

The role of nectar sources for oviposition decisions of the common blue butterfly *Polyommatus icarus*

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Neural limitations on information processing have been shown to play an important role for host plant specialization in herbivorous insects. The necessity of fast and accurate decisions favors the adoption of a few high-contrast signals, which selects against the use of multiple resources. Many species face a similar problem when searching for adult food sources and the simultaneous need to fulfill both search tasks can lead to a potential conflict. Some insects use the same host plant species for both adult and larval nutrition, which makes it possible to decrease the number of search images and thus potentially increase efficiency of the choices. The aim of this study was to investigate if there is a connection between choice of nectar sources and choice of oviposition host plant. In a laboratory experiment, females of *Polyommatus icarus* preferred to oviposit on *Lotus corniculatus* plants with flowers over those without flowers. Observations of behavioral sequences also revealed that oviposition often followed immediately after nectaring. The results suggest that nectar availability could play an important role in oviposition decisions of *P. icarus* and can provide one explanation to why some phytophagous insects not always choose the host plant that gives the best offspring performance.

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Recent studies have pointed at the importance of female oviposition strategies for determining patterns of host use among herbivorous insects (Sirost and Bernstein 1996, Janz and Nylin 1997, Nylin et al. 2000, Scheirs et al. 2000). Neural limitations among phytophagous insects lead to a tradeoff between the ability to use several different host plant species and the speed and/or accuracy of host choices (Bernays 2001). For example, more specialized females of *Polygonia c-album* were more successful than less specialized females in choosing oviposition sites (Janz and Nylin 1997, Nylin et al. 2000).

During oviposition, females must first search for and locate a potential host, evaluate its suitability as a larval host and then decide to accept or reject the plant for oviposition. It is of importance that these tasks are

executed within a minimum of time expenditure and with maximal accuracy.

Visual cues like shape and color play an important role for butterflies in host finding (Bernays and Chapman 1994, Renwick and Chew 1994), and an adoption of high contrast signals should be expected to maximize speed and accuracy of choices (Bernays 2001). Conspicuous search images have been shown to increase the flight speed of female butterflies when searching for suitable host plants (Rausher 1978, Stanton 1984). In many flowering plants the inflorescences are much more conspicuous than the other parts of the plant, and could potentially be used as visual cues to fulfill both search tasks. This would be particularly true for insect-pollinated plants, where the ovipositing female is often herself a target of the floral display. Most adult

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butterflies are nectar feeders and require frequent “re-fueling” of the carbohydrates that the nectar provides. Hence, in those cases where the host plant is insect-pollinated and nectar producing, the female could potentially use the more conspicuous inflorescences as cues for both adult feeding and oviposition (provided that the plant flowers at the time of oviposition).

Wiklund (1977) recognized three tasks that are important for the survival of most butterfly populations: (1) that females and males can find each other and mate, (2) that adult females can deposit their eggs so the larvae can find their host plant, and (3) that adults can find food in order to live long enough to fulfill the two first tasks. Depending on flight ability and resource patchiness a female must either use a limited area, which contains all three functional types of habitats (“mating habitat”, “breeding habitat” and “foraging habitat”), or she must move between areas that provide these functions separately (Wiklund and Åhrberg 1978, Murphy et al. 1984, Stanton 1984).

As the third task above is a prerequisite for the others, it can be argued that it should be of overriding importance for the female; without sufficient adult nutrition to sustain herself no other tasks can be accomplished. Accordingly, Scheirs et al. (2000) showed that optimal foraging for adult food influences oviposition preference in a study of preference patterns of the grass miner *Chromatomyia nigra*. Females of the grass miner oviposited where they fed and had an oviposition preference for hosts which enhanced adult performance more than larval performance; the adult performance but not the larval performance was strongly correlated with host preference. This behavior increases the female’s fitness by making her capable of laying many eggs (because of her higher nutritional status) rather than a small amount of eggs on the optimal host plants in terms of larval performance.

For butterflies, there can be a possible conflict between searching for nectar or for oviposition sites, as they are often not provided by the same plant species or individuals. Hence, it would be a great advantage if both resources can be obtained from the same plant individuals. In these cases, search efficiency can be increased by combining both search types into one.

Females of the common blue butterfly *Polyommatus icarus* use several plants in Fabaceae as larval host plants, many which could also potentially function as nectar sources. It is thus conceivable that these butterflies have evolved search images that converge on inflorescences. By primarily searching for adult nutrition females get oviposition sites for free, to the extent that nectar sources and larval food plants converge. The synergy may be even larger, as it has been suggested that performance of *P. icarus* larvae is actually higher when feeding on inflorescences than on green leaves (Burghardt and Fiedler 1996).

