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The Relationship Between Habitat Selection and Preference for Adult and Larval Food Resources in the Polyphagous Butterfly *Vanessa cardui* (Lepidoptera: Nymphalidae)

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Search strategies can have profound fitness-effects for plant-feeding insects. Here I focus on the potential conflict between searching for nectar plants and for larval food plants. I test if the butterfly Vanessa cardui*, which can use some of its larval food plants as nectar sources, is able to rationalize this search problem by combining the two search tasks. Lab-experiments revealed a higher oviposition preference for* Cirsium arvense *over* Urtica dioica *and a corresponding difference in larval performance. Contrary to predictions, there was no effect of inflorescences on oviposition. However, experiments in large outdoor cages showed a higher occupancy and a higher level of oviposition in patches with access to nectar sources, even on* U. dioica*. Hence, while there was no preference for individual plants with flowers, the results suggests that* V. cardui *is simplifying its search task to primarily search for hosts in nectar-rich patches. This strategy allows females to increase oviposition rate, but it is likely that it comes at the expense of not always using optimal host plants in terms of offspring performance.*

KEY WORDS: neural limitations; search behavior; preference–performance; nectar preference; patch preference.

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INTRODUCTION

Conflicting behavioral tasks can force organisms into making compromises, leading to seemingly suboptimal choices. Host plant selection by plant-feeding insects is probably a good example of this. The question of how and why eggs are distributed across potential hosts by ovipositing females has historically been dominated by the "preference–performance problem" (reviewed in Thompson, 1988), under the assumption that host preference has evolved to assure maximal offspring performance. While this has sometimes been a successful approach, it has become increasingly clear that other factors often need to be incorporated in order to explain patterns of egg distribution, which are far from always well correlated with optimal offspring performance (e.g., Mayhew, 1997). As a consequence, recent years have seen an renewed interest in the factors directly affecting the ovipositing female while searching for potential hosts (Janz and Nylin, 1997; Karban, 1997; Bernays, 1998, 2001; Scheirs *et al.*, 2000; Mayhew, 2001; Scheirs and de Bruyn, 2002). An ovipositing female is faced with some intricate problems. She has to gather and process sufficient information to locate and evaluate potential host plants for oviposition, and she has to do this fast and accurately (Bernays, 2001). This is in itself a complex and resource-intensive task, especially when the range of possible host plants or prey types increases (Dukas and Ellner, 1993; Bernays and Wcislo, 1994; Janz and Nylin, 1997; Nylin *et al.*, 2000; Bernays, 2001; Dukas, 2002). The "information processing hypothesis" states that females from species and populations with a wide range of different hosts to search for will pay a cost in either time (Bernays and Funk, 1999; Janz, 2003) or accuracy (Janz and Nylin, 1997; Nylin *et al.*, 2000) of their oviposition decisions, both of which can have serious fitness consequences by reducing vigilance, realized fecundity, or offspring survival (Bernays, 2001).

Moreover, the ovipositing female also has to search for and evaluate potential resources for adult feeding, and the need to find such resources may well be more immediately pressing, as the cost of adult food stress can be severe (Boggs and Ross, 1993). These two search tasks are very similar in nature, but will have different objectives and involve different visual and chemical cues. Hence, there is a potential conflict between search tasks in terms of search efficiency (time and accuracy) that could have important consequences for how the eggs become distributed across hosts.

Optimal food selection will often differ for adults and larvae, either because they have different host plant requirements or because they feed on different plant structures. A recent study on the oligophagous grass miner *Chromatomyia nigra* (Diptera), where the adult feed on leaf saps exuding from oviposition punctures, have also shown that host preference in this species was better correlated with adult performance (longevity and fecundity) than offspring performance (Scheirs *et al.*, 2000). Most butterflies acquire all of their nutrition during larval development; adults are typically only capable of "refueling" on carbohydrates, often in the form of nectar. While nectar and other adult food sources can also provide some amino acids, sometimes even to compensate for poor larval resources (Mevi-Schutz and Erhardt, 2003), adult and larval feeding requirements are very different. Compared to the leaf-miners studied by Scheirs *et al.* (2000), adult and larval resources are typically found on different plant species and are thus less tightly spatially coupled. Consequently, adult and larval resources are likely to be more diverse in terms of search cues, which together with the higher spatial separation should lead to a more pronounced conflict (c.f. Stanton, 1984). Indeed, time-budget analysis of *Colias* butterflies have revealed that when females used between 7 and 22% of their time for oviposition, they spent between 12 and 41% of their time feeding (Nielsen and Watt, 1998). There are several possible ways to handle the conflict between searching for these two resource types. The female can search for both resources simultaneously, leading to a cost in reduced search efficiency on both resources (Bernays, 2001), or she can primarily search for one resource, and take a cost in reduced encounter rates of the other (Scheirs *et al.*, 2000). Finally, she can divide her search into distinct temporal phases, which allows the female to achieve high search efficiency on each resource type, but she will take a cost in the amount of time she can spend searching for any of the resources (Wiklund, 1977; Stanton, 1984). This latter solution will be the only option available when the resource types are widely separated in space (c.f. Brommer and Fred, 1999). Hence, Stanton (1984) found that host plant searching accuracy in *Colias* butterflies was low after periods of nectar feeding, but increased with time during host plant searching. McNeely and Singer (2001) found a similar increase in search accuracy with time in *Euphydryas* butterflies during nectar search, but not when searching for host plants.

