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ORIGINAL ARTICLE

Host-plant leaf-surface preferences of young caterpillars of three species of *Pieris* (Lepidoptera: Pieridae) and its effect on parasitism by the gregarious parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae)

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Key words. Lepidoptera, Pieridae, *Pieris melete*, *Pieris napi japonica*, *Pieris rapae crucivora*, Hymenoptera, Braconidae, *Cotesia glomerata*, parasitism rates, herbivore, host, *Brassica oleracea* var. *capitata, Armoracia rusticana*, *Rorippa indica*, *Arabis flagellosa*, leaf-surface preference, larva

Abstract. Preferences of young caterpillars of three species of *Pieris* (*P. rapae crucivora* Boisduval, *P. melete* Ménétriès, and *P. napi japonica* Shirôzu) (Lepidoptera: Pieridae) for the upper and lower surfaces of the leaves of their host plants (Brassicaceae) were investigated in the laboratory. On horseradish *Armoracia rusticana* Gaertn. Mey. et Scherb., which was provided as a common food for three species, second and third instar larvae of the respective species preferred the lower to the upper surface of horizontally placed leaves, irrespective of whether they hatched on the upper or lower surface. First instar larvae seemed to remain on the surface on which they hatched. However, first instar larvae of *P. melete* on *Rorippa indica* (L.), a natural food of *P. melete* in the field, and first instar larvae of *P. napi japonica* on *Arabis flagellosa* Miq., a natural food of *P. napi japonica*, preferred the lower to the upper surface, just as second and third instar larvae did. To elucidate the effects of leaf-surface preference, the percentage parasitism of *P. rapae crucivora* on *Arm. rusticana* and *Ara. flagellosa* by the parasitoid *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) was investigated. On *Arm. rusticana*, the percentage parasitism of the larvae on the upper surface was higher than that of larvae on the lower surface. On *Ara. flagellosa*, however, percentages parasitism were nearly equal on both surfaces. Leaf-surface preference by the larvae of *Pieris* is discussed in terms of avoidance of parasitism by the parasitoid *C. glomerata*.

INTRODUCTION

Pieris butterflies such as *P. rapae crucivora* Boisduval, *P. melete* Ménétriès and *P. napi japonica* Shirôzu (Lepidoptera: Pieridae) are well-known in Japan as small white butterflies. The larvae feed mainly on crucifer plants such as cabbage, radish, yellowcress and rockcress. The common habitats and principal food plants of these three species of butterfly differ (Ohsaki & Sato, 1999). *Pieris rapae crucivora* larvae feed mainly on cabbage and to some degree on radish or other crucifers in open sunny fields. *Pieris melete* and *P. napi japonica* feed mainly on wild crucifers growing at the edges of forests (Ohsaki, 1980). The larvae of *P. melete* occasionally feed on vegetables as do the larvae of *P. rapae crucivora*. *Pieris napi japonica* larvae are found almost exclusively on rockcress, *Arabis* plants. For that reason, their habitat is rather limited (Ohsaki & Sato, 1994).

The larvae are adversely affected by predation and parasitism by many natural enemies such as spiders, bugs, paper wasps, parasitoid flies and wasps, and birds. Large larvae are expected to be at higher risk of predation than small ones; small larvae are reportedly more vulnerable to parasitoids than are large ones (Slansky, 1986; Van Driesche, 1988; Reavey, 1993). The gregarious parasitoid wasp *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) attacks young *Pieris* larvae and strongly affects the population dynamics of *Pieris* butterflies, particularly *P. rapae crucivora* (Matsuzawa, 1958; Ohsaki & Sato, 1990, 1994). *Cotesia glomerata* females seek hosts on and near feeding marks on leaves by detecting cues such as chemical substances synthesized at wounds caused by host larvae (Sato, 1979; Horikoshi et al., 1997). When being attacked by the parasitoid, *P. rapae crucivora* larvae seem to resist being parasitized by thrashing their body, sometimes spitting saliva at the attacking wasp. However, these behaviours are useless if performed by first or second instar larvae, which are regarded as the principal hosts of *C. glomerata* (Matsuzawa, 1958), as in *P. brassicae* (L.) (Johansson, 1951;

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Slansky, 1986). Apparently, the deterrent behaviours of small larvae are ineffective against attacking parasitoids. However, the small larvae have a means of reducing their risk of being parasitized. Tagawa et al. (2008) report that young, 1st–3rd instar larvae on cabbage leaves prefer the lower to the upper surface, although 4th–5th instar larvae show no such leaf-surface preference. The lower-surface preference exhibited by young larvae is regarded as a behavioural mechanism for avoiding parasitism because the percentage parasitism of the caterpillars on the lower surface is lower than that of caterpillars on the upper surface (Tagawa et al., 2008).