We tested the hypothesis that females of *P. icarus* use inflorescences to find both nectar sources and oviposition sites, and that foraging for adult nutrients is the proximate cause of this behavior. The specific predictions were that *P. icarus* females (1) should prefer to oviposit on plants with than without flowers, and (2) that nectar feeding should precede oviposition in behavioral sequences.

Material and methods

Study species

Polyommatus icarus is a widely distributed butterfly in the group of Lycaenidae. It flies in two overlapping generations from May to September, except for the northern part of Scandinavia, Scotland, and Northern Ireland. The larvae live on several plants in Fabaceae, among them *Lotus corniculatus*. The adults are nectar-feeding on plants from several plant species and families, including their fabaceous host plants (Ebert 1993). We used *L. corniculatus* in the oviposition trials, as it is a preferred host (Thomas and Lewington 1991) that is also commonly used as nectar source. It is a perennial herbaceous plant with yellow flowers. The main flowering season is June to July. It is dependent on pollinating insects to reproduce sexually and offers nectar to attract pollinators. *Lotus corniculatus* is abundant in the whole of Sweden except for the north. It grows in meadows, pastures, verges and moors on both dry and humid ground.

Preparation

Wild female butterflies were caught in June 2001 in two localities (Tävelsrum and on Alvaret outside Vickleby) on the Swedish island Öland and in the area around the Stockholm University. From these females, eggs were collected for breeding of the F₁-generation. The *L. corniculatus* plants used in the experiment were collected in the vicinity of Stockholm University, Stockholm, Sweden and were transferred to pots.

When the eggs hatched, each larva was transferred into a separate plastic jar, covered with net. The jars were kept in an environmentally controlled growth room set to 26°C and a photoperiod of 22/2 h L/D to promote direct development. The larvae had free access to fresh *L. corniculatus* during the whole larval period. After eclosion, adults were individually marked with a thin felt tip color pen and sexed. The butterflies were then fed with sugar solution (approximately 20% sucrose) and kept cold until the beginning of the experiments.

The marked butterflies were placed together in a circular mating cage (H70 cm, D50 cm) where they

could choose partners freely and were monitored for matings.

Experimental setup

After mating, females were placed in individual cages, 50 × 50 × 50 cm, covered with cloth on the sides and with a transparent top. The number of cages that were used simultaneously varied between six and eight. Each cage was illuminated from above with a 75 W light bulb, using a 6 h light regime. Two potted plants of *L. corniculatus*, cut to the same size, were placed at opposite sides in each cage, one with and one without flowers. The positions of the plants were switched twice per day to avoid position effects. We strived to keep the two plants as identical as possible, so that the only difference between them was the presence of inflorescences. Hence, only fully developed flowers, that could provide nectar, were removed.

Eggs were counted daily, allowing each female to lay at least 20 eggs before exchanging her for a new female. The plants were replaced when they showed signs of senescence.

During the oviposition experiment we recorded data on behavioral sequences. During these observations, we noted the temporal sequences of nectar feeding, oviposition, flying, landing, resting and basking. Each period of observation lasted for five minutes from when we noticed activity in the cage. We recorded the sequences of behavior and on which plant the behavior took place.

Results

Oviposition preference

As predicted, females had a significant preference for plants with flowers over plants without flowers (Wilcoxon matched pairs test, $N = 24$, $z = 4.289$, $P \ll 0.001$). Of a total number of 24 individuals, 20 females laid at least 75% of their eggs on plants with flowers and 86% of the total number of eggs was found on plants with flowers (Fig. 1). None of the females preferred plants without flowers. The females also often oviposited on or close to the flowers.

