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The *Pieris napi/bryoniae* hybrid zone at Pont de Nant, Switzerland: broad overlap in the range of suitable host plants

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Abstract. 1. The butterflies *Pieris napi* and *Pieris bryoniae* hybridize in a narrow zone at ≈ 1200 m in the Alps and Carpathians of Europe. They feed as larvae on a variety of hosts in the Brassicaceae, and few host species occur on both sides of the hybrid zone.

2. Females were captured on either side of the hybrid zone at Pont de Nant, Switzerland, eggs obtained, and larvae were offered plants from nineteen species of Brassicaceae and *Reseda lutea* (Resedaceae).

3. Nine of the hosts were found to have eggs or larvae already on them. Only *Capsella bursa-pastoris* and *R. lutea* were unsuitable.

4. Significant survivorship differences among suitable hosts were found. There was no interaction between butterfly species and host plant, which would indicate adaptation by these taxa to their respective suites of hosts.

5. Among suitable hosts, larvae of both taxa had higher mortality on plants with hairy leaves and on older plants beginning to senesce.

6. Differential selection on host use, if it occurs at all, is likely to be a very minor factor in the dynamics of the *Pieris napi/bryoniae* hybrid zone.

Key words. Brassicaceae, herbivory, host-plant relationships, oligophagy

Introduction

Pieris napi (L.) is a multivoltine butterfly that is widespread in Europe at elevations below ≈ 1200 m. The closely related taxon *Pieris bryoniae* (Ochs.) occurs in the Alps and Carpathians above 1200 m, and is univoltine or at most bivoltine. These taxa form hybrid zones wherever their ranges contact (Petersen, 1963). The extreme difference in habitats used by these butterflies over very short distances in the Alps, in combination with relatively high natural densities and ease of manipulation in the laboratory, makes this system a convenient model for the study of ecological and evolutionary processes in hybrid zones.

Theoretical work has shown that the width of a hybrid zone is determined by an equilibrium established between the competing microevolutionary forces of gene flow that broadens the zone and selection that narrows it, and the dynamics of this process are well studied (reviewed by Barton & Gale, 1993). It is convenient to consider hybrid zones as collections of clines at different genetic loci, 'hybrids' as the continuum of recombinant genotypes of varying ancestry, and to use the terms 'intrinsic' and 'extrinsic' to distinguish types of selection in hybrid zones (Harrison, 1993). Intrinsic selection may be thought of as a function of the internal, physiological environment of an organism; such selection occurs against recombinant genotypes when incompatibilities among alleles at different loci result in hybrid dysfunction (e.g. infertility or embryonic death). Extrinsic selection is then a function of the external, ecological environment; it occurs when adaptation to different ecological conditions occurs on each side of the hybrid zone, such that genetically 'pure' individuals are well adapted in their respective habitats and recombinant genotypes are nowhere well adapted. The remaining hypothesis, that extrinsic selection favours recombinant genotypes only in the centre of the zone, has received less theoretical and empirical support (Barton & Hewitt, 1985), and seems likely only when the scale of dispersal is small relative to the breadth of the ecotone. Because of the dynamics between dispersal and selection, hybrid zones make excellent 'natural laboratories' for the study of adaptation to current ecological conditions (Hewitt, 1988; Harrison, 1993).

A transect from 400 to 2000 m elevation was established near Bex, Switzerland to study the *P. napi/bryoniae* hybrid

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Table 1. Potential host plants assayed in this study. Taxonomy follows Lauber & Wagner (1992). See Materials and Methods for classification into host location, leaf hairiness, habitus and host age.

Plant species	Location	Frequency	Hairiness	Habitus	Host age
Brassicaceae					
**Alliaria petiolata* (M.B.) Cavara & Grande	valley	common	glabrous	erect	flowering
*†*Arabis alpina* L.	alpine	common	hairy	low	flowering
Arabis ciliata Clairv.	both	very common	hairy	low	flowering
**Arabis pauciflora* (Grimm) Garke	alpine	rare	glabrous	erect	flowering
Arabis soyeri Reut. & Huet	alpine	infrequent	glabrous	low	flowering
Barbarea intermedia Boreau	both	rare	glabrous	erect	in seed
Barbarea vulgaris R. Br.	valley	rare	glabrous	erect	in seed
*†*Biscutella laevigata* L.	alpine	very common	hairy	low	flowering
Capsella bursa-pastoris (L.) Medikus	both	very common			
**Cardamine amara* L.	valley	infrequent	glabrous	low	flowering
*†*Dentaria heptaphylla* Vill.	both	very common	glabrous	erect	flowering
*†*Dentaria pentaphylla* L.	alpine	very common	glabrous	erect	flowering
Draba azoides L.	alpine	common	hairy	low	flowering
**Erucastrum gallicum* (Willd.) Schulz	valley	very common	hairy	erect	in seed
†*Hesperis matronalis* L.	valley	rare	hairy	erect	in seed
Nasturtium officinale R. Br.	valley	rare	glabrous	low	flowering
Sinapis arvensis L.	valley	very common	glabrous	erect	
†*Sisymbrium officinale* (L.) Scop.	valley	rare	hairy	erect	in seed
**Thlaspi rotundifolium* (L.) Gaud.	alpine	common	glabrous	low	flowering
Resedaceae					
Reseda lutea L.	valley	common			