Parasitism avoidance in the three *Pieris* species is reported by Ohsaki & Sato (1990, 1994) as an ecological or an immunological mechanism, but they did not consider the behaviour of host larvae. Such behaviour might serve as an added avoidance mechanism against parasitoids, as evidenced in *P. rapae crucivora*, if young caterpillars of *P. melete* and *P. napi japonica* show a preference for a particular leaf surface when feeding on their food plants. This study was designed to ascertain whether or not leaf-surface preference exists in young caterpillars of three species of *Pieris*. In addition, the effect of the larvae feeding on different leaf surfaces on parasitism by the parasitoid wasp *C. glomerata* was determined.

MATERIALS AND METHODS

Caterpillar

From fields in Okayama, Japan in 2008 and 2009, eggs, larvae and adult butterflies of three species of *Pieris* were collected: *P. rapae crucivora* (*Pr*), *P. melete* (*Pm*) and *P. napi japonica* (*Pn*). Eggs were allowed to hatch at room temperature in the laboratory. Newly hatched larvae and larvae collected in the field were reared at room temperature, principally on their food plants (*Brassica oleracea* var. *capitata*, *Rorippa indica* and *Arabis flagellosa*, respectively) in 350 ml plastic cups until pupation or parasitoid egression, with absorbent paper placed beneath the lids. Occasionally, the larvae were offered horseradish (*Armoracia rusticana*) leaves. After pupation, pupae of each species were put in a butterfly cage (l × w × h = 130 × 49 × 136 cm) placed in a room. Adult butterflies that emerged from these pupae were fed a dilute solution of honey.

Parasitoid

Parasitoids were obtained from parasitized larvae of *P. rapae crucivora* collected in the field. Within a day after egression from the hosts, the cocoon clusters of *C. glomerata* were put in 30 ml vials and kept at 20°C under a 16L : 8D photoperiod. To assure mating after adult emergence, both sexes were kept together in the vials for more than 3 days with a drop of honey and water. Then, females were allowed to parasitize young *P. rapae crucivora* larvae. These artificially parasitized hosts were reared under the conditions described above.

Food plants of *Pieris*

Cabbage, *B. oleracea* var. *capitata*, and horseradish, *Arm. rusticana*, leaves were collected from the field. Variable leaf yellowcress, *R. indica*, and rockcress, *Ara. flagellosa*, were collected from the field and were planted individually in small pots (8 × 8 × 8 cm). Immediately after collection, all eggs and animals on their leaves were removed carefully. Leaves of *R. indica* and *Ara. flagellosa* were smaller and softer than those of horseradish or cabbage.

Leaf-surface location of three *Pieris* specis larvae on *Arm. rusticana*

In the field, the three *Pieris* butterflies were observed to oviposit on horseradish leaves. Therefore, to collect new eggs of each *Pieris* species, fresh horseradish leaves, *Arm. rusticana*, of ca. 15 cm in length were placed in a butterfly cage in which the butterflies of one species were flying. Eggs on a randomly chosen surface were removed; those on the other surface were left to ascertain whether *Pieris* larvae preferred the upper or lower surface of the leaves. The number of eggs left on a single leaf was set as five. Each of these leaves was kept horizontally with the egg surface either facing up or down in a transparent plastic case (22 × 16 × 12 cm) at room temperature. The difference between adaxial and abaxial surfaces was ignored because the larvae did not discriminate between anatomical surfaces (Tagawa et al., 2008; prelim. obs.). One day after hatching, the first instar larvae on the respective surfaces were counted. Thereafter, the larvae on each leaf surface were counted on the day after each larval moult until the fourth instar. Unhealthy or dead larvae were excluded from the count. Horseradish leaves were exchanged with fresh leaves of similar size every other day. When changing leaves, each larva was allowed to move freely to new leaves.