On the other hand, longer feeding bouts will lead to an increased wingload (Corbet, 2000), which can interfere with flight and hence oviposition search. Hence, shorter but more frequent feeding bouts should be favored when resource distribution so allows. In situations where there is some degree of spatial overlap between resources, the need to temporally divide the search effort between resource types becomes less critical (c.f. Wiklund and Åhrberg, 1978; Murphy *et al.*, 1984). In cases when host plants also produce nectar, there is a particularly high spatial overlap between resources. Females utilizing such a resource will be able to rationalize their search effort by searching for both types of resources more or less simultaneously; by primarily searching for one resource, the other resource will be found "for free." Such a search strategy was demonstrated in the lycaenid butterfly *Polyommatus icarus*, which uses fabaceous hosts both as larval and adult food sources. It was found that the proximate driving force behind landings on host plants was to forage for nectar, even if this was often followed by oviposition (Janz *et al.*, 2005). However, even in such cases there may still be a conflict, similar to that reported by Scheirs *et al.* (2000), because the suitability of a plant as a larval and adult resource will not necessarily be well correlated on the level of individual plants. Because there is a clear spatial component to this problem, it would be interesting to investigate how choice of adult and larval resources is affected by spatial scale.

In this study, I have investigated the relationship between oviposition and nectar plant preference in the butterfly *Vanessa cardui*, the painted lady. It is a marked opportunist, capable of rapid colonization of vast areas in the temperate parts of the world each year, as these areas become favorable in spring. Many of its hosts, including Asteraceae and Malvaceae, are also good nectar sources, which makes it an interesting species with respect to the conflict between searching for adult and larval feeding resources. As already mentioned, this problem can be solved in different ways, but the information processing/neural limitation hypothesis predicts that search behavior should be rationalized to solve any complex search problem in the simplest possible way (Bernays, 1998). Hence, female *V. cardui* should be able to decrease their search effort by combining the two search types into one. I test this with a series of lab and field experiments designed to measure host searching and selection on three levels of resolution: the choice of patch to search in, the choice of plants within patch, and the preference for plant individual once encountered. As nectar provides the necessary "fuel" needed to perform any other activity, such as searching for host plants, the specific predictions are that females should preferentially occupy patches with available adult food resources in the form of nectar, and as a consequence they should oviposit more in nectar-rich patches than in patches without nectar sources. On the level of individual plants they should prefer to oviposit on nectar-producing plants compared with wind-pollinated plants, and they should favor flowering over nonflowering plants.

METHODS

Study Species

Vanessa cardui (Lepidoptera: Nymphalidae) is a highly migratory butterfly, present all over the world except South America. In Europe it is considered to be able to survive the winter only in the southern Mediterranean, but during the warmer seasons it habitually migrates to the rest of Europe as far north as Scandinavia. However, the magnitude of these northward migrations varies greatly from year to year (Pollard *et al.*, 1998). The painted lady is arguably the most polyphagous butterfly species in the world, reported to be capable of using plants from 25 families as hosts (Scott, 1986). The most preferred hosts appear to be plants in Asteraceae (mainly *Cirsium* and *Carduus*) and Malvaceae, but Urticaceae is also widely used (Stefanescu, 1997). The butterflies used in these experiments derive from eggs collected in Catalonia, Spain in June 2002.