* = plants found with eggs or larvae; † = females seen ovipositing on these plants.

zone. The hybrid zone is centred at 1200 m at Pont de Nant, and is being described in detail elsewhere (A. H. Porter *et al.*, unpublished data. The *P. napi/bryoniae* hybrid zone is narrow, with a width of only 2.36 km (A. H. Porter *et al.*, unpublished data). Dispersal in the transect is high, estimated at $s = 2$ km/gen$^{-1/2}$ (A. H. Porter *et al.*, unpublished data). The combination of high dispersal and narrow width implies a very strong effective selection differential occurring across the hybrid zone, at approximately $s = 0.65$ (95% CI 0.23–2.2). Some intrinsic selection probably occurs against hybrids (Petersen & Tenow, 1954; Lorkovic, 1962; Bowden, 1966). The most important extrinsic selection pressure is probably on the propensity to enter pupal diapause, the physiological trait responsible for the sharp difference in voltinism across the hybrid zone (A. H. Porter *et al.*, unpublished data). However, in the *Papilio* butterfly hybrid zone in North America, host plants comprise an important extrinsic selection pressure (Lindroth *et al.*, 1988b) probably contributing substantially to hybrid zone dynamics. In the *P. napi/bryoniae* literature, numerous hosts in the Brassicaceae are reported and few occur in the habitats of both butterfly taxa. Varga (1967) proposed, based on anecdotal observations, that in the Carpathian hybrid zone at Bükk, Hungary, a series of populations of *P. napi* and *P. bryoniae* had adapted to particular host plant species at a very local scale, in a way that leads to partial reproductive isolation. However, most crucifer-feeding pierids (Pierini and Euchloini) worldwide have broad and overlapping host ranges, suggesting that local adaptation to hosts rarely occurs in pierine butterflies (Courtney & Chew, 1987).

In this study, the proposition is addressed that adaptation for larval performance on host plants in these different habitats is an important selection pressure contributing to the dynamics of the *P. napi/bryoniae* hybrid zone. Broad overlap in host suitability would indicate that such selection is unimportant in the overall dynamics of the hybrid zone. It must be emphasized that this study concerns the extrinsic selection pressures in the different habitats on either side of the zone, and addresses neither the issue of intrinsic selection nor the genetic basis for any differences in larval performance. Chew (1975, 1977, 1980; Renwick & Chew, 1994) and Courtney (1982, 1986; Courtney & Chew, 1987) have identified several host attributes that lead to variance in *Pieris* larval performance on different crucifer species, and the secondary goal of this study is to document the potential host range and verify these factors in the *Pieris napi/bryoniae* hybrid zone. Controversy remains about what constitutes species and subspecies in the *Pieris napi* group, with an abundance of opinion and few relevant data. The problem will not be resolved here, and binomials and the term 'butterfly species' will be used for literary convenience; no conclusion about their taxonomic status is implied.

Materials and Methods

In June 1993, potential host plants in the study transect in the vicinity of the *P. napi/bryoniae* hybrid zone at Pont de Nant, in Canton Vaud, Switzerland, were identified using Lauber & Wagner (1992) (Table 1). Plants were classified as to their location in *P. napi* ('valley') habitat, *P. bryoniae* ('alpine') habitat, or in both habitats based on their ranges in the study transect and those reported in Lauber & Wagner (1992) (Fig. 1).