Leaf-surface location of *P. melete* larvae on *R. indica*

Several pots of *R. indica*, a natural food of *P. melete* larvae, were placed in the butterfly cage of *P. melete* to collect new eggs. After harvesting leaves, eggs on one surface of the harvested leaves were removed. Those on the other surface were left intact. The number of eggs left on a single leaf was set as 1–3. The petiole of each leaf was wrapped with a water-moistened cotton ball. Then the leaf was kept horizontally in a 1500 ml plastic cup at room temperature with the egg surface facing either up or down. Thereafter, the same procedure as that described above was performed.

Leaf-surface location of *P. napi japonica* larvae on *Ara. flagellosa*

Several pots of *Ara. flagellosa*, an ordinary food of *P. napi japonica* larvae, were placed in the butterfly cage of *P. napi japonica* to collect new eggs. After removing eggs from one surface of the leaves, each pot was placed on a water-moistened cotton sheet in a 1500 ml plastic cup and kept at room temperature. The number of eggs left on a single leaf was set as 1–3. Thereafter, the same procedure as that described above was performed.

Parasitism differences between the leaf surfaces

Oviposition-experienced, mated females of *C. glomerata*, younger than 7 days old, were used in the parasitism experiments. The experienced females were prepared by offering young *P. rapae crucivora* larvae once within a day before the experiment. As hosts in this parasitism experiment, *P. rapae crucivora* larvae were provided because they were the most easily obtained.

To examine the parasitism difference between the leaf surfaces of *Arm. rusticana*, ca. 5 larvae of first, second, or third instar *P. rapae crucivora* were put on the upper or the lower surfaces of the leaves. Each leaf was then placed horizontally in a transparent plastic case (22 × 16 × 12 cm) 4 cm above the bottom of the case. A female parasitoid was then introduced into this case and was allowed to attack the hosts freely for 24 h at room temperature. After removing the wasp, the host larvae were collected, irrespective of their position, and were reared under standard conditions. This procedure was replicated 2–4 times for each setting. Larvae that died during rearing were dissected under a binocular micro-

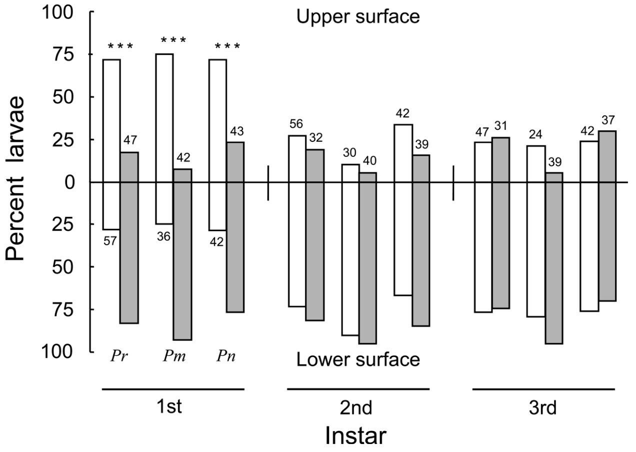

Fig. 1. Leaf surface locations of 1st–3rd instar larvae of three species of *Pieris* on horseradish leaves. The eggs hatched on the upper (white bars) or the lower (grey bars) surface: *Pr – P. rapae crucivora*; *Pm – P. melete* and *Pn – P. napi japonica*. Figures associated with the bars are the numbers of larvae. For every species, distribution patterns of first instar larvae are significantly different between the groups (χ^2-test: *** $p < 0.001$).

scope. Then parasitoid eggs and larvae were counted. For larvae that yielded parasitoids, the cocoons were counted. Dead hosts were dissected to ascertain the number of parasitoid larvae that failed to egress.

Parasitism of *P. rapae crucivora* larvae on *Ara. flagellosa* was also examined. Nearly five larvae of first, second, or third instar *P. rapae crucivora* were put in a small pot (ca. 300 ml) on the upper or lower surfaces of the leaves of plants of *Ara. flagellosa*. Each pot was then placed in a plastic case (22 × 16 × 12 cm). Thereafter, the same procedure as that described above was performed and replicated 2–4 times for each setting.

Statistical analyses

Distributions of larvae on the leaf surfaces and percentage parasitism of larvae on leaf surfaces were analyzed using χ^2-tests. Clutch sizes of *C. glomerata* females were examined using a Mann-Whitney U-test (Zar, 1999).