Behavioral sequences

Out of 23 observations on behavioral sequences 15 of which included both nectar feeding and egg-laying. These sequences involved six females. Oviposition after nectar feeding was significantly more common than nectar feeding after oviposition (Wilcoxon matched pairs test, $N = 6$, $z = 2.214$; $P = 0.0269$). Indeed, no female was

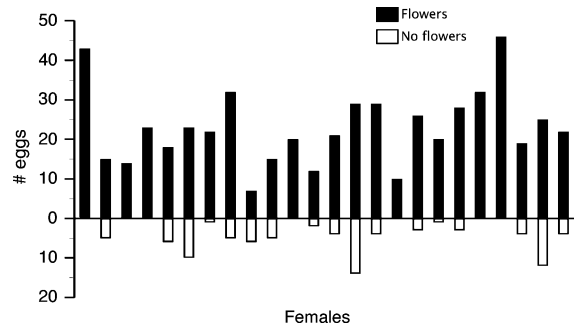


Fig. 1. Number of eggs oviposited by *Polyommatus icarus* females on potted plants of *Lotus corniculatus* with (black bars) and without (white bars) inflorescences in a simultaneous choice trial. Each bar represents the preference of one female.

ever observed landing for oviposition followed by nectar feeding.

Discussion

The results strongly indicated a correlation between the presence of nectar flowers and the females' choice of oviposition host plant; *P. icarus* females showed a significant oviposition preference for plants that also offered flowers for nectaring (Fig. 1).

In behavioral observations, nectar feeding preceded oviposition in all recorded behavioral sequences. This suggests that the proximate driving force when searching for host plants is more related to adult nutrition than to finding an optimal host plant for egg and larvae. By using the same plant both for adult nutrition and oviposition *P. icarus* is able to minimize search time while at the same time maintaining a high nutritional state. Even if the plant individual thus found may not necessarily be optimal in terms of either larval performance (Mayhew 1997) or nectar composition (Rusterholz and Erhardt 2000), the greatly reduced search time could still make this a favored strategy. The exposure to predators will decrease as the total number of flights will be lower, compared to if the female had to shift between host searching and food searching.

Burghardt and Fiedler (1996) showed that *P. icarus* larvae can assimilate nutrition from flowers and that fourth instar larvae achieved higher weight on *L. corniculatus* flowers than on leaves from two other host species. This could provide yet another reason for oviposition on flowers of *L. corniculatus*, further increasing the efficiency of primarily searching for flowers. However, if the ovipositions in or around flowers are to be primarily explained by their enhanced nutritional value, the flower must remain in bloom at least until the larvae hatch, which would take at least one week in nature (Bink 1992). However, *L. corniculatus* only flowers for 3–5 days, and consequently, the presence of inflorescences at the moment of oviposition is a poor

predictor for their availability as larval food. The behavioral sequences showed that nectar-feeding almost always preceded oviposition after landing, which also supports the hypothesis that *P. icarus* females use the search image for inflorescences also to find oviposition sites, and that foraging for nectar is the proximate cause of the behavior, i.e. landings were primarily driven by foraging for adult food.

P. icarus seems to have evolved a rational strategy for host plant searching that makes it possible to use the same host plant individual for both adult nutrition and oviposition. What is unique in this case is that the host plant, *L. corniculatus* is a favored plant both for adult nutrition and as food for larvae. This allows females of *P. icarus* to fulfill two of its important tasks by searching for only one of the resources. The flowers of *L. corniculatus* are more conspicuous than the green foliage, providing a higher-contrast signal and a more efficient search (Rauscher 1978, Stanton 1984, Bernays and Wcislo 1994, Bernays 1996). According to the neural limitation hypothesis (Bernays 2001), limitations in the ability to gather and process information would cause natural selection to favor such a combined search strategy. Obviously, this strategy is not available for many other butterflies and other herbivorous insects, where adult and larval nutrition are provided by different plants, more or less spatially separated. However, there will always be selection for more efficient search strategies, and nectar foraging can have an impact on host plant use even in cases where the different resources are not necessarily well correlated in space. Murphy et al. (1984) showed that the distribution of nectar sources affect the distribution of adult *Euphydryas chalcedona* and their offspring. They suggested that the choice of host plant is correlated with nectar availability in habitats where the host plant species are spatially separated. They suggested that the distribution of nectar may have an impact on the selection of host plant individuals as well as on the selection of host plant species (Murphy et al. 1984). This means that food plants growing in the vicinity of nectar plants will be more likely to be used as larval hosts, and will run a larger risk of being colonized by herbivorous insects that also utilize nectar as adult food. Indeed, the floral displays of insect pollinated plants, intended to attract pollinators, will make them an even more likely target for colonization. As the insects already have the ability to search for and recognize the plant, and already will spend much time on it, they are more likely to receive some of the stray eggs that many insects lay on non-hosts ("oviposition mistakes" Larsson and Ekblom 1995, Nylin et al. 2000). We believe that this is a possible pathway for host plant colonization that deserves more attention.

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