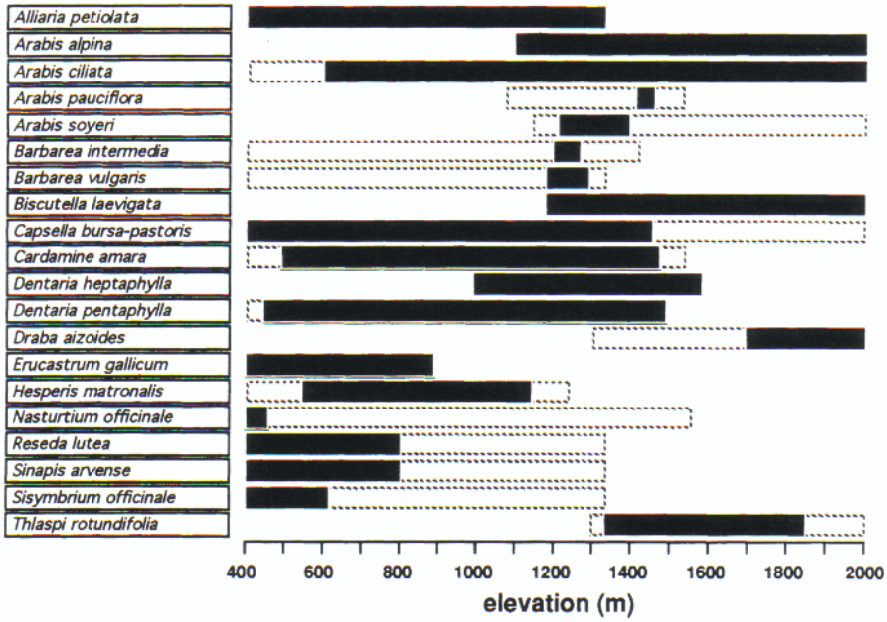

Fig. 1. Approximate elevational ranges of potential hosts at Pont de Nant, Switzerland. Solid lines indicate the ranges within the region of the transect; dotted lines indicate general ranges in Switzerland, adapted from Lauber & Wagner (1992). The hybrid zone occurs between 1050 and 1300 m, centred at 1200 m.

Table 2. ANOVA of the effects of host, brood and butterfly species on arcsin-square root transformed larval survivorship. Brood is nested within butterfly species.

Source	d.f.	SS	MS	*F*	*P*	Error term
Host	17	4.908	0.289	4.811	0.0007	residual
Butterfly species	1	0.463	0.463	6.237	0.0371	brood
Brood (butterfly species)	8	0.594	0.074	1.237	0.3314	residual
Host * butterfly species	16	1.018	0.064	1.060	0.4467	residual
Residual	19	1.140	0.060			

Reseda lutea was included in the study because it is an occasional host of related pierids (Courtney & Chew, 1987; Higgins & Hargreaves, 1991). Other cruciferous plants that occur in the study area were rare (< three plants encountered) or had already senesced, such that sufficient plants were not available.

Three dams (females) of *P. napi* and seven of *P. bryoniae* were obtained from the low (400–600 m) and high (1400–2000 m) elevations, respectively, of the transect. Only dams with wing pattern phenotypes typical of 'pure' taxa were used. Dams were induced to oviposit individually in transparent plastic boxes containing cuttings of *Alliaria petiolata*. Upon hatching, larvae were transferred to 12 × 1.5 cm Petri dishes, each containing cuttings of the hosts in Table 1. Environmental chambers and greenhouses were not available at the transect site and the larvae were reared indoors at ambient temperatures on cuttings taken from the field. The cuttings were kept fresh by wrapping their stems in wet tissue paper and replaced every 2–4 days or sooner if the larvae had eaten them. The foliage was inspected for predators and the presence of wild *Pieris* larvae before use, and the larvae found were transferred to separate dishes for rearing. The number of plants per host varied with the size of the plant, but at least ten individuals of the largest plants were used. Naturally occurring ovipositions encountered over the duration of the study were also recorded.

The dependent variable was the proportion of larvae per (original) Petri dish that survived to pupate, and analysis of variance was used on these scores. Three factors were controlled: host plant, butterfly species (dam was *P. napi* or *P. bryoniae*), and brood (the individual dams). Replication consisted of ten larvae brood^{-1}, and two broods (butterfly species)$^{-1}$ host^{-1} where host material permitted. Brood was treated as a random effect, and all others treated as fixed. Further data relevant to selection on larval growth on different hosts, including developmental times and pupal weights, were not studied because temperature and host quality could not be controlled sufficiently.

There were several logistical constraints and steps were taken to include or limit their effects. First, dams laid different numbers of eggs, so that it was not possible to give each host plant to larvae from each dam, precluding a fully factorial design. Even if enough eggs had been available, some host species were rare enough that sufficient foliage would not have been available (e.g. *Arabis pauciflora*). Second, foliage and

Table 3. Larval survivorship on potential hosts. n = number of broods, q = proportion surviving to pupation.

