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Food for protection: an introduction

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It has long been recognized that plants provide floral nectar and pollen to attract pollinators. In addition, plants also provide specific foods as part of a protection strategy. By producing extrafloral nectar or food bodies, plants attract predators that can act as bodyguards, clearing the plant of its antagonists. A wide range of arthropods with a primarily carnivorous lifestyle require plant-provided food as an indispensable part of their diet (Table 1.1). In some arthropod groups, the adult stages depend on nectar or pollen for survival and reproduction, whereas in other groups all stages feed on plant-provided food in addition to prey. Only recently have we started to appreciate the implications of non-prey food for plant–herbivore–carnivore interactions. Insight into these food-mediated interactions not only helps in understanding the functioning of multitrophic interactions in natural ecosystems, it also has direct implications for the use of food supplements in biological control programs. In this introductory chapter we first sketch a historical perspective on the topic of plant-provided foods. Subsequently, we present an outline of the book and briefly introduce the different chapters.

The scientific discovery of plant-provided foods

Humans have always shared the sweet tooth of many arthropods. However, for long we lacked the ability to obtain sugars directly from plants, and thus were entirely dependent on insects as intermediaries. Therefore, it is not surprising that nectar and honeydew in connection with insects attracted the attention of naturalists early on.

The Old Testament provides the first accounts of honeydew. The biblical “manna” (Exodus 16:13–36) is believed to be honeydew from the scale insect

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Coccus manniparus feeding on the shrub *Tamarix mannifera* (Bodenheimer 1947). In the Sinai, this honeydew is still collected as an alternative to honey under the local name of “menn” or “menu”. Based on references by Al-Birūnī (973–1051) in his book on materia medica, Persian and Arab scholars of the medieval period already knew that honeydew originated from insects. Nevertheless, European naturalists argued for many centuries about the nature and origin of honeydew, before Leche (1765), basing himself on observations in Réamur’s *Mémoires sur les insectes* (1734–42), described the production of honeydew by sap-feeding insects as well as the fact that ants tend them to obtain the sugar-rich solution.

Written records on floral nectar date back to antiquity as well. The Greek physician Dioscorides (50 BC – AD 10) wrote about floral nectar as the basis of honey production and the medicinal uses of the latter. The Roman naturalist Pliny the Elder (AD 23–79) in his *Naturalis Historiae* provides detailed accounts of nectar types secreted by flowers as well as their collection by bees as a basis for honey production:

The honey that we see formed in the calix of flowers is of a rich and unctuous nature; that which is made from rosemary is thick, while that which is candied is little esteemed. Thyme honey does not coagulate, and on being touched will draw out into thin viscous threads, a thing which is the principal proof of its heaviness.

Both Pliny and Dioscorides already recognized that the phenomenon of toxic honey relates to its floral origin. They correctly attributed the toxicity of honey from the Black Sea region to the nectar from particular flowers (a.o. *Rhododendron* spp. and oleander (*Nerium oleander*)). The ecological role of nectar as a pollination reward was studied experimentally for the first time by Sprengel (1793), who did groundbreaking work on pollination ecology, recognizing and describing a range of pollination-related phenomena. Darwin (1855) built upon Sprengel’s work by placing nectar production in the context of plant–pollinator co-evolution.

Hall (1762) is believed to have been the first to make the distinction between floral and extrafloral nectaries. In 1855, Glover reported that glands (extrafloral nectaries) of cotton (*Gossypium* spp.) secrete a sweet substance, which ants, bees, wasps, and plant bugs avail themselves of as food (Trelease 1879). Around that time, Darwin (1855) described that extrafloral nectaries on *Vicia* spp. are visited by bees, ants, and flies and suggested that they have a function other than pollination. Delpino (1873) recognized the specific functions of floral and extrafloral nectaries and proposed the terms “nuptial” and “extra-nuptial” nectaries as phrases that indicate their different ecological roles. He observed that “extra-nuptial nectar glands, by their secretion, attract to the plant that bears them,

hordes of ants (rarely wasps)” and asserted that these “constitute a temporary and changing bodyguard”. Around the same time, Thomas Belt (Belt 1874) argued that plants obtain a defensive benefit from insects visiting extrafloral nectaries and/or food bodies. The actual protective function of extrafloral nectaries was first demonstrated by Von Wettstein (1889). He excluded ants from bracteal nectaries on the flowering heads of two Compositae species, and was able to show that ant-tended plants suffered less damage to seeds by beetles and hemipteran bugs.