Cirsium arvense (Asteraceae) is a widespread perennial herb with a native Palearctic distribution. It has, however, been introduced to North America and occurs throughout northern USA and Canada. It is insect-pollinated and spreads efficiently both *via* root fragments and seeds, and is a common agricultural weed. *Urtica dioica* (Urticaceae) is also a perennial herb with a similar distribution to *C. arvense*. Also like *C. arvense*, it is capable of spreading both *via* root fragments and seeds, but it is wind-pollinated and dioicous.

Larval Growth

Newly hatched larvae were placed on fresh leaves of either *Cirsium arvense* or *Urtica dioica*. The larvae were reared individually in small plastic containers in environmental chambers at 22°C and 16/8 h L/D, and were supplied with fresh leaves of their respective host during the whole development. Larvae that failed establishment were replaced as long as there were newly hatched larvae available. Survival after establishment, pupal weights, and development times were measured after pupation.

After eclosion all butterflies were placed in one of four mating cages, approximately 1 m × 1 m × 1 m, where they were fed with a solution of sucrose and water and were monitored for matings.

Small-Cage Choice Trial

Mated females were transferred from the mating cages to smaller cages, 0.5 m × 0.5 m × 0.5 m. A total of 14 females were placed individually in these cages and were supplied with diluted sucrose (approximately 20%) throughout the experiments. The cages were illuminated by free-hanging light bulbs (75 W) hanging approximately 50 cm above the transparent cage roof. The light bulbs also provided an additional source of heat.

Each female was given three treatments, consisting of all possible pairwise combinations of *C. arvense* with inflorescences, *C. arvense* without inflorescences, and *U. dioica*. The order of treatments was randomized for each female and each treatment lasted for one whole day. Plants were cut to approximately the same size and were kept in bottles with water, and were exchanged upon signs of senescence. They were presented to the butterflies at equal distance from the central light and food sources, and their relative position in the cage was randomized for each day of the experiment. Eggs were removed from the plants and counted after each day.

Large-Cage Choice Trial

This experiment was carried out in a large outdoor cage of oblong shape with a half-circle shaped cross section (dimensions $W \times L \times H$: $8\,\mathrm{m} \times 30\,\mathrm{m} \times 4\,\mathrm{m}$). The cage was located in an open pasture at the Tovetorp research station, 100 km southwest of Stockholm, and has an east-westerly orientation. The cage was covered with fine-meshed net that reduces solar radiation by approximately 25% and the bottom of the cage consisted of the natural grassland vegetation, cut to about 0.2 m height. It was divided into two compartments by a 4 m wide barrier of camouflage nets, hanging freely from the ceiling of the cage all the way to the ground. The camouflage nets were 4 m tall and 1–2 m wide. They were hung in the barrier zone in an irregular pattern that prevented visual contact between the compartments. The maze-like barrier served the function of creating two distinct, similarly sized patches, while still allowing migration between the patches. A set of eight plants was placed at the far end of each cage compartment (away from the barrier) in a 2 × 4 grid, with four each of *U. dioica* and *C. arvense*. The difference between the treatments (cage compartments) was the presence or absence of *C. arvense* inflorescences. There was no additional source of adult food in the cage.

A total of 28 mated and individually marked females were released in the cage at the beginning of the first day of the experiment (9 A.M.), 14 in each of the compartments. At three times during the day (12 A.M. and 15 and 18 P.M.), the position (cage compartment) was recorded for each female that could be found. At the end of the flight period, eggs were collected from all plant individuals and the treatments were shifted between the compartments (using new plants). Before the flight period at the beginning of day 2, the remaining 18 butterflies were redistributed to once again create an even distribution between the compartments. Out of the original 28 females, 10 butterflies were lost to spider predation but 4 of these survived long enough to provide occupation data during the first day. The procedure from day 1 was then repeated. Weather conditions were very similar during the 2 days of experimental trials: sunny, 20–25°C, calm. Hence, varying weather conditions were not likely to confound the data. Although there may have been diurnal movements caused by other factors than host plants or nectar plants, they were not likely to influence the data much, since treatments were shifted between days.

Patch occupancy was analyzed by recording the time passing between two consecutive counts where a female was found in the same compartment. The accumulated time in each treatment were then summed up, giving a total time spent in each treatment by each female. To assure equal influence of the data from the 2 days, the data from day 2 were weighted for the reduced number of females left in the trial.