RESULTS

Leaf-surface location of three *Pieris* species larvae on *Arm. rusticana*

For every *Pieris* species, when the eggs hatched on the lower surface of an *Arm. rusticana* leaf, more than 75% of the first instars remained on the lower surface for one day after hatching (Fig. 1). Distribution patterns of the three species were not different ($\chi^2 = 4.2$, d.f. = 2, ns). When the eggs hatched on the upper surface, more than 70% of the first instar larvae of every species remained on that surface, as they do when they hatched on the lower surface. Distribution patterns were not different among the three species ($\chi^2 = 0.1$, d.f. = 2, ns). First instar larvae of every *Pieris* species showed a tendency to remain on the surface where they hatched. Therefore, for all species, the distribution patterns of first instar larvae were significantly different between the groups (*Pr*, $\chi^2 = 31.2$; *Pm*, $\chi^2 = 37.7$; *Pn*, $\chi^2 = 19.8$; all d.f. = 1, $p < 0.001$).

After the first moult, however, most second instar larvae of all species remained on the lower surface. Accordingly, the significant differences in the distribution patterns between the surfaces where they hatched disappeared thereafter for every species. The second and third instar larvae showed a lower-surface preference (2nd – *Pr*, $\chi^2 = 24.0$; *Pm*, $\chi^2 = 51.4$; *Pn*, $\chi^2 = 20.8$; third – *Pr*, $\chi^2 = 20.5$; *Pm*, $\chi^2 = 38.1$; *Pn*, $\chi^2 = 17.3$; all d.f. = 1, $p < 0.001$).

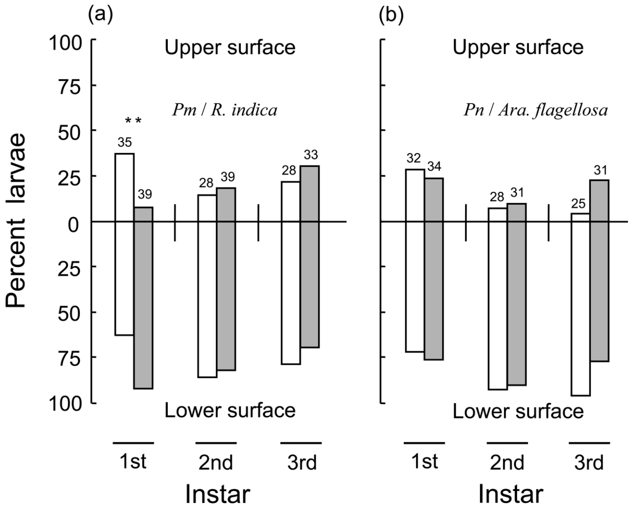

Fig. 2. Leaf surface locations of 1st–3rd instar larvae of *P. melete* on *R. indica* (a) and of *P. napi japonica* on *Ara. flagellosa* (b). The eggs hatched on the upper (white bars) or the lower (grey bars) surface: *Pm – P. melete* and *Pn – P. napi japonica*. Figures associated with the bars are the numbers of larvae. Distribution patterns of first instars of *P. melete* on *R. indica* are significantly different between the groups (χ^2-test: ** $p < 0.01$).

Leaf-surface location of *P. melete* larvae on *R. indica*

When the eggs of *P. melete* hatched on the lower surface of *R. indica* leaf, more than 90% of the first instars remained on the lower surface for one day after hatching (Fig. 2a; $\chi^2 = 27.9$, d.f. = 1, $p < 0.001$). However, when the eggs hatched on the upper surface, fewer than 40% of the first instars remained on the upper surface, indicating there was a tendency not to remain stationary ($\chi^2 = 2.3$, d.f. = 1, ns). Nevertheless, the distribution patterns of first instar larvae were significantly different between the groups ($\chi^2 = 9.4$, d.f. = 1, $p < 0.01$).

After moulting, *P. melete* larvae showed a lower-surface preference, irrespective of whether they hatched on the upper surface or on the lower surface. More than 70% of larvae remained on the lower surface (2nd, $\chi^2 = 30.2$; and 3rd, $\chi^2 = 13.8$; d.f. = 1, $p < 0.001$).