For almost a century following the seminal publications by Delpino and Belt, the protective function of plant-provided food was subject to intense debate (Bentley 1977). For many decades the concept of food as an indirect defense mechanism was discarded, before Janzen (1966) and others in the 1960s revived the idea. Through extensive experimental work, they were able to substantiate the fact that ants recruited to extrafloral nectaries and food bodies can benefit plant fitness.

Plant-provided food and biological control

The role of food supplements in plant–herbivore–carnivore interactions is not only an important topic in basic ecology, but is also directly linked to the applied discipline of biological pest control. Defensive food provision has evolved repeatedly and independently, suggesting that it constitutes a powerful mechanism through which plants can enhance the effectiveness of carnivores. We pursue the same objective in biological control programs. Here too, we aim at enhancing the efficacy with which carnivores control herbivorous pests.

The possibility of using predators for biological control of insect pests was recognized in China as far back as the fourth century AD. Hsi Han (AD 304) described in *Records of the Plants and Trees of the Southern Regions* how bags holding ant nests were traded in southern China. The bags were placed in citrus trees in order to protect the fruits from insect attacks. Farmers interconnected trees by means of bamboo bridges allowing ants to move between trees.

In biological control textbooks, this example is widely featured as the first known case of biological control. However, it is much less known that it also represents the first instance in which food supplements were used to enhance the efficacy of the biological control agent. Farmers provided food supplements, such as intestines and silkworm larvae, to help ants establish (Beattie 1985). The use of ants for biological control was not restricted to the Far East. In the New World, Indians independently developed methods to use ants as biological control agents. Rather than bringing the ants to the crop, they took the opposite approach by sowing cotton plants in the vicinity of ant nests (Cook 1905). Here

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again, food supplements played an integral role. The effectiveness of this practice can be explained by the fact that cotton features a range of extrafloral nectaries (Mound 1962) that are eagerly visited by ants (Rudgers 2002). By sowing cotton in the proximity of ant nests the Indians exploited this natural food-mediated association between cotton plants and predaceous ants.

In the twentieth century, awareness grew among biological control workers that the absence of non-prey food sources in agriculture or forestry could impose a serious constraint on the effectiveness of natural enemies (Illingworth 1921; Schneider 1940; Wolcott 1942; Hocking 1966). Hocking (1966) pointed out that lack of food availability can also prevent introduced parasitoids from establishing in classical biological control programs. Adding food sources to agroecosystems could be a simple and effective way to enhance the effectiveness of biological control programs.

Three types of approaches have been proposed to alleviate the shortage of food in modern monocultures. The first approach involves the diversification of agroecosystems, either through the use of non-crops in undergrowth or field margins (Van Emden 1965; Altieri and Whitcomb 1979) or through mixed cropping, e.g., with crops featuring flowers or extrafloral nectaries. A second approach involves the use of food sprays or other types of artificial food supplements to cater for the food needs of biological control agents (Hagen 1986). Finally, some crops produce suitable food supplements themselves. Examples of extrafloral nectar producing crops include *Prunus* spp. (cherry, plum, peach, almond), cassava, faba bean, zucchini, pumpkin, cashew, and cotton. These crop-produced foods may suffice as food sources for predators and parasitoids. In other cases, there may be room for plant breeding to improve the timing, quantity, and quality of food production, to better match the nutritional needs of biological control agents (Rogers 1985).

