

Host plant exposure determines larval vulnerability – do prey females know?

B. TSCHANZ, E. SCHMID and S. BACHER†

Zoological Institute, Community Ecology, University of Bern, Baltzerstr. 6, CH-3012 Bern, Switzerland

Summary

1. In heterogeneous environments, the risk of predation and parasitism for phytophagous insects varies among different microhabitats. Adult females can escape natural enemies by depositing their eggs on sites unfavourable for prey-searching predators or parasitoids. Host plant characteristics can determine the availability of such spatial refuges.
2. We assessed the importance of host plant exposure for the predation probability of shield beetle (*Cassida rubiginosa* Müller) larvae by paper wasps (*Polistes dominulus* Christ), hypothesizing that prey on exposed (i.e. free-standing) plants are more likely to be found and eaten by predators than prey on hidden (i.e. surrounded by other vegetation) plants. Because larval predation is a major mortality factor in shield beetles, we further hypothesized that the prey would adapt and avoid high-risk plants for oviposition. Finally, we investigated the influence of egg parasitism on the prey's host plant choice.
3. Host plant exposure significantly affected predation probability of Shield Beetles. Larvae on hidden host plants were less likely to be killed by the wasps than larvae on exposed shoots. However, females did not prefer the low predation risk environment of hidden plants for oviposition. The rate of parasitism was equal on exposed and hidden plants, and thus probably does not contribute to the oviposition habitat selection of prey.
4. Our study shows experimentally that characteristics of the first trophic level (i.e. host plant exposure) can affect the foraging success of insect predators. Different reasons, potentially responsible for the apparent non-selective host plant choice in beetle females, are discussed.

Key-words: *Cassida rubiginosa*, multitrophic, oviposition habitat selection, *Polistes dominulus*, predation

Functional Ecology (2005) **19**, 391–395
doi: 10.1111/j.1365-2435.2005.00999.x

Introduction

In phytophagous insects, larvae of many species are unable to move from one host plant to another, and are thus forced to complete their development on the plant selected by the adult female. Females are therefore expected to choose an optimal oviposition site, in order to indirectly maximize their fitness. In heterogeneous environments, microhabitats vary in their suitability for juvenile development and survival. Several microhabitat characteristics have been shown to drive the oviposition habitat selection of female insects: physical and chemical suitability for larval development (e.g. Jaenike 1978; Kessler & Baldwin 2002), habitat size and resource availability (e.g. Kagata & Ohgushi 2002), the presence and abundance of conspecific competitors (e.g. Kiflawi, Blaustein & Mangel 2003) and the presence of predators and parasitoids (e.g. Meiners & Obermaier 2004). Factors influencing larval growth and perform-

ance (e.g. nutritional value of the host, temperature) certainly are of importance for oviposition habitat selection; however, factors which directly affect offspring mortality (e.g. natural enemies) may be even more important, since they have greater net impacts on fitness and are more likely to drive the evolution of oviposition behaviour (Rieger, Binckley & Resetarits 2004). In fact, predator avoidance is thought to play a major role in host plant selection of phytophagous insects (Bernays & Graham 1988).

We investigated two major mortality factors, predation and parasitism, of shield beetle larvae (*Cassida rubiginosa* Müller, Coleoptera: Chrysomelidae) in heterogeneous vegetation patches, and their impact on the oviposition habitat selection of shield beetle females. *Cassida rubiginosa* predominantly feeds on Creeping Thistle (*Cirsium arvense* (L.) Scop., Asteraceae), one of the world's worst weeds (Holm *et al.* 1977), and therefore is considered as a biocontrol agent (Bacher & Schwab 2000). In the field, thistle shoots differ in their exposure: they are either concealed by dense, surrounding vegetation ('hidden thistles') or solitary, free-standing

(‘exposed thistles’). We hypothesized that such differences in host plant exposure affect predation risk by creating natural variation in the vulnerability of prey to predators (Abrams 1994). In previous studies, paper wasps (*Polistes dominulus* Christ, Hymenoptera: Vespidae) were identified to be the almost exclusive predators of shield beetles (Schenk & Bacher 2002; Bacher & Luder 2005; Schenk, Bersier & Bacher 2005). Since paper wasps hunt visually, we anticipated them to find prey on exposed, free-standing plants with a higher probability than prey on plants hidden by surrounding vegetation. In particular, we tested the hypothesis that *C. rubiginosa* larvae on exposed thistle shoots suffer from higher predation rates by paper wasps than larvae on hidden plants.

Since larval predation is a major mortality factor in shield beetles (Schenk & Bacher 2002), and host plants with high predation risk are expected to be predictable according to their degree of exposure, we hypothesized that shield beetle females prefer to oviposit on low-risk (i.e. hidden) host plants.