Leaf-surface location of *P. napi japonica* larvae on *Ara. flagellosa*

When the *P. napi japonica* eggs hatched on the lower surface of *Ara. flagellosa* leaves, more than 70% of the first instar larvae remained on the lower surface one day after hatching (Fig. 2b). However, when the eggs hatched on the upper surface, less than 30% remained on the upper surface. Therefore, for first instar larvae, the distribution patterns did not differ according to the surfaces on which they hatched ($\chi^2 = 0.2$, d.f. = 1, ns). Young larvae of *P. napi japonica* on *Ara. flagellosa* leaf showed a lower-surface

Table 1. Parasitism by *Cotesia glomerata* of young *Pieris rapae crucivora* larvae placed on the upper and lower surfaces of horseradish *Armoracia rusticana* (a) and rockcress *Arabis flagellosa* (b) leaves for 1 day. Figures in parentheses are the numbers of parasitized larvae. Figures in brackets are the proportions parasitized; *n* denotes the sample size.

Larval stadium	Upper surface		Lower surface	
	n	No. eggs laid in a host Mean ± SD	*n*	No. eggs laid in a host Mean ± SD
(a) *Armoracia rusticana*				
1st	19	41.5 ± 18.6 (6)	10	40.8 ± 16.5 (5)
2nd	19	29.5 ± 13.8 (13)	15	23.8 ± 5.3 (4)
3rd	15	26.7 ± 18.2 (6)	19	52.0 ± 46.7 (2)
Total[1]	53	31.7 ± 16.4 (25) [0.47]	44	36.6 ± 21.4 (11) [0.25]
(b) *Arabis flagellosa*				
1st	20	48.0 ± 28.9 (16)	16	42.2 ± 25.1 (9)
2nd	18	37.2 ± 4.7 (6)	20	36.9 ± 11.2 (8)
3rd	14	28.4 ± 8.0 (5)	10	35.2 ± 19.7 (5)
Total	52	42.0 ± 23.6 (27) [0.52]	46	38.7 ± 19.1 (22) [0.48]

[1] Proportions parasitized differ between the leaf surfaces (χ^2-test: $p < 0.05$).

preference (1st – $\chi^2 = 15.5$; 2nd – $\chi^2 = 40.7$; 3rd – $\chi^2 = 28.6$; all d.f. = 1, $p < 0.001$).

Differences in the parasitism on the different leaf surfaces

Larvae on *Arm. rusticana*

When 1st–3rd instar larvae of *P. rapae crucivora* were put on the upper surface of an *Arm. rusticana* leaf, the percentages of first, second, and third instars parasitized were, respectively, 32% (6/19), 68% (13/19) and 40% (6/15). Nearly half of all larvae (47%, 25/53) were parasitized (Table 1a). However, when larvae were put on the lower surface, the percentages parasitism of first, second and third instars were, respectively, 50% (5/10), 27% (4/15) and 11% (2/19). In total, 25% (11/44) of larvae were parasitized. The percentage parasitism of all larvae on the upper surface was significantly higher than that of larvae on the lower surface ($\chi^2 = 5.1$, d.f. = 1, $p < 0.05$). The number of eggs laid in a host were equal for both surfaces (Mann-Whitney U-test: ns), but very variable.

Larvae on *Ara. flagellosa*

When *P. rapae crucivora* larvae were put on the upper surface of *Ara. flagellosa* leaves, the percentages parasitism of first, second, and third instars were, respectively, 80% (16/20), 33% (6/18) and 36% (5/14). More than half of all larvae (52%, 27/52) were parasitized (Table 1b). When larvae were put on the lower surface, the percentages parasitism of first, second, and third instars were, respectively, 56% (9/16), 40% (8/20) and 50% (5/10). Nearly half of all larvae (48%, 22/46) were parasitized. No significant difference in percentage parasitism was recorded between the upper and lower leaf surfaces ($\chi^2 = 0.2$, d.f. = 1, ns). The numbers of eggs laid in a host were inferred as equal on both surfaces (ns) and very variable.