Cultivated cotton also provides a prominent example in which the potential for negative effects of food supplements became apparent. Cotton extrafloral nectaries are not only used by predators and parasitoids, but several major cotton pest species are known to feed on cotton extrafloral nectar as well. The generous use of broad-spectrum insecticides in the mid twentieth century not only temporarily eliminated herbivores from cotton fields, it also proved effective in clearing the field of predators and parasitoids. As a result, the indirect defensive function of extrafloral nectaries became obsolete. Under these conditions, nectar-bearing cotton varieties sometimes suffered higher levels of herbivore damage than nectariless varieties (Lukefahr *et al.* 1965; Adjei-Mafo and Wilson 1983). The replacement of broad-spectrum insecticides by more selective control methods rekindled the interest in cotton extrafloral nectar as a food source for beneficials (Rogers 1985; Schuster and Calderon 1986). Whereas the conditions of cotton

production during the green revolution were obviously a far cry from the conditions of modern-day conservation biological control programs, this example nevertheless shows that we cannot ignore herbivore benefits when studying the impact of food supplements on biological control programs.

Outline of this book

This historical overview indicates how the provision of food by plants, and its impact on the effectiveness of predators and parasitoids, gradually gained interest. In the last two or three decades this interest seems to have accelerated. This has stimulated us to compose a book that reviews the current state of knowledge, and indicates directions of future research on this specific aspect of multitrophic (plant–herbivore–carnivore) interactions.

In the first section of this book, the spotlight is on the plants. What types of food supplements do they provide, why does food provision evolve and how does it affect plant–insect interactions? In the second section, the arthropods that feed on plant-provided food are at center stage. Why do they feed on this food, and how does it affect their behavior and life history? In the third section, we focus on the dynamics of the interactions between plants, carnivores, and herbivores. How do these interactions affect herbivore population levels, and what factors define the success of biological control?

Part I: Food provision by plants

Plants employ nutritional supplements to obtain a range of services. Best known are the mutualistic interactions in which sessile plants provide food in return for dispersal. This includes floral nectar to attract pollinators (Faegri and Van der Pijl 1979), and the fleshy fruit tissues and elaiosomes promoting seed dispersal. Other plant-provided foods, such as extrafloral nectar and food bodies, are likely to have evolved primarily to attract carnivores in order to obtain their protective services (Turlings and Wäckers 2004). As such they represent the most suitable models to study the evolution and functioning of food-for-protection strategies. Plant-provided foods are not only used by the intended consumers, they may also be exploited by arthropods from other guilds. Some of these unintended interactions are to the benefit of the plant, others to the detriment.

A separate category of food supplements comprises those that have evolved for functions other than arthropod nutrition. Pollen, for instance, primarily serves as a vehicle for gene transfer, but may serve a secondary function in attracting pollinators. Honeydew, the plant-derived waste product of phloem-feeding insects, can also be an important food source for (predaceous) arthropods. When ants tend

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sap-feeders to collect the honeydew, this sugar source can serve a (secondary) defensive function that may benefit both the sap-feeders and the plants.

Finally, some predators can feed directly on photosynthetic or reproductive plant tissue without special adaptations from the plant. It is obvious that these different food categories will differ in their implications for plant-carnivore interactions.

In this book, Wäckers (Chapter 2) presents an overview of the food sources provided by plants, and reviews their suitability in terms of their availability, detectability, accessibility, nutritional value, and mortality risks for the various arthropods that feed on them. The identified differences can be helpful in understanding the evolution and functioning of food supplements, and in selecting food supplements for use in biological control programs.

Koptur (Chapter 3) discusses the evolutionary origin of extrafloral nectar. A comparison is made between floral and extrafloral nectar, with respect to nectar composition, its consumers, and the ecological factors modifying its production. A strong emphasis is laid on ant-plant interactions.

Sabelis, van Rijn, and Janssen (Chapter 4) focus more closely on the evolutionary stability of extrafloral nectar production and of other nutritional rewards in the food-for-protection mutualism: how can they persist in the face of cheaters and other organisms ready to reap the benefits?