Larval predation risk may not be the exclusive force driving the shield beetle’s host plant choice. Other natural enemies, e.g. parasitoids, may also be of importance (e.g. Meiners & Obermaier 2004). Herbivorous insects might escape egg or larval parasitism by ovipositing on locations unfavourable for parasitoids. At our investigation sites, the endoparasitoid *Foersterella reptans* (Hymenoptera: Tetracampidae) is the major parasitoid species (Magun 1999). Searching for hosts, these small egg parasitoids mostly walk up and down plant stems or leaves, but were rarely observed flying (Bacher & Luder 2005). Thus, *F. reptans* (and similarly behaving parasitoids) probably are more effective in parasitizing hosts in dense vegetation patches as opposed to exposed, isolated plants. We tested the hypothesis that the rate of parasitism is lower on exposed plants. Prey females would thus face a decision between high larval predation and low egg parasitism risk.

Materials and methods

LIFE HISTORY OF *C. RUBIGINOSA*

Cassida rubiginosa hibernates as an adult. Oviposition takes place from March to early July. During this time, females produce a number of egg clutches, each containing three to eight eggs, which are preferentially deposited on the lower surface of thistle leaves (Magun 1999). All five larval instars collect their faeces and exuviae on two movable spines at the end of their abdomen (Bacher & Luder 2005). The development to adult takes about 20–30 days, depending on the temperature.

EXPERIMENTAL SITE AND SET-UP

Fourth and early fifth instar larvae of *C. rubiginosa* used in the experiments were reared on cut Creeping

Thistle shoots in the laboratory. In 2001, the experiment was integrated in a study on density-dependent predation conducted on an ecological compensation area within arable farmland in Belp, near Bern, Switzerland (Schenk & Bacher 2002). Thirty-five *C. arvensis* shoots within an area of 50 m² were searched for naturally occurring *C. rubiginosa* larvae, which were removed prior to the experiment. Thistles were marked individually and their location was classified as either hidden ($N = 8$), i.e. shoots were concealed by dense surrounding vegetation, or exposed ($N = 27$), i.e. free-standing shoots without contact to neighbouring vegetation. Early in the morning, at six dates in July and August, between 13 and 69 beetle larvae (fourth and fifth instars) were distributed uniformly (as close as possible) over the experimental thistles. Plants were searched for all remaining larvae early in the following morning, and daily predation rates were calculated for each shoot (number of missing larvae divided by the total number of larvae placed on the shoot). Preceding experiments established that *C. rubiginosa* larvae do not leave the host plant they are placed on and that mortality from causes other than predation is practically non-existent in late larval instars (S. Bacher, unpublished observations; Kaufmann 2001). Thus, all larvae vanished were attributed to predation. Simultaneous video surveillance of individual Shield Beetle larvae identified the paper wasp *P. dominulus* as the almost exclusive predator species, responsible for more than 99% of predation events (Schenk & Bacher 2002).

In 2003, a similar experiment was carried out in the garden of the Zoological Institute, on a patch of 30 m², where the naturally growing vegetation predominantly consisted of *Solidago canadensis* L. (Asteraceae) and *C. arvensis*. This patch belonged to a larger, partly uncultivated meadow with a mixture of flowering plants and was surrounded by orchard trees and hedges. The same site had been used in earlier studies on paper wasp predation of *C. rubiginosa* (Schenk & Bacher 2002; Schenk *et al.* 2005; Bacher & Luder 2005). Video surveillance revealed that also on this site *P. dominulus* represented the predominant predator species. Forty thistle plants of about the same height and stature were chosen and assigned to either the hidden or the exposed treatment (each $N = 20$). Shoot heights were compared between groups by an independent-samples *t*-test ($P = 0.735$). Before each experiment, all naturally occurring *C. rubiginosa* larvae were removed from the experimental plants and neighbouring vegetation was removed from thistles assigned to the exposed treatment, if necessary. Early in the morning, before the activity period of the paper wasps began, one fourth or fifth instar shield beetle larva was placed on each thistle and, early the next day, the number of surviving larvae was recorded for each plant. At the same time, we counted all daily laid egg clutches of *C. rubiginosa* on the experimental shoots, in order to determine differences in the beetle’s oviposition rate on hidden and exposed plants. Data were collected between 16 June and 8 July

(predation: 10 experimental days; oviposition: 15 experimental days). No experiments were conducted on rainy days. For each investigation year, we calculated the daily predation rates per shoot of exposed and hidden thistles and compared the daily group means using a paired-samples *t*-test (2001: $N = 6$ days; 2003: $N = 10$ days).