DISCUSSION

On horseradish leaves, first instar larvae of three *Pieris* species showed a tendency to remain on the surface on which they hatched. After moulting, however, the larvae of all species showed a preference for lower surfaces. The tendency of recently hatched larvae not to move and the degrees of lower-surface preference of 2nd–3rd instar larvae are similar in the three species (Fig. 1). For *P. rapae crucivora* on cabbage leaves, Tagawa et al. (2008) report the same behaviour of 1st–3rd instar larvae as observed in this study. The tendency of first instar larvae to remain stationary is interpreted as showing that newly hatched larvae are weak and that they have little mobility (Tagawa et al., 2008). First instar larvae are expected to behave similarly to second and third instar larvae if food leaves are softer and/or smaller than cabbage or horseradish leaves. This idea is supported by the surface locations of the larvae on *R. indica* and *Ara. flagellosa* (Fig. 2), the leaves of which are smaller and softer than those of cabbage or horseradish. The different distribution patterns of *Pieris* larvae on different food plants evidently resulted from differences in the size and/or softness of their leaves. These results indicate that young larvae of species of *Pieris* intrinsically prefer the lower surfaces of leaves.

In the field, more than 80% of *Pieris* eggs are laid on the lower surface of leaves (Kobayashi, 1965; Watanabe & Yamaguchi, 1993). Together with this fact, the lower-surface preference of young *Pieris* larvae is expected to result in a strong bias for the larvae to remain on the lower surface of food leaves in the field (Kobayashi, 1963), although large larvae exhibit no such tendency (Mauricio & Bowers, 1990; Tagawa et al., 2008). The lower-surface preference is characteristic of young instar larvae.

Lower-surface preference in the young larvae of *P. rapae crucivora* on cabbage leaves is regarded as an effective way of avoiding parasitoids because the percentage parasitism of the larvae on the lower surface is less than that of larvae on the upper surface (Tagawa et al., 2008). In the present study also, young larvae on the upper surface of horseradish leaves were parasitized more easily than those on the lower surface (Table 1a), suggesting that a lower-surface preference on both cabbage and horseradish is an effective way of avoiding being encountered by parasitoids.

Nevertheless, larvae on the lower surface of *Ara. flagellosa* leaves do not benefit from a reduced risk of parasitism (Table 1b). A plausible reason is that the leaves of *Ara. flagellosa* are smaller and softer than those of horseradish or cabbage. First instar larvae of *P. napi japonica* on the upper surface of *Ara. flagellosa* leaves can move easily to the lower surface (Fig. 2b). Under such conditions, the parasitoid might also easily move to the lower surface while searching for hosts. Accordingly, the benefit for larvae of remaining on the lower surface is expected to be slight. The effectiveness of avoiding parasitoids by remaining on the lower surface of leaves is regarded as dependent on the kind of food plant. However, the difference in the food plants does not directly reflect the percentage parasitism of larvae of *Pieris* recorded in the field.

In the field, *Ara. flagellosa* is fed on mainly by *P. napi japonica* (Sato & Ohsaki, 1987; Ohsaki & Sato, 1994, 1999). The percentage parasitism of *P. napi japonica* larvae on

Arabis plants by *C. glomerata* is reportedly as low as 0–3% (Sato & Ohsaki, 1987; Ohsaki & Sato, 1994). *Arabis* plants normally grow below surrounding vegetation. The parasitoid-escaping efficiency is influenced strongly by the natural environment of these food plants in the field. The importance of the habitat of food plants has been discussed in terms of host-parasitoid relations. The *Arabis* plant environment has been shown to have a strong effect on parasitoid avoidance in *P. napi japonica* (Sato & Ohsaki, 1987; Ohsaki & Sato, 1994). Under natural conditions, other parasitoid-avoidance mechanisms work well for *P. napi japonica*, even if the lower-surface preference is not so effective. Moreover, in cases of occasional use of radish and cabbage by *P. napi japonica* (pers. obs.), lower-surface preference is expected to be effective.

Pieris melete actually escapes from *C. glomerata* by having a strong immune response (Azuma & Kitano, 1971; Sato, 1977), which seems to be sufficient for resisting parasitism. Nevertheless, the larvae show a lower surface preference. Niogret et al. (2009) report that the growth of larvae, which have strong immune response against parasitoids, is retarded by their own immune response, resulting in small adults even if parasitism fails. Therefore, it might be beneficial that young *P. melete* larvae avoid parasitoid attacks by means of leaf-surface preference.

Our results demonstrate that young larvae of three related species of *Pieris* prefer lower surfaces of leaves, suggesting that this behaviour is associated with avoiding parasitoids. To elucidate the ecological meaning of this behaviour further, additional investigations must be conducted, including the host-parasitoid relations of other pierid caterpillars.

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