At the end of the flight period, all eggs were collected from the plants and counted. The number of eggs laid per plant individual in relation to treatment (nectar/no nectar), plant species (*U. dioica/C. arvense*), and days was analyzed with multiple two-sample Wilcoxon rank-sum (Mann–Whitney) tests, using Bonferroni adjustments of the α-values to account for multiple tests on the same data. To further compensate for the risk of pseudo-replication (the same females were used on both days), an additional correction was made, by adding the amount of eggs oviposited on a plant in day 1 to the amount oviposited on the corresponding plant (same treatment, different section) in day 2. This combined measure was then used in the analysis, thus producing one data point for each plant position over the whole experiment, which reduced the number of data points from 32 to 16.

RESULTS

Larval Growth

There was no doubt that larval performance under lab conditions was higher on *C. arvense* than on *U. dioica* (Table I) Larvae reared on thistles had shorter development times (t-test: $df = 94$, $t = -3.95$, $P < 0.001$) and attained higher pupal weights (t-test: $df = 95$, $t = 3.42$, $P < 0.001$) than larvae reared on nettles. However, there was no difference between plants in term of larval survival under lab conditions (Fisher's exact test: $N = 154$, $P = 0.32$). Mortality was high on both plants; 40% of the larvae died before pupation on *U. dioica* and 32.5% on *C. arvense* (Table I), and most mortality occurred during establishment. It is hard to say what caused this high mortality. Eggs and first instar larvae of *V. cardui* are small, and initial feeding position could be crucial for successful larval establishment. On the other hand, *V. cardui* females do not seem to be very good at selecting optimal oviposition sites (Janz and Nylin, 1997).

Table I. Larval Performance of *Vanessa cardui* on the Two Natural Host Plants Used in the Study: *Cirsium arvense* and *Urtica dioica*

	Cirsium arvense	*Urtica dioica*	Test	Significance
Larval development time (d) (means ± SE)	22.9 ± 0.54 ($N = 52$)	26.7 ± 0.84 ($N = 44$)	t-test	***
Pupal weight (mg) (means ± SE)	461.8 ± 8.8 ($N = 53$)	421.8 ± 7.2 ($N = 44$)	t-test	***
Survival	44 of 74 (40.5%)	54 of 80 (32.5%)	Fisher's exact	NS

***$p < 0.001$.

Small-Cage Choice Trial

In both treatments involving *U. dioica*, the females showed a significant preference for *C. arvense*, mirroring the difference in larval performance demonstrated in the larval growth experiment (Wilcoxon matched-pair signed-rank tests: $P = 0.05$, Fig. 1). There was no significant difference in preference for *C. arvense* with or without inflorescences (Wilcoxon matched-pair signed-rank test: $P = 0.63$, Fig. 1). The data set was relatively small and it cannot be ruled out that a difference would have been found with a larger material. However, there was no clear trend in the data, so it does not seem very likely that *V. cardui* females do prefer to oviposit on thistles with flowers.

Large-Cage Choice Trial

The accumulated time between consecutive recordings from the same patch (corrected for differences in total number of butterflies) were used as an indication of patch occupancy. Individual females were used as data points, comparing the accumulated time each female spent in the two treatments. With this measurement, there was a strong bias in occupancy toward the patch that contained flowering *C. arvense*, (two-sample Wilcoxon rank-sum (Mann–Whitney) test: $N = 22$, $z = -3.299$, $p = 0.001$), implying that the butterflies spent more time in the patch where there are nectar sources available (Fig. 2).

The combined egg count measure over the 2 days of experiment (see Methods) gave a similar picture as the occupancy data (Fig. 3). Once again, there was a significant effect of treatment (Wilcoxon rank-sum test, $N = 16$, $z = -2.688$, $p = 0.0072$), but no effect of host plant (Wilcoxon rank-sum