In 2004, we conducted an additional experiment on the oviposition choice of *C. rubiginosa* in an ecological compensation area (a sown wildflower field) of about 10 000 m² in Dürdingen, 25 km from Bern. At this site, *C. rubiginosa* was very abundant. On 4 June, 40 potted thistles of about the same height, grown from standardized root pieces, were arranged in pairs on the experimental area. Half of the pots were distributed in the field, about 1 m from the field margin. These pots were hidden by dense surrounding vegetation (hidden thistles). The remaining 20 pots were placed in the margin of the field, where the vegetation was sparse (exposed thistles), each pot about 2 m from a hidden pot. Pairs were separated by a distance of at least 5 m. Twice a week, on six different dates between 9 June and 1 July, we collected and recorded all newly laid *C. rubiginosa* egg clutches on the experimental plants (six experimental periods, consisting of 3–4 days). The daily number of egg clutches laid on exposed or hidden shoots was compared by means of a paired-samples *t*-test (2003: $N = 15$ days; 2004: $N = 6$ periods).

At the same time, naturally grown thistles were searched for egg clutches in the surroundings of Bern ($N = 118$ thistles with egg clutches). We classified the exposure of every plant bearing eggs as either exposed ($N = 61$) or hidden ($N = 57$). The egg clutches were collected and kept singly in wells of microtitre plates (Immulon 4 flat bottom, Dynatech Laboratories Inc., Chantilly, VA). Each well was sealed by a foam rubber cap, and the plates were stored on a moist filter paper in a closed plastic box (16 cm × 11 cm × 6 cm) at room temperature until shield beetle larvae and/or parasitoids hatched. We recorded for each egg clutch whether it was parasitized or not and determined the emerging parasitoids. Only egg clutches where either beetle larvae or parasitoids emerged were considered for analysis. The parasitism rates of egg clutches originating from exposed or hidden plants were compared with an exact χ^2 test (software StatXact 6.0, Cytel, Cambridge, MA).

Results

We recorded an average daily larval predation rate on all experimental plants of 66.7% in 2001 and 74.8% in 2003. In both years, *C. rubiginosa* larvae on exposed plants suffered from a significantly higher mortality than larvae on hidden plants (2001: $P = 0.009$; 2003: $P < 0.001$; Fig. 1). Despite the higher predation pressure on exposed plants, *C. rubiginosa* females oviposited as frequently on exposed as on hidden thistle shoots (2003: $P = 1.000$; 2004: $P = 0.892$; Fig. 2). From 56 egg clutches of a total of 118 collected either beetle larvae

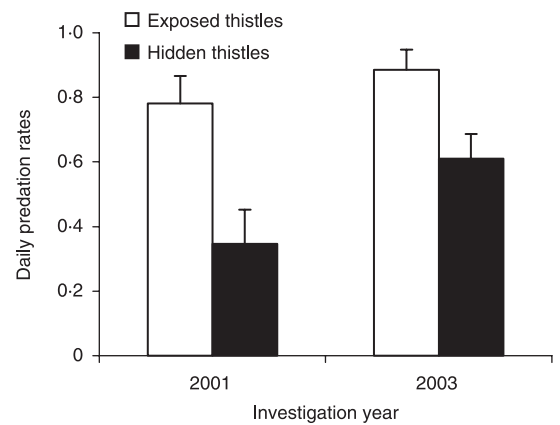


Fig. 1. Daily larval predation rates (mean + standard error) on exposed and hidden thistles. (2001: 6 experimental days; 2003: 10 experimental days).

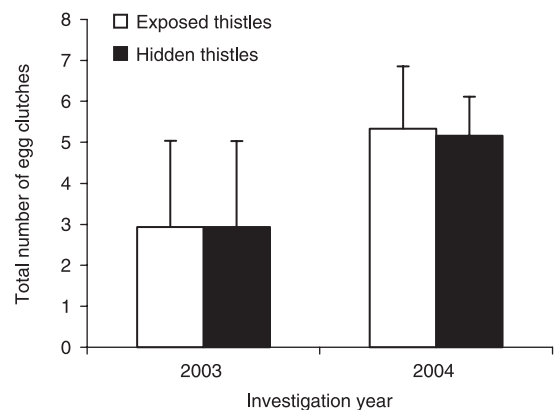


Fig. 2. Total number of *C. rubiginosa* egg clutches (mean + standard error) on 20 exposed and 20 hidden thistles. (2003: 15 experimental days; 2004: 6 experimental periods, each consisting of 3–4 days).

or parasitoids hatched. The emergence rate did not differ between egg clutches on hidden (47.4%) and exposed thistles (47.5%; $P = 1.000$). The 111 parasitoids that emerged from the egg clutches were 96.4% *F. repletans*, 2.7% *Pediobius cassidae* and 0.9% Trichogrammatidae. Parasitism rates did not differ between egg clutches on exposed (79.3%) and hidden host plants (81.5%; $P = 0.575$).