Part II: Arthropods feeding on plant-provided food

As most arthropod predators and parasitoids are able to feed on prey as well as on plant-provided food, they could actually be called omnivores. However, the need for plant food of these arthropods has long been overlooked. This has a number of reasons. Many species feed specifically on plant-provided food (nectar and/or pollen) and cause no visible damage to the plants. In some of these insects the stages that are carnivorous are not the stages that feed on plant substances. In other arthropods, carnivorous stages can also feed on plant tissue, but without obvious adaptations in their feeding apparatus.

In order to structure the great variety in plant-feeding among predators and parasitoids, we propose the following typology (see also Table 1.1).

- Life-history omnivory. Many holometabolic insects change their lifestyle during metamorphosis, and some of these insects shift from carnivory in the larval stage to herbivory (or nectarivory) in the adult stage. The larvae of some hymenopterans, such as parasitoids, most ants, and social wasps, only feed on animal prey (or hosts). Some of the nutrients obtained during larval stages are transferred to the adult stage, allowing the adults to survive and reproduce while feeding on nectar or

honeydew only. An ontogenetic diet shift from herbivory to carnivory is much less common. Nymphs of stink bugs may start life as herbivores and later become predators or mixed feeders (McGavin 2000). The term “life-history omnivory” was first coined by Polis and Strong (1996).

- Temporal omnivory. Some predators and host-feeding parasitoids can supplement their carnivorous diet with plant food during part of their life cycle only. As an example, both juvenile and adult tiger beetles (Cicindelidae) forage on ground-dwelling prey, whereas adults also feed on plant seeds.
- Permanent omnivory. Many plant-inhabiting “predators” can feed on both prey and plant material in their juvenile as well as their adult phase. Typical are the heteropteran predators that can use their stinging mouthparts to feed on prey and plant tissue. Other predators only use pollen and/or nectar to supplement their diet (e.g., predatory mites and ladybirds).

The impact of plant-provided food on arthropods, and on their role in plant protection (herbivore suppression), depends on the type of omnivory. For life-history omnivores, such as parasitoids, the availability of the right plant material will typically extend survival of the adult insects, and will thereby expand their reproductive capacity. Olson, Takasu, and Lewis (Chapter 5) discuss the specific morphological and behavioral adaptations to this nectarivorous lifestyle and its ecological consequences. Heimpel and Jervis (Chapter 9) review the empirical evidence for nectar use by parasitoids under field conditions. They also address the impact of nectar feeding on parasitoid survival and reproduction, as well as on population establishment and pest control.

For real (temporal or permanent) omnivores, such as predatory bugs, the effect of plant-based feeding may be less clear, as it can be partly substituted by feeding on prey. The impact of plant food on the various life-history components (development, survival, reproduction) of these omnivores should therefore be studied at different, but fixed, prey densities. Another complicating factor is that plant feeding may go at the expense of the per capita prey consumption. Eubanks and Styrsky (Chapter 6) review the experimental studies on the various effects of omnivory, including its impact on herbivore suppression.

Not only predators and parasitoids shift their diets during development, also some herbivorous species change from tissue-feeding larvae to nectar or pollen-feeding adults. Romeis, Städler, and Wäckers (Chapter 7) review the foraging and feeding requirements of adult herbivorous butterflies, flies, and beetles. They discuss the implications of this adult feeding for herbivore reproductive fitness, herbivore–plant interactions, and pest management.

Table 1.1 Types of omnivory among “carnivorous” arthropods

Type	Plant-feeding stage	Arthropod examples can be found within:	Type of plant food utilized	Reference	
Life-history omnivory	Adult	Neuroptera	Nectar, pollen	Stelzl 1991	
		Diptera	Nectar, pollen	Hickman <i>et al.</i> 1995 Opit <i>et al.</i> 1997	
	Hymenoptera	Cecidomyiidae (gall midges)	Nectar	Gilbert and Jervis 1998	
		Tachinidae (parasitoid flies)	Nectar	Jervis 1998, Lewis <i>et al.</i> 1998, Wäckers 2001	
		a.o. Ichneumonidae, Braconidae (parasitoid wasps)	Nectar	Cuautle and Rico-Gray 2003	
		Vespididae (social wasps)	Nectar, fruit	Beattie 1985	
	Juvenile	Coleoptera	Nectar	Adams and Selander 1979	
		Heteroptera	Meloidae (blister beetles) Pentatomidae (stink bugs)	Plant juice	McGavin 2000
	Temporal omnivory	Adult	Hymenoptera	Nectar	Jervis 1998, Lewis <i>et al.</i> 1998
			Coleoptera	Seeds	Zerm and Adis 2001
Juvenile		Araneae	Nectar, pollen Pollen	Traugott 2003 Smith and Mommsen 1984	

Permanent omnivory	Adult and juvenile	Acari: Mesostigmata	Phytoseiidae (predatory mites)	Nectar, pollen	Van Rijn and Tanigoshi 1999a, b
		Heteroptera	Pentatomidae (stink bugs) Miridae (mirid bugs)	Plant juice Plant juice	Ruberson <i>et al.</i> 1986 Gillespie and McGregor 2000
			Geocoridae (big-eyed bugs)	Plant juice	Eubanks and Styrsky, Chapter 6
			Anthocoridae (flower bugs)	Pollen	Eubanks and Styrsky, Chapter 6
		Neuroptera	<i>Chrysopa</i> , Hemerobiidae (brown lacewings)	Nectar, pollen	Stelzl 1991, McEwen <i>et al.</i> 1993
		Thysanoptera	Aeolothripidae, Phlaeothripidae	Leaves, pollen	Kirk 1997
		Coleoptera	Coccinellidae (ladybirds)	Nectar	Pemberton and Vandenberg 1993
			Carabidae (ground beetles)	Pollen Seeds	Cottrell and Yeagan 1998 Goldschmidt and Toft 1997

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Part III: Plant-provided food and biological control

Food-for-protection strategies have evolved independently in many plants, suggesting that food supplements can be a powerful tool to enhance the effectiveness of predators and parasitoids in the reduction of herbivores. In biological control programs, we rely on carnivorous arthropods to control herbivorous pest insects. Therefore, it seems an obvious step to emulate the food-for-protection strategies in our cropping systems.

The use of food plants and artificial food sprays has been advocated as a means to enhance biological and natural control. Some of the efforts seem successful, but in general the results remain variable and unpredictable (Bugg and Waddington 1994; Landis *et al.* 2000). The strategy is certainly promising, but we need to improve our understanding of the underlying mechanisms in order to increase the effectiveness of our efforts.

In theory, the enhanced performance of a carnivore supplied with plant food does not necessarily improve herbivore suppression. The positive effect on carnivore fitness can be canceled out by factors such as reduced attack rate or increased herbivore reproduction. Population feedback and modified distribution patterns may also reduce the effect on herbivore suppression. In a series of model exercises, Van Rijn and Sabelis (Chapter 8) investigate the conditions required for a positive relationship between food provision and plant protection. They consider food quality, life history, spatial structure, and food web structure.

The empirical verification of the food-for-protection hypothesis may be easier for parasitoids than for predators, for two reasons: the relative ease with which the strength of interaction between herbivore and parasitoid can be quantified (by means of percentage parasitism), and the fact that parasitoids often depend on a single food type (nectar). Heimpel and Jervis (Chapter 9) consider the assumptions underlying this nectar-limitation hypothesis, and discuss to what extent empirical evidence matches the predicted host parasitism and suppression.

When “companion” plants are grown, this may not only provide food for predators and parasitoids, but also other services such as shelter and alternative hosts. Wilkinson and Landis (Chapter 10) discuss the different spatial scales at which the plant resources can be present in the landscape, and how this eventually affects pest control.

Finally, Gurr and colleagues (Chapter 11) discuss how the implementation of food-for-protection strategies in agriculture can benefit from a directed approach that brings together general ecological theory, well-focused empirical studies, and case-specific modeling.