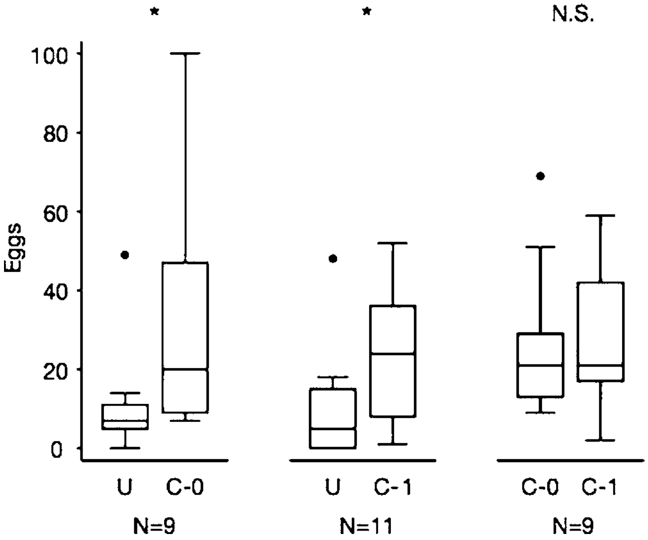

Fig. 1. Relative oviposition preference of *Vanessa cardui* for *Cirsium arvense* (with and without inflorescences) and *Urtica dioica*, as revealed by two-way simultaneous choice trials. U = *U. dioica*, C-0 = *C. arvense* without inflorescences, C-1 = *C. arvense* with inflorescences. Significant comparisons are marked with asterisks for significance on the 5% level. Medians, upper and lower quartiles, and ranges. Outside values (outliers) are represented as black, filled, circles.

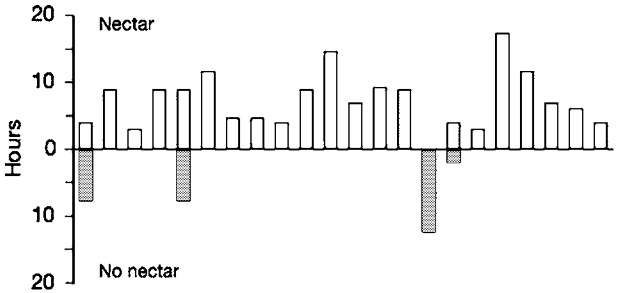

Fig. 2. Patch preference in the large outdoor flight cage experiment. Patch preference was measured as the accumulated time of occupancy for each female in the two treatments (nectar, no nectar) during 2 days. Each female is represented by a vertical bar, unfilled bars denote time spent in the treatment with available nectar, filled bars denote time spent in the treatment without nectar.

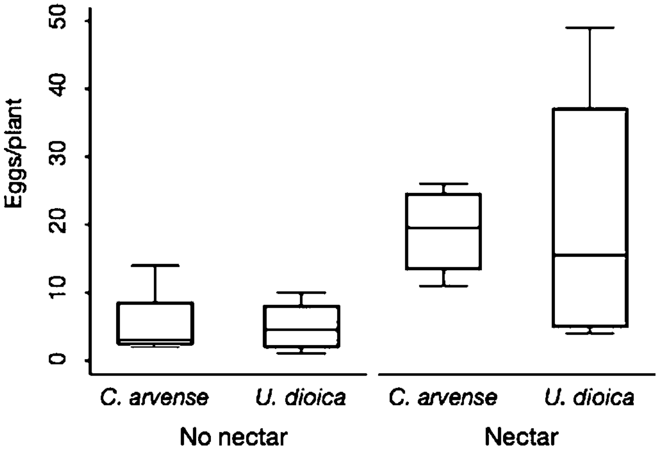

Fig. 3. Distribution of eggs across treatments (nectar, no nectar) and plants (*Cirsium arvense*, *Urtica dioica*) in the large outdoor cage experiment. Medians, upper and lower quartiles, and ranges.

test, $N = 16$, $z = 0.316$, $p = 0.7518$), using a Bonferroni-adjusted α-value of 0.025. The rather strong preference for *Cirsium* over *Urtica* found in the small cages was not found in this experiment. Thus, the experiment demonstrated a strong preference on the patch level (butterflies seemed to prefer to lay eggs in patches where there were adult food sources available), but showed no preference between plant species within patches.

DISCUSSION

Both relative oviposition preference (Fig. 1) and larval performance (Table I) under laboratory conditions were higher on the nectar-producing *Cirsium arvense* than on the wind-pollinated *Urtica dioica*, which was in accordance with predictions, and also with data on actual host use in the field (Stefanescu, 1997). However, contrary to predictions, there was no difference in preference of *C. arvense* with or without inflorescences (Fig. 1). This also differs from a previous study on *Polyommatus icarus* using an identical experimental design (Janz *et al.*, 2005), where there was a clear preference for flowering plants. Use of nectar sources by *V. cardui* in the field is largely determined by local abundance and availability and only rarely are the same plant species used as both nectar and larval food plants at a given locality (Stefanescu, 1997). The reason for this could simply be an effect of phenology, reflecting the likelihood that the locally abundant larval host plant is flowering at the time of observation. However, it may also be that the ovipositing *V. cardui*, as opposed to *P. icarus*, interpret flowering as a sign of imminent senescence, so that oviposition preference on the level of individual plants does not favor flowering plants.