	Pieris napi			*Pieris bryoniae*			Totals		
Plant species	n	q	SE	n	q	SE	n	q	SE
Dentaria heptaphylla	3	0.97	0.03	2	0.95	0.05	5	0.960	0.024
Thlaspi rotundifolia	1	1.00		2	0.90	0.10	3	0.933	0.067
Barbarea vulgaris	2	0.90	0.10				2	0.900	0.100
Arabis soyeri	2	1.00		2	0.70	0.10	4	0.850	0.096
Alliaria petiolata	1	1.00		1	0.70		2	0.850	0.150
Hesperis matronalis	2	0.90	0	2	0.90	0	4	0.900	0
Biscutella laevigata	2	0.95	0.05	2	0.70	0.20	4	0.825	0.111
Dentaria pentaphylla	2	0.90	0	2	0.85	0.05	4	0.875	0.025
Arabis pauciflora	1	0.80		2	0.90	0	3	0.867	0.033
Cardamine amara	2	0.90	0	2	0.80	0.10	4	0.850	0.050
Barbarea intermedia	1	0.70		2	0.85	0.05	3	0.800	0.058
Arabis ciliata	1	0.90		2	0.70	0.10	3	0.767	0.088
Nasturtium officinale	1	0.90		2	0.65	0.15	3	0.733	0.120
Sinapis arvense	2	0.85	0.05	2	0.25	0.25	4	0.550	0.202
Arabis alpina	2	0.55	0.05	2	0.40	0	4	0.475	0.048
Erucastrum gallicum	2	0.65	0.05	2	0.20	0.20	4	0.425	0.155
Draba aizoides	1	0.60		1	0.10		2	0.350	0.250
Sisymbrium officinale	2	0.36	0.36	2	0		4	0.182	0.182
Reseda lutea	2	0		2	0		4	0.000	
Capsella bursa-pastoris	2	0		2	0		4	0.000	

Table 4. ANOVA of the effects of host genus, brood and butterfly species on arcsin-square root transformed larval survivorship. Brood is nested within butterfly species. This serves as a partial control for phylogenetic effects, in the absence of a phylogeny of the hosts. There is no qualitative difference from the results of Table 2.

Source	d.f.	SS	MS	F	P	Error term
Host genus	11	4.224	0.384	5.569	0.00009	residual
Butterfly species	1	1.114	1.114	11.280	0.0100	brood
Brood (butterfly species)	8	0.790	0.099	1.433	0.2237	residual
Host genus * butterfly species	11	0.782	0.071	1.031	0.4453	residual
Residual	30	2.069	0.069			

Table 5. Results of a multifactorial ANOVA on arcsin-square root transformed larval survivorship.

Source	d.f.	SS	MS	F	P
Butterfly species	1	1.589	1.589	18.961	0.00007
Host hairiness	1	1.827	1.827	21.806	0.00002
Host age	1	2.197	2.197	26.218	0.000005
Host habitus	1	0.239	0.239	2.846	0.0978
Hairiness * host age	1	0.437	0.437	5.212	0.0267
Hairiness * habitus	1	0.123	0.123	1.473	0.2306
Butterfly species * hairiness	1	0.008	0.008	0.096	0.7578
Butterfly species * host age	1	0.319	0.319	3.805	0.0567
Butterfly species * habitus	1	0.116	0.116	1.386	0.2447
Butterfly species * hairiness * habitus	1	0.006	0.006	0.072	0.7894
Butterfly species * hairiness * host age	1	0.031	0.031	0.368	0.5469
Residual	50	4.190	0.084		

space were limited so larvae were reared by brood in groups of ten dish^{-1}, split to five dish^{-1} during the fourth instar. Thus, brood × host plant interactions could not be tested, and brood effects were considered only to see if they might have confounded the butterfly species × host plant and butterfly species × host location interactions.

Third, there may be factors common to several hosts that affect larval survivorship. These effects were explored by

classifying hosts as to habitus and leaf hairiness. Two factor levels of each were assigned: 'erect' vs. 'low' habitus and 'hairy' vs. 'glabrous' leaves (Table 1). Only plants very near the ground or found standing in water (*Cardamine*, *Nasturtium*) were considered 'low' and only those with very hairy leaves were considered 'hairy'. Also, cuttings from old plants were more likely to senesce quickly than those from young plants. This was studied by classifying hosts to their phenological stage, with two factor levels (Table 1). The level 'in seed' refers to older plants with numerous mature seeds and few remaining flowers; 'flowering' refers to plants in earlier phenological stages (all were flowering except *Alliaria petiolata*, in the rosette stage, and about half of the individuals of the two *Dentaria* species). All these were treated as fixed effects.

