores that produce no eggs or only very few in the absence of floral resources will not maintain a population in habitats lacking those resources. Even when the floral resources are not strictly essential, they may nevertheless have a large impact on herbivore population dynamics.

Such impacts can be quantified by calculating the intrinsic rate of population increase, r_m , from life tables made in the absence and presence of floral resources. For example, the r_m of *Frankliniella occidentalis* on susceptible cotton increases from 0.16 to 0.22 per day when pollen is added. This means that after 2 months (about two generations) the population will have increased 16,000-fold in the absence of pollen and nearly a million-fold when pollen is permanently available! Also sugar feeding can have a strong effect on the r_m . When adding glucose to a diet of water, the r_m of *Pieris brassicae* increases from 0.079 to 0.096 per day (106) (assuming 50% juvenile mortality).

Given this potential impact of adult feeding on herbivore population growth, it is not surprising that fluctuations in nectar or pollen availability can have a profound effect on herbivore population dynamics. Several studies

comparing herbivore pressure between nectarless cotton varieties and varieties producing extrafloral nectar show larger herbivore populations on the latter (1, 87, 114). Herbivore population dynamics may be driven by pollen availability as well. The numbers of pear thrips (*Taeniothrips inconsequens*) and their damage to stands of sugar maple (*Acer saccharum*) vary dramatically from year to year. Detailed studies by Leskey et al. (84) revealed that this could be attributed to the irregular occurrence of spring flowering in sugar maple stands.

The above examples show that adult food sources can be an important factor in shaping the structure and dynamics of herbivore populations. As herbivore populations are linked directly to both plants and carnivores, the spatial and temporal pattern of nectar and pollen availability can have obvious indirect effects for these adjoining trophic levels. While this adds intriguing direct and indirect interactions to multitrophic systems (Figure 1), it also adds complexity. To avoid confusion, we focus first on the impact of nectar and pollen feeding in a bitrophic (plant-herbivore) context before addressing the role of pollen and nectar in more intricate multitrophic interactions.

IMPLICATIONS FOR PLANT-HERBIVORE INTERACTIONS AND PLANT FITNESS

Some flower-visiting herbivores are important pollinators (39). The efficiency with which they collect and transfer pollen has resulted in the coevolution of many highly specialized pollination syndromes. Whereas the mutualistic benefits in interactions between flowering plants and pollinators among Lepidoptera, Diptera, or Coleoptera have been extensively covered (39, 100), the costs often remain relatively unexplored (17), even though the attraction of adult herbivores may carry particular costs for the flowering plant.

r_m : intrinsic rate of population increase

Multitrophic: involving several trophic levels, with plants, herbivores, and carnivores constituting the first three levels

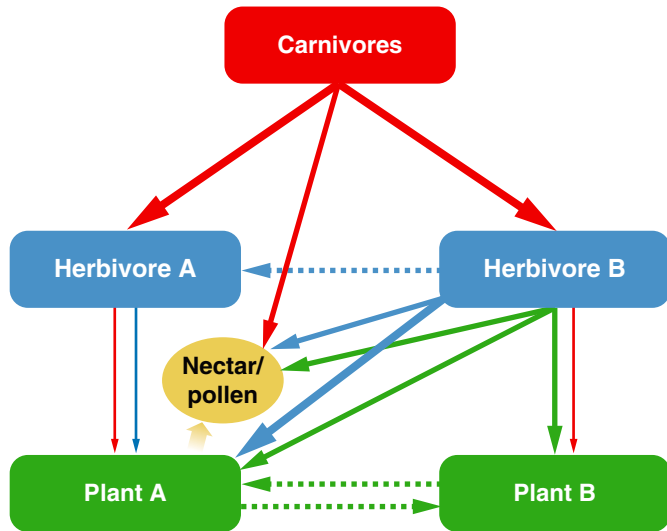


Figure 1

Food web diagram showing main direct and indirect interactions affected by feeding on nectar or pollen. Solid arrows indicate direct exploitation (consumer-resource interactions): fat when negative impact on resource is enhanced by nectar/pollen, thin when negative impact on resource or positive impact on consumer is reduced. Dotted arrows indicate negative indirect interactions possibly enhanced by nectar/pollen. Green: herbivore-mediated, plant-plant interactions; blue: plant-mediated, herbivore-herbivore interactions; red: tritrophic level interactions. See main text for detailed explanations.

Producing floral rewards represents a direct cost in terms of invested metabolites. These costs are usually limited (but see References 52, 102) and they are typically outweighed by the benefits of achieving pollination. However, floral rewards are also exploited by insects that contribute little or nothing to pollination, so-called nectar/pollen thieves (59, 80, 143).

Some nonpollinating insects use their biting mouthparts to create a shortcut to the often hidden floral rewards (60). Among herbivores this nectar/pollen robbery has been described to occur in several coleopteran species (60). For the plant, the fitness consequences of the damage inflicted during the robbery of floral rewards can be substantial (61).

Ineffective flower visitors may also interfere with actual pollination, either through

physical interactions with potential pollinators (interference competition) (72) or through reward depletion (exploitative competition) (22, 78). Unlike nectar feeding, pollen feeding constitutes a depletion of the reward as well as the gametes. Studies show that a substantial fraction of pollen can be consumed by flower and bud herbivores (75).

Additional indirect costs may apply when flower-visiting herbivores live up to their name and supplement their nectar and pollen diet with plant tissue. Feeding damage may be inflicted directly by the flower-visiting adults or by their offspring, when nectar-/pollen-feeding adults use their feeding plant as an oviposition site.

Adult herbivores with biting or piercing mouthparts may combine nectar or pollen consumption with feeding on either floral tissue or vegetative structures. Floral herbivory may include damage to floral nectaries, stamens, or the ovary. As feeding on floral tissue commonly involves destruction of gametes, it often has a stronger direct impact on plant fitness than does foliar herbivory (118, 149). Damage to the inflorescence may negatively affect the pollen quality as well as quantity (3) and may make the flower, the flowering plant, or even patches of flowering plants less attractive to pollinators (78).

An additional category of costs may arise if the presence of adult food increases a plant's chance to be selected as an oviposition site (2, 15, 64, 65). For the plant, oviposition can be considerably more costly than adult herbivory, given that larval stages typically consume more tissue and are usually less mobile and thus less likely to leave the plant. The fitness costs of oviposition can be particularly high in species whose females cluster their eggs and/or show oviposition aggregations.

Nectar or pollen feeding by herbivores may furthermore undermine plant resistance mechanisms when it allows herbivores to circumvent or neutralize the impact of plant secondary chemistry. In plant species whose pollen contains relatively low levels of

secondary metabolites (30), this evasive pollen feeding can render the antibiosis type of resistance ineffective (63, 125).

Effect of Adult Food on Oviposition Patterns

Given that the distribution of feeding sites affects the distribution patterns of adult herbivores, it is not surprising that the spatial pattern in which female herbivores distribute their eggs can be affected by adult food as well. By feeding in the vicinity of oviposition patches or selecting oviposition hosts near adult food plants, herbivores save time and energy and reduce predation risks. Using the same plant as an oviposition and feeding site furthermore simplifies a herbivore's search task. On the basis of the concept that neural limitation may constrain the speed and accuracy of herbivore decisions (10), Janz et al. (65) proposed that neural conflicts associated with performing multiple tasks may explain ovipositions on (suboptimal) nectar plants.

There is ample evidence that the availability of adult food sources is a factor shaping the choice of oviposition sites in Lepidoptera (2, 16, 47, 64, 69, 94, 95), Diptera (6, 101), Coleoptera (23), and Thysanoptera (74). The impact of floral food on oviposition decisions may depend on the scale at which interactions are studied. Janz (64) showed that the butterfly *Vanessa cardui* distributes its eggs evenly among flowering and nonflowering *Cirsium arvense* when offered in close proximity, whereas it spends more time and lays more eggs in flowering versus nonflowering patches when these plants are spatially separated.

It often remains unclear to what extent the impact of food sites on oviposition decisions is due to adult food use, or whether enhanced oviposition can be (partly) explained by the enhanced apparency of the flowering plant (40, 149). For herbivore species whose larvae preferably develop in reproductive structures, a preference for flowering plants may reflect optimal oviposition as well as optimal

foraging. When given a choice between non-flowering tobacco and flowering tobacco, with flowers either removed or intact, *Helicoverpa armigera* prefers the latter for oviposition (43). Moreover, oviposition by this species on a number of crop plants peaks at time of flowering (99). However, the fact that this match between oviposition frequency and flowering phenology also applies to nectarless plants such as maize (99) shows that the preference for flowering plants is not strictly based on adult food needs.

Adler & Bronstein (2) circumvented these confounding factors by artificially manipulating nectar quantity rather than removing flowers. They demonstrated that nectar supplementation enhanced the chance for plants to receive *Manduca sexta* eggs, whereas nectar removal did not result in a concomitant reduction in egg deposition. Further evidence for the effect of food resources on oviposition patterns was presented by Murphy (94), who observed an increased effect of nectar on activity patterns of *Euphydryas chalcedona* females at the end of the season, coinciding with the increase in nectar dependence in aging females of this species.

The impact of adult feeding on oviposition patterns is particularly evident in systems in which female feeding forms an integral part of the oviposition sequence. Floral oviposition by the noctuid moth *Hadena bicurvis* is typically preceded by nectar feeding on the same flower. When the nectar-feeding behavior is suppressed by satiating females with a sugar solution, floral ovipositions are replaced by (nonviable) random ovipositions (15).

The proximity of adult food may result in the acceptance of inferior host plants (20, 101). In some instances this may actually lead to oviposition on novel plants. When larvae manage to survive, this mechanism may extend the host range of herbivorous insects. Chew & Robbins (20) suggest that host range expansion is likely in herbivores whose larvae feed on flowers, given that flowers often contain lower levels of secondary metabolites.

Optimal oviposition theory:

the theory that an animal's oviposition behavior should maximize its reproductive fitness

Optimal foraging theory:

the theory that foraging behavior should maximize an animal's net rate of food or nutrient intake

Parent-offspring conflict:

conflict derived from conditions at which genetic interests of parents and offspring are not identical

Dioecy: plant species with unisexual male and female flowers on separate plant individuals

Herbivores have long been assumed to select oviposition sites primarily on the basis of their suitability for larval development (89). However, many studies report weak or even negative correlations between female preference and larval performance (89, 112, 123). Jaenike (62) was the first to realize that these apparently maladaptive choices may be reconciled with the optimal oviposition theory when we consider that a female can increase her reproductive success by selecting oviposition sites that are optimal in terms of her own survival, rather than primarily optimizing offspring performance. Subsequent studies have provided evidence that selection of oviposition sites may be driven partly or primarily by the proximity (35, 46, 64, 94) and quality (62, 110–112) of adult food sources. Scheirs and colleagues (110–112) analyzed oviposition choices by two dipteran leafminers and a chrysomelid (*Alicia carduorum*) that feed on their host plants before oviposition. The authors demonstrated that plant choice is correlated more closely to the performance of the ovipositing adult than to offspring performance. In these cases the optimal behavior of female herbivores should be predicted by considering its overall impact on net reproduction (maximizing the number of surviving offspring) (110), thus integrating optimal oviposition theory (maximizing offspring survival) and optimal foraging theory (maximizing female survival and fecundity). In some cases in which plants are highly suitable as an adult food source while relatively unsuitable as larval host plants this may generate a parent-offspring conflict. As herbivore plant choices in the above studies do not compromise larval performance, these examples do not represent such a conflict. However, other studies show that nectar-feeding females may concentrate oviposition on flowering plant species even when the oviposition plant is relatively unsuitable as a host for their offspring (20, 25, 43), indicating that a parent-offspring conflict in host plant choice can occur.

Plants with sexual dimorphism (dioecy) provide a unique system to study the effect

of floral rewards on plant-herbivore interactions, given that in dioecious species pollen is available only from staminate (male) individuals. Herbivory in dioecious plants is often biased toward pollen-bearing plants (24). Whereas this male bias is most pronounced in herbivores attacking flowers and buds, it also extends to herbivores attacking vegetative structures (5). Various mechanisms have been proposed to explain this sex-biased herbivory, including a range of morphological and biochemical factors (24). However, the possibility that pollen exploitation by herbivores may concentrate herbivores on staminate plants has been largely overlooked. To our knowledge, the study by Feller et al. (41) is the only example to have considered this mechanism. The authors show that the specialist thrips *Heterotrips arisaemae* occurs in higher numbers and causes more damage on *Arisaema triphyllum* with male flowers than on female or asexual plants. Because female and male plants in their experiments did not show differences in nitrogen levels or plant defensive chemistry, the difference was attributed to pollen feeding by adult thrips.

IMPLICATIONS FOR HERBIVORE-MEDIATED PLANT-PLANT INTERACTIONS

When herbivores oviposit in direct proximity to their foraging sites, this may result in enhanced herbivore pressure on the nectar-/pollen-producing plant itself (2, 15, 64, 65) or, alternatively, on plants in its direct vicinity (64, 69, 95). These two scenarios likely have opposing fitness consequences for the nectar-/pollen-producing plant (**Table 2**). Whereas the former scenario may represent substantial fitness costs, the latter scenario may actually generate competitive benefits to the flowering plant when recruited herbivores effectively weaken the competitive strength of its neighbors. The potential fitness costs or benefits to the nectar-/pollen-producing plant depend on the host range and host preference of the

Table 2 The potential fitness costs or benefits to the nectar-/pollen-producing plant of attracting foraging herbivores

Foraging plant used for oviposition?	Oviposition host range	Tendency to move between plants	Impact on foraging plant ^a	Examples			Reference	
				Adult food plant	Herbivore	Herbivore		
Yes	Narrow (monophagous, oligophagous)	High (long range)	–	<i>Cirsium arvense</i> <i>Lotus corniculatus</i>		<i>Africa carduorum</i> <i>Polymnatus icarus</i>	139 65	
		High (short range)	– ^b	<i>Gossypium</i> spp. <i>Vicia faba</i>		<i>Anthonomus grandis</i> <i>Kakothrips pisivorus</i>	74	
	Broad (polyphagous)	Low	–	<i>Arisaema triphyllum</i>		<i>Heterothrips arisamae</i>	41	
		High (long range)	–					
		High (short range)	–/+	<i>Cirsium arvense</i> <i>Helianthus annuus</i>		<i>Vanessa cardui</i> <i>Helicoverpa armigera</i>	64 43	
	No	Narrow (monophagous, oligophagous)	Low	–				
			Long range	0/+	Adult food plant <i>Monardella odoratissima</i> , a.o. <i>Cirsium japonicum</i> a.o.	Oviposition plant <i>Penstemon newberryi</i> Brassicaceae	Herbivore <i>Euphydryas chalcedona</i> <i>Pieris rapae</i> ^c	94 97
		Broad (polyphagous)	Short range	+	<i>Brassica napus</i> <i>Eriastrum densifolium</i>	<i>Vicia faba</i> <i>Nicotiana attenuata</i>	<i>Kakothrips pisivorus</i> <i>Manduca quinquemaculata</i>	74 69
			Long range	0/+				
			Short range	+	<i>Lamium amplexicaule</i>	<i>Citrus</i> spp.	<i>Frankliniella occidentalis</i>	92

^a Assuming no significant role in pollination.

^b Possible benefit when direct competitors are conspecifics.

^c May change to area-restricted search following nectar feeding (12).

Polyphagous:

herbivores feeding on several plant families

Monophagous

herbivores feeding on one plant species

Oligophagous

herbivores feeding on several species within one family

Apparent competition:

indirect interaction defined as a negative effect of one species on another species, mediated through action of shared natural enemies

herbivore, as well as on its pattern of movement (**Table 2**).

When adult herbivores use the foraging plant for oviposition, the plant likely incurs a net cost. This cost will be most pronounced when the herbivore is an oviposition specialist on the foraging plant and has a low tendency to move between plants. Some of the fitness costs, however, may be outweighed when herbivores, in addition to ovipositing onto the foraging plant, also deposit eggs onto neighboring plants with which the foraging plant competes for resources. This scenario might occur if the herbivore is polyphagous or if the plant's competitors are conspecifics (**Table 2**). The fitness balance may even become positive when the foraging plant is not included within the herbivore's range of oviposition hosts, especially when the herbivore is rather polyphagous and tends to stay in the proximity of its foraging plant (**Table 2**), e.g., when feeding induces herbivores to change to an area-restricted host search (6, 12).

Enhanced herbivory has been recognized as an important fitness cost for the nectar-/pollen-producing plant, potentially shaping both floral traits (5, 108) and the production of extrafloral nectar (108, 136). To our knowledge, the fitness benefits of recruiting herbivores of neighboring plants through the production of nectar or pollen have not yet been considered.

The concept that plants may increase their fitness by unloading herbivores onto their neighbors has been previously proposed (34, 127, 128). However, these papers focused on tissue-feeding herbivore larvae deterred by herbivore-induced plant defense. Although the expulsion of tissue-feeding larvae may relieve the induced plant from herbivory, the impact on neighboring plants is often limited. As most insect herbivores tend to be monophagous or oligophagous, they are expected to primarily compromise neighbors in stands of conspecific plants (128; but see 98, 122). Attracting herbivores of neighboring plants by providing pollen or nectar (**Figure 1**, green arrows) may have a broader

impact, given that herbivores are often less specialized with regard to adult nectar/pollen feeding (97).

Herbivore-Mediated Apparent Competition Between Plants

When plant traits increase herbivory on associated plant species, thereby reducing their local abundance, this qualifies as herbivore-mediated apparent competition (18, 55). A number of studies (18, 98, 104, 122) have shown that sharing a herbivore species can result in reduced coexistence of host plant species. Similar effects are expected to occur (**Figure 1**, green arrows) when one plant serves as the adult food plant and the other serves as the oviposition host (6, 64, 69, 95).

In addition to short-term apparent competition between plants, which results from plant-mediated herbivore foraging and oviposition behavior, the presence of other plant species may also give rise to long-term apparent competition that acts through the herbivore numerical response (45, 50). In theory this is a likely scenario for indirect interactions between a larval host plant and nectar plants, because many herbivores can only persist and build up populations in the presence of both plant types. That these long-term indirect interactions have not yet been reported may have several reasons: (a) When these interactions result in competitive exclusion (or habitat segregation) the plants may no longer be observed together. (b) The interactions can be highly diffusive when many different species act as nectar source or host plant. Long-term indirect interactions are most likely to become apparent in systems in which the herbivore is (locally) monophagous with regard to host plant and adult food. (c) When herbivore species are highly mobile they may obtain nectar from other habitats.

Most herbivore-mediated indirect interactions are to some extent asymmetric (18), with one plant species suffering from the interaction more than the other species. When the interaction is between one plant species

serving as larval host plant and another providing adult food, the interaction is often negative for one species only (**Table 2**).

Until now we have considered interspecific interactions. Another, still theoretical possibility is that conspecific neighboring plants are negatively affected by the action of nectar- or pollen-feeding herbivores. This intraspecific enemy-mediated apparent competition can be seen as a special case of the Janzen-Connell hypothesis. This hypothesis explains the spacing of conspecific plants by enhanced herbivory on young plants in the vicinity of parent plants (57, 66). The tendency of some herbivores to oviposit onto plants of the same species used for adult feeding (2, 26, 65) may give rise to such density-dependent interactions.

IMPLICATIONS FOR HERBIVORE-HERBIVORE INTERACTIONS

Herbivores feeding on the same host plant species likely interact competitively (29). Apart from a mutual reduction in host plant density, a negative impact may also result from interactions at the individual plant level. Some common mechanisms include intraguild predation (116), resource preemption (29), and indirect interactions mediated by herbivore-induced changes in primary or secondary metabolites, changing the quality of the host plant (96). The presence of floral resources may affect competitive interactions when only one of the competing herbivores feeds on nectar or pollen (**Figure 1**, blue arrows) or when adult feeding has an asymmetrical effect on the reproductive fitness of the two herbivores (**Table 1**).

When *Frankliniella occidentalis* invaded Northern European greenhouses, it rapidly replaced the native *Thrips tabaci* as the main thrips pest. This could not be explained through differences in their intrinsic rate of increase, as this is similar for the two species (129). Both species also act as intraguild predators of mite eggs and thrips (145). The

dominance of *F. occidentalis* may, however, result from its more active foraging on pollen and nectar in flowering crops relative to *T. tabaci* (92).

At the individual plant level, root feeding can have a strong negative effect on the development of shoot-feeding herbivores (11). In interactions between the root-feeding anthomyiid fly (*Delia radicum*) and the large cabbage white butterfly *Pieris brassicae* feeding on *Brassica nigra* (117), nectar feeding is essential for egg production by the root fly and less so for the butterfly (**Table 2**). Nectar availability may thus have an indirect negative effect on the butterfly.

In certain cases the indirect interaction between herbivores on a host plant may be facilitative (29). The larva of the pyralid butterfly *Omphalocera munroei* regularly defoliate its shrub host plant (*Asimina*), thereby inducing young growth during summer. Another specialist herbivore, *Eurytides marcellus*, requires young foliage for successful larval development and therefore benefits from the presence of the other herbivore (27). Having suitable nectar plants available for the butterfly *O. munroei* could in this case indirectly benefit *E. marcellus*.

IMPLICATIONS FOR TRITROPHIC LEVEL INTERACTIONS AND (BIOLOGICAL) PEST CONTROL

Up to this point we have focused on how communities of herbivores and plants are affected by feeding on nectar or pollen. We thereby deliberately assumed the third trophic level to be absent or at least ineffective. However, when natural enemies of herbivores are important components of the systems we consider, this may have implications for the impact of floral resources on these systems (**Figure 1**). First, when different herbivores share a common enemy they may perform negative or positive indirect interactions (enemy-mediated apparent competition or mutualism) (18, 133), and it is not yet clear how nectar or pollen

Adult food fecundity index

(AFFI): impact of adult feeding on fecundity expressed as mean fecundity realized by adults provided food divided by fecundity of unfed individuals

feeding by one of the herbivores may affect this type of interaction. Second, many predators and parasitoids of herbivores utilize these food sources as well (137a), which may support their top-down control on the herbivores and may modify or even override the direct effect of these food sources on the herbivores. The top-down control may be stronger on nectar-/pollen-producing plants (**Figure 1**), in which case the food production may become part of a plant's indirect defense (77, 108a, 136). Nectar/pollen production may even divert predators and parasitoids from neighboring plants, which as a result may suffer from reduced herbivore control. In other cases the predators and parasitoids recruited by the nectar-/pollen-producing plant may spillover onto neighboring plants (**Figure 1**). In the latter case the food production can be seen as an ecosystem service enhancing herbivore control (7, 49).

Biological control workers have long been aware that the scarcity of flowering plants in simplified agricultural systems can severely impede the survival and reproduction of parasitoids and predators (58, 148). Flowering noncrop elements are increasingly advocated and used as a simple and potentially powerful tool to resolve this impediment and thus enhance the effectiveness of biological pest control (49).

In many instances, however, herbivorous pests benefit from the food as well. A range of nectar-feeding herbivores reach higher population densities and inflict more damage on extrafloral nectar-producing cotton varieties than on nectariless varieties (1, 87, 113), showing that nectar availability can enhance herbivory. It also underlines that one cannot ignore nectar and/or pollen feeding when studying the impact of biodiversity on herbivore levels.

Other studies confirm that the presence of adult food can enhance herbivore population densities in a range of agricultural systems (101, 119). Cabbage (*Brassica oleracea*) appears to be the most thoroughly studied crop with regard to effects of flowering vegetation on

pest densities. Several studies (81, 147, 150) have reported increased ovipositions by *P. rapae* onto *B. oleracea* in the presence of flowering companion plants. Borders of flowering *Iberis umbellata* surrounding *B. oleracea* increased oviposition by *Trichoplusia ni*, but not by *P. rapae* (12).

Whereas these results may point to nectar feeding by the adult herbivores as the mechanism explaining enhanced oviposition, the complex interactions underlying such field studies make it difficult to single out the effect of nectar. One further piece of evidence was provided by a recent study (145a) showing that herbivores in cabbage plots adjacent to flowering margins have significantly elevated sugar levels relative to individuals in control fields lacking nectar.

The important question therefore is, How will floral resources affect a system in which both the herbivores and their natural enemies feed on flowers? The study by van Rijn et al. (132) provides an experimental and theoretical framework to analyze this problem (130). One important aspect affecting the balance between herbivores and natural enemies is the relative impact of the resource on their life histories, expressed in the AFFI (adult food fecundity index). For Lepidoptera and bruchid beetles listed in **Table 1**, this index varies from 1 to 10. The parasitoids attacking these herbivores, however, generally obtain larger lifetime fecundity benefits from adult feeding, with AFFI values ranging between 10 and 100 (146). For thrips and its acarid predators a similar difference in response to pollen feeding can be observed. The maximum AFFI of thrips on susceptible host plants is about 4 (**Table 1**). For the different predatory mites, pollen makes the difference between no reproduction and maximum reproduction as long as prey are scarce (131). In these systems floral resources stimulate the fecundity of the natural enemies more than the fecundity of their herbivore prey. However, this does not hold for the dipteran herbivores in **Table 1**, as they fully depend on nectar for reproduction.

The impact of floral resources likely depends on the timescale at which the results are measured (130, 132). On a very short timescale herbivores can merely be stimulated by the floral resources. Only at longer timescales (relative to their generation time) can natural enemies build up sufficient numbers to impede herbivore population growth and convert the floral resources into a significant mortality factor for the herbivores. When the herbivores have higher AFFI values relative to that of their natural enemies, the interaction periods must be longer before floral resources benefit biological control.

Not all flowers are equally suitable as food source for herbivores and natural enemies. Wäckers (135) discusses how availability, apparency, accessibility, and nutritional suitability of flowers may differ between insect groups. Understanding these factors may allow us to select food sources that provide nutritional benefits for natural enemies without providing suitable food for the herbivores (7, 56, 134, 135).

CONCLUSIONS AND FUTURE RESEARCH

Nectar and pollen play an important role as food sources in plant-pollinator interactions. Their role in shaping food web interactions, however, has been largely overlooked. This in spite of the fact that many insects that are characterized as either herbivores, carnivores, or detritivores on the basis of the juvenile lifestyle depend on nectar or pollen in their adult life. For herbivorous insects this dependence can significantly affect their population dynamics, distribution, and host plant choice. These processes also have consequences at the plant level. Plants that produce nectar and/or pollen or grow in the proximity of a nectar/pollen source may increase or decrease specific types of herbivory. Nectar/pollen feeding may also affect direct or resource competition among plants through herbivore-mediated apparent competition. Finally, through its impact on herbivores as well as carnivores, nectar/pollen

feeding may alter the balance between top-down and bottom-up effects.

Despite their potential impact on the evolution and ecology of trophic interactions, the following aspects have not yet received sufficient scientific attention.

- The benefits of nectar and pollen feeding in terms of survival and fecundity can be different among species and insect groups. Estimating and comparing the AFFI values for a wider range of species may help researchers to understand the patterns and mechanisms underlying this variation. To fully appreciate nectar as an energy source for adult herbivores, (semi)field studies are required in which the insects have to forage for both their food and host plants.
- More studies are needed to test if and how the availability of pollen or nectar is limiting the population growth and/or population distribution of herbivores with high AFFI.
- The relationship between food plant choice and host plant choice of polyphagous herbivores should be studied in different experimental combinations of flowering and nonflowering plant species. This may reveal the potential costs of enhanced herbivory associated with nectar/pollen production, as well as the effects on neighboring plants.
- Field observations and experimentation may reveal the potential negative impact of nectar-/pollen-producing plants on specific neighboring plants through herbivore-mediated apparent competition, both at the behavioral and population-dynamical timescale.
- If such apparent competition occurs, it needs to be established whether this ultimately benefits the nectar-/pollen-producing plants by reducing direct and resource competition.
- Feeding on nectar and pollen during part of the insects' life cycle

can be seen as life-history omnivory/polyphagy (99a) and creates additional weak trophic links, which may con-

tribute to the stability of the ecosystem (95a). This thesis requires further theoretical and experimental validation.

SUMMARY POINTS

1. The current review brings together widely scattered literature to quantify the impact of adult feeding on herbivore reproductive fitness among insect herbivores from several orders.
2. Different ways in which adult food use can shape herbivore population structure and population dynamics are shown.
3. The role of adult nectar or pollen feeding as an indirect mechanism mediating plant-herbivore-carnivore interactions is explored.
4. Previously unrecognized nectar-/pollen-mediated interactions, such as the effect of floral food on plant-plant competition are identified.
5. Conditions under which nectar or pollen feeding by herbivores may result in increased pest problems are explored.
6. Implications for biological pest control are addressed as well as ways in which we can optimize herbivore biological control through use of selective food sources.

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