The situation in the large flight cages was noticeably different, though. As predicted, females clearly spent more time in patches with flowering *C. arvense* (Fig. 2). Thus, availability of adult resources appears to be important for patch preference of ovipositing females of *Vanessa cardui*. The higher level of occupancy in patches with available nectar also resulted in more eggs deposited on plants in these patches (Fig. 3). An interesting observation is that oviposition was higher in the nectar treatment on both plants (Fig. 3). In fact, *U. dioica* received as many eggs in this experiment as did *C. arvense*, which was a bit surprising considering the results from the lab trials. In any case, this indicates that host use of *V. cardui* is influenced by the availability of adult food sources. Host plants growing in patches with abundant nectar sources will be more likely to be oviposited on than plants growing in a patch with no nectar plants, even if eggs are not necessarily laid on the nectar plants themselves. This is in accordance with earlier observations of Murphy *et al.* (1984) that the distribution of nectar sources affected the distribution of adults and larvae of the butterfly *Euphydryas chalcedona* and of Karban (1997), who found that proximity to nectar plants increased herbivore damage on tobacco plants by the tobacco hornworm (*Manduca quinquemaculata*).

Interestingly, in the small cage experiment, the correlation between preference and performance on the level of individual plants was rather good (Fig. 1, Table I). The suboptimal egg distribution in relation to offspring performance (a large number of eggs on *Urtica*) was caused by patch-level preference for nectar sources. This means that the distribution of eggs in nature across potential host plants will not necessarily be optimal with regard to offspring performance, even where there is a good correspondence between host plant preference and offspring performance. The females can probably increase their total realized fecundity by rationalizing search behavior to mainly search for nectar-rich patches (Boggs and Ross, 1993; Scheirs *et al.*, 2000), and accepting the cost of not always finding optimal host plants.

These results demonstrate the importance of taking the adult into consideration when trying to understand host plant selection (c.f. Janz and Nylin, 1997; Bernays and Funk, 1999; Scheirs *et al.*, 2000; Bernays, 2001; Mayhew, 2001; Scheirs and de Bruyn, 2002). It also shows that preferences on different levels of resolution in the host selection process can reveal different results. For practical reasons, most experimental designs to test for oviposition preference only involve the last phases of the selection process (often only postencounter decisions). If habitat preference favors patches with a high abundance of the preferred plant, selection at the habitat level can reinforce the association with the preferred host (Thomas and Singer, 1987; Kuussaari *et al.*, 2000). But it is also conceivable that the two types of preference can be in disagreement. If so, the preferences early in the sequence could influence the final egg distribution by “masking” decisions made later in the decision sequence. In extreme cases, preference on the level of the patch could entirely preclude encounters of certain hosts. In this case, the plant will not be used for oviposition in the field, regardless of within-patch preference for it. This situation would be functionally similar to the examples of apparently maladaptive behavior, where females have been found to have a high preference for hosts that do not exist in the habitat of the insect, either because the insects have colonized a new habitat type, or because the plant has gone locally extinct (Singer *et al.*, 1992; Thompson, 1993; Wehling and Thompson, 1997). A situation like this could potentially evolve where habitat selection is primarily governed by other factors than the abundance of a favored host, such as the availability of adult food resources. In this case, selection at the habitat level will weaken the association with the preferred hosts, which fits well with the opportunistic nature of host selection of *V. cardui* in the field (Stefanescu, 1997).

As mentioned in the Introduction, *V. cardui* is in many ways a typical opportunist. It is strongly migratory and extremely polyphagous. It is also very fecund and has unusually small eggs (N. Janz, unpublished data). Apparently, these butterflies prioritize quantity of offspring over quality, something that was perhaps responsible for the high larval mortality in this study (Table I). Most hosts of this butterfly are ruderals and good nectar plants. It is tempting to suggest that the repeated colonization of nectar plants by *V. cardui* and its ancestors (Janz *et al.*, 2001) has to some extent been driven by adults foraging for nectar. Indeed, this is a potential general pathway for host plant colonization that may deserve more attention. Nectar producing plants may take a risk when attracting insects to take care of their pollination. As these insects will spend more time on these plants than on other nonhosts that do not offer nectar, they will become more exposed targets for colonization.

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