Discussion

In accordance with our hypothesis, host plant exposure clearly affected predation probability of herbivores in the system investigated. In natural habitats, variation in thistles' exposure creates a heterogeneous predation risk for shield beetle larvae. Individual paper wasps primarily detected and attacked *C. rubiginosa* on exposed thistle shoots, whereas hidden shoots represented refuges harbouring a fraction of the prey population. Refuges are likely to be responsible for the sigmoid form of the functional response of paper wasps found in this system (Schenk & Bacher 2002), as they increase

the predator's searching time at low prey densities. In general, refuges and sigmoid functional responses both are considered to stabilize prey population dynamics (Crawley 1992). Variation in prey vulnerability in a heterogeneous environment can also cause indirect predator interference (Abrams 1994), which was designated as decisive mechanism creating predator-dependent functional responses (e.g. Free, Beddington & Lawton 1977). Our finding of variable prey vulnerability due to host plant exposure therefore may at least partly explain the predator-dependence of the functional response in paper wasps (Schenk *et al.* 2005). Thus, not only physical or chemical plant characteristics (e.g. Da Silva, Hagen & Gutierrez 1992; Geitzenauer & Bernays 1996; Messina & Hanks 1998; De Clercq, Mohaghegh & Tirry 2000) and plant architectural traits (e.g. Clark & Messina 1998), but also the immediate environment of a plant (in this case the density of surrounding vegetation) can influence the third trophic level. We conclude that predator-prey systems can only be understood in a multitrophic context.

In contrast to our expectation, *C. rubiginosa* females did not prefer the low predation risk environment of hidden thistle shoots for oviposition. Different reasons may be responsible for our finding. First, shield beetle females may be unable to find cues for discriminating between high and low predation risk host plants. Chemical cues indicating the presence of predators are well known from aquatic predator-prey systems (e.g. Blaustein *et al.* 2004), but to our knowledge are not yet documented in terrestrial habitats. Furthermore, beetle females searching for suitable host plants probably face the problem of a time-lag between oviposition and larval predation risk, since paper wasps prefer late larval instars as prey (S. Bacher, unpublished observations; Kaufmann 2001). During egg and larval development, the exposure of an individual thistle and, as a consequence thereof, the predation risk of developing *C. rubiginosa* larvae may change fundamentally, depending on the relative growth of the thistle and the surrounding vegetation. A second explanation may be that the paper wasp, the almost exclusive predator of *C. rubiginosa* (Schenk & Bacher 2002; Bacher & Luder 2005), is mostly bound to anthropogenic habitats (Witt 1998) and therefore probably does not co-occur with *C. rubiginosa* at each site. Thus, a special adaptation by beetle females to the wasps' hunting strategy may not be required in general. Thirdly, shield beetles may not prefer hidden plants over exposed, because losses through predation at exposed locations may be outbalanced by biotic or abiotic advantages not only for the larvae, but also directly for the adult female (e.g. Scheirs, De Bruyn & Verhagen 2000; Meiners & Obermaier 2004). Higher temperatures on free-standing thistle shoots, for example, may allow an increased oviposition rate (Eidmann & Kühlnhorn 1970) and a shorter larval development (Laudien 1973). Because parasitism rates were equal on exposed and hidden shoots, we conclude that enemy-free space does not play a decisive role in driving the

prey's oviposition habitat selection. Comparing larval performance parameters on exposed and hidden plants in the absence of natural enemies is necessary in order to identify the potential mechanisms determining the host selection of *C. rubiginosa* females.

In conclusion, we demonstrated that characteristics of the first trophic level must be taken into account in order to understand complex predator-prey interactions in natural systems. Surprisingly, prey females do not seem to adapt their oviposition behaviour to the predation risk and we found no satisfactory explanation for this unexpected phenomenon. However, the potential explanations we presented for this finding are experimentally testable. Investigations on the possible forces determining the apparent non-selective host plant choice in this shield beetle may greatly advance our understanding of its spatial distribution and its population dynamics. This kind of information is needed to assess the suitability of *C. rubiginosa* as potential biocontrol agent against its host *C. arvensis* (Bacher & Schwab 2000).

Acknowledgements

We thank Daniel Engimann for assistance in technical matters. This study was funded by the National Centre of Competence in Research (NCCR) Plant Survival, research programme of the Swiss National Science Foundation.

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Received 8 December 2004; revised 10 March 2005; accepted 15 March 2005