Finally, plant species were treated as independent in this analysis. There is presently no phylogeny available for these taxa to rectify this problem, so a reanalysis was performed grouping hosts by genus instead of species. In doing so, *Cardamine* and *Dentaria* were pooled conservatively as a single genus as these are sometimes regarded as 'splitter's genera'. Statistical analyses were performed on a Macintosh® computer using SUPERANOVA® (v. 1.11; Abacus Concepts, Berkeley, CA, U.S.A.), with Type III sums of squares, and sequential Bonferroni corrections (Rice, 1989) were applied.

Results

Eggs or larvae of *P. napi* or *P. bryoniae* were found on nine species of Brassicaceae in the region of the transect (Table 1), and females were also observed ovipositing on six of these. After the experiment ended, larvae were also found on *Hutchinsia alpina* (L.) R. Br. above 1300 m and *P. bryoniae* females were later observed ovipositing on them. All eggs and larvae were reared to pupation on their respective hosts (including *Hutchinsia*) with little mortality, and were confirmed not to be from the related butterfly species, *Pieris rapae*.

Two hosts did not support larval growth. All larvae placed on *Capsella bursa-pastoris* began wandering immediately and died without feeding. About half of the larvae on *Reseda lutea* survived the moult to the third instar, but declined thereafter and perished before reaching fourth instar. At least some larvae of both taxa survived to pupation on each of the remaining hosts. In 1994, individuals from two *bryoniae* broods and one *napi* brood were also reared to pupation on *Kernera saxatilis* (L.) Rchb., a subalpine, low-density species of rocky outcrops, with rosettes too small to sustain even a single larva to pupation in the field. *Capsella* and *Reseda*, with zero survivorship, were omitted from all further analyses.

There were highly significant differences in larval survivorship among hosts (Table 2). A breakdown of the host main effect (Table 3) shows a broad range of host suitabilities. A significant difference between the butterfly species can be seen in Table 2, but this was not significant (but see below) after a Bonferroni correction (including *P*-values of Table 2 and Table 5). The butterfly species effect was that *P. napi* showed slightly better average survivorship than did *P. bryoniae*

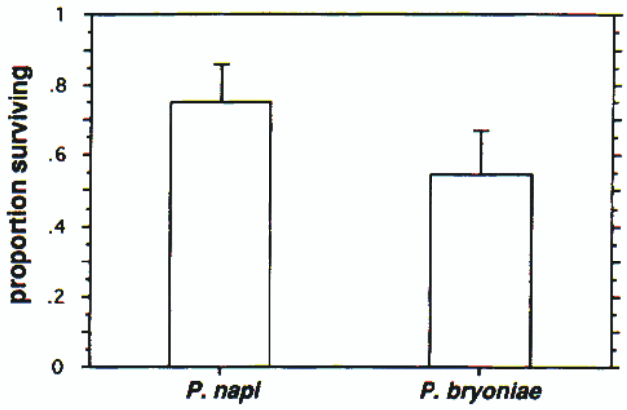

Fig. 2. Main effect of butterfly species on survivorship (95% CI).

(Fig. 2). There was no effect of broods nested within butterfly species.

There was no indication of an interaction between host plants and butterfly species, as would be expected if *P. napi* and *P. bryoniae* were adapting to different hosts on different sides of the hybrid zone (Table 2).

As a control for phylogenetic effects, the analyses of Table 2 were repeated replacing host species with host genus, with very similar results (Table 4). There was a strong host genus effect, and a slightly stronger butterfly species effect than in the previous analysis, and the brood effect was not detected. The species effect was not significant after the sequential Bonferroni correction (including *P*-values of Table 4 and Table 5). There was no detectable interaction between butterfly species and host genus.

To better understand the effects of host species, traits correlated with hosts were investigated. The ANOVA configuration that permitted the greatest number of simultaneous comparisons of host factors is shown in Table 5. Two of the three host-associated traits had highly significant effects on survivorship, as did the butterfly species (Fig. 2). Plants with glabrous leaves were significantly more palatable than those with hairy leaves (Fig. 3), and plants in the later stages of their phenologies were significantly less palatable. The interaction between plant age and hairiness ($P = