THE EFFECT OF FOOD SUPPLEMENTS ON PARASITOID-HOST DYNAMICS

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IntroductionParasitoids can be an important factor in regulating insect population dynamics (Utida, 1957). The potential impact of a parasitoid on the population of its host depends, among other factors, on the parasitoid's longevity, its fecundity, and the efficiency with which it locates its hosts. The vast majority of adult parasitoids require sugar solutions, such as nectar or honeydew, as their main source of energy (Jervis and Kidd, 1986). Sugar feeding can increase parasitoid longevity (Pielou and Glasser, 1953; Wäckers, 1998, 2001; Siekmann *et al.*, 2001) as well as fecundity (Olson and Andow, 1998; Schmale *et al.*, 2001). In addition, well-fed parasitoids are usually also more active and more focused in seeking out their herbivorous hosts (Van Emden, 1962; Wäckers, 1994; Takasu and Lewis, 1995). Each of these three fitness parameters is directly linked to the number of hosts a parasitoid can attack. Therefore, the availability of sugar sources can be a key factor in the population dynamics of a parasitoid-host system.

Lack of suitable food sources has long been suspected to be an important constraint to the success of biological control programs (Illingworth, 1921; Wolcott, 1942; Hocking, 1966). While the provision of food sources as a strategy to raise the impact of parasitoids has often been proposed, the validity of this basic concept remains to be proven. To date, only circumstantial evidence is available to indicate that natural enemies benefit from the availability of food supplements and that feeding actually translates into better herbivore regulation.

Field data on the effects of sugar supplements are often confounded by two inherent factors: migration and ecological complexity. In open field systems, spatial dynamics are an integral part of population dynamics. Food supplements may both attract additional individuals from adjacent areas (Wäckers, 1994; Patt *et al.*, 1999) or increase the retention of individuals within a given area (Stapel *et al.*, 1997). This entanglement of migratory and nutritional effects makes it difficult to use open systems to study whether and how the nutritional quality of food supplements contributes to host-natural enemy interactions.

The ecological complexity of field systems, in which various herbivores and their (shared) antagonists interact, represents an additional complication if one wants to single out the effect of food provision. The impact of food supplements is generally not limited to the herbivore-carnivore system under study. Artificial or natural food sites can also be used by other players in the system, which in turn may impact the target organisms, e.g., through competition or intraguild predation. The intricate web of multitrophic interactions in diversified habitats makes it difficult to attribute changes in natural enemy populations to one particular factor (food).

In this study, a storage system was chosen to specifically address the question of how food supplements (honey) affect parasitoid-host dynamics. This choice was primarily based on the fact that storage systems are closed entities, thereby excluding migratory effects. A second advantage of the storage system is the fact that ecological complexity can be reduced to a minimum by limiting each of the three trophic levels to a single species. Based on previous studies (Wäckers, 1998), I chose to use cowpea (*Vigna unguiculata* [L.]), the bruchid weevil *Callosobruchus chinensis* (L.), and its pteromalid parasitoid, *Anisopteromalus calandrae* (Howard), as a model for tritrophic systems. Finally, stored

beans have the advantage that the presence of accidental sugar sources commonly occuring in the field (honeydew, flowering weeds) can be excluded. This combination of factors makes it possible to single out the variable of food supplements and to unambiguously attribute changes in parasitoid-host dynamics to this one parameter.

MATERIAL AND METHODS

Organisms and Climatic Conditions

Both the rearing of insects used in the experiments and the experiments themselves were done at 25 °C, 65% RH, and 16 L:8D. Cowpeas (*V. unguiculata*) from Haeflinger (Herzogenbuchsee, Switzerland) were used both in the experiments and for bruchid and parasitoid rearing.

Callosobruchus chinensis used in the experiments had been reared on cowpeas for more than 50 generations. In order to obtain bruchid eggs or larvae of controlled age for the experiments, weevils were allowed to oviposit on uninfested beans for 24 h. Subsequently beans were sieved to remove the weevils and weevils were kept isolated according to date in Plexiglas containers. Under the climatic conditions used for the rearing it took approximately 13 days before weevil larvae developed to a stage that parasitoids could use for oviposition or host feeding. Adult weevils (mated, 2-d old) used in the experiments were collected upon emergence and provided with water only.

Anisopteromalus calandrae used in the experiment were from a colony that had been reared on *C. chinensis*-infested cowpeas for more than 50 generations. To obtain parasitoids (mated, 2-d old) for the experiments, newly emerged individuals were collected daily and kept in Plexiglas boxes with water only until used. Undiluted honey (Langnese) was used as a food source throughout the experiments.

Experimental Arena and Treatments

Plexiglas containers (26 x 26 x 45 cm) were used as arenas for the experiment. To provide ventilation, open containers were covered with fine mesh lids, which were inpenetrable to both parasitoid and weevil. Six containers were filled with 10 kg uninfested cowpeas, to a height of about 20 cm. Each container was subsequently inoculated by adding 12 cowpeas infested with three 1 to 2-day old bruchid eggs. Ten days after the onset of the experiment, 10 *A. calandrae* females were introduced into each container, creating a parasitoid/host ratio of 1: 3.6. In three of the containers, honey was provided as a food supplement. This was done by placing 0.5 g of honey droplets on the Plexiglas walls of each container. The honey would run down alongside the container wall, providing a food source accessible to bruchids and parasitoids at all layers of the bean-filled container. The remaining three containers did not receive any food supplements and served as controls. Daily counts were made of the number of bruchids and parasitoids visible on the surface of the stored beans. Counts started at the beginning of the experiment and were continued for 100 days. Under the conditions used, 100 days is sufficient for the emergence of the bruchids as well as that of the F1 and F2 generations. When population levels were too high to allow direct counts, the count was restricted to the insects present within a narrow Plexiglas ring (12 cm diameter) which had been centrally placed on the surface of the beans. Since the surface area enclosed by the ring made up 10% of the total bean surface, these counts were multiplied by a factor of 10 to obtain an estimate for high population densities. Daily counts were averaged over the three replicates per treatment.

RESULTS

Without Food Supplements

Anisopteromalus calandrae. In the absence of food supplements, the parasitoids did not establish in any of the containers. The initially introduced parasitoids were recorded for six days after their release. In two of the three containers a maximum of two individuals were recorded between days 30 and 40, representing the F1 generation. In one container, the F2 generation was represented by sporadic recordings at days 58 (1 parasitoid), 59 (2 parasitoids), and 62 (1 parasitoid). In the remaining 38 days, no living parasitoids were recorded, and subsequent analysis of the beans revealed no living individuals either. Throughout the experiment, an average of only 4.3 parasitoids were recorded per container (Table 1).

Callosobruchus chinensis. In contrast to the low number of parasitoids, weevil recordings per container added up to a total of 4,302 (Table 1). The bruchid recordings showed three discrete peaks representing the initial bruchids, as well as their F1 and F2 generations (Wäckers, 1998). The relatively short lifespan of the weevils in the absence of adult food sources translated into discrete curves for the individual generations. The initial bruchids peaked at 24 individuals (day 31), the second generation at 193 (day 55) and the third at 330 (day 84). By the time of the third generation, all beans had multiple holes, indicating that population growth was likely limited by substrate availability.

With Food Supplements

Anisopteromalus calandrae. In contrast to the treatment without food supplements, parasitoids established readily when honey was provided. As parasitoids lived longer as a result of food availability, no discrete generation peaks could be distinguished. The maximum parasitoid count (8) was recorded on day 41, and the parasitoid population persisted for weeks after the bruchids had been eradicated. Over the course of the experiment an average of 270 parasitoids were recorded on the surface of the container (Table 1).

Callosobruchus chinensis. In contrast to the treatments without food supplements, cumulative weevil recordings were very low, adding up to 13 live weevils per container (Table 1). The initial bruchid generation appeared to have been decimated by parasitoids. This generation peaked at a mere 1.7 weevils (day 31-36). During what should have been the second bruchid generation, the bruchid population was reduced to two recordings of a single weevil each (day 54 and day 55) in one of the replicates. Since no further bruchids were seen during the remaining 40 days of the experiment and subsequent analysis of the beans revealed no living individuals, it can be concluded that the parasitoids eradicated *C. chinensis* in all three replicates.

Table 1. Cumulative counts (days 20-100) of live bruchids and parasitoids on top of bean containers (n=3) with and without food supplements.

	Without supplements	With supplements
Callosobruchus chinensis	4302.0 + 612	13 + 4.3
Anisopteromalus calandrae	4.3 + 1.68	270 + 33.6

DISCUSSION

The present study shows that nonhost food supplements can have a profound effect on the population dynamics of parasitoid-host systems. To my knowledge, this represents the first case in which changes in parasitoid-host dynamics can be unambiguously attributed to the presence of non-host food. These findings confirm strong indications from field studies (Zhao et al., 1992; Patt *et al.*, 1997; Baggen and Gurr, 1998), as well as earlier model predictions in predator-prey systems (van Baalen *et al.*, 2001).

The differences in this study were especially pronounced, due to the fact that parasitoids failed to establish in the absence of food supplements, while in the food treatment parasitoids eradicated the bean weevils. The low number of parasitoid offspring recorded in the non-food treatment could either be a consequence of high host-feeding rates or could indicate a failure by the parasitoids to locate the infested beans. It is likely that a combination of both mechanisms contributed to the poor parasitoid performance.

Given the high number of weevils emerging from the initial population (peak count of 24 weevils out of the inoculation with 36 eggs), we can conclude that the sugar-deprived parasitoids were not very succesful in locating their hosts during their restricted lifespan. Parasitoids in our experiments were introduced to beans that had been inoculated 10 days previously. Under the experimental conditions, it took approximately 12 days before weevil larvae had developed to a stage in which parasitoids could start using them for oviposition or host feeding. As food deprived *A. calandrae* live on average only 6.6 days, this leaves a narrow window of time for reproduction. Moreover, parasitoids often use small larvae for host feeding or deposition of male eggs (van den Assem *et al.*, 1984; Kidd and Jervis, 1991). The fact that the few parasitoids recorded in the F1 generation were all male, indicates that this mechanism contributed to the failure of *A. calandrae* to establish.

The provision of honey as a food supplement enhanced parasitoid performance dramatically. The extended lifespan likely increased the time window during which bruchid larvae were exposed to parasitoid attack. Through this extension, *A. calandrae* lived long enough to encounter larger larval stages that are preferably used for the production of daughters (van den Assem *et al.*, 1984). In addition, sugar satiation might suppress the parasitoid's tendency to engage in host-feeding, thereby increasing offspring production.

Using a model approach, KYivan and Sirot (1997) showed that food foraging can stabilize host-parasitoid dynamics due to a trade-off in time spent searching for hosts and nonhost food. At low host densities, parasitoids in their model were assumed to search for food only. While in the present experiments food provision had a clear effect on host-parasitoid dynamics, it did not stabilize the system. In all three replicates, nectar-fed parasitoids drove bruchids to (rapid) extinction. This is probably due to the fact that in this experiment surplus food was provided in close proximity to the host patch. Under these conditions the trade-off between food foraging and host search would be limited. Time devoted to food foraging would be minimal, while food-satiated parasitoids may encounter more hosts through an increase in host searching activity and longevity. These results show that the impact of food supplements will depend on the spatial distribution of food sites relative to host patches. Under field conditions parasitoids may have to invest considerably more time in locating food sources if food sites are located outside of the host habitat and food quantity per site is limited. Under these conditions, the stabilizing trade-off predicted by KYivan and Sirot (1997) is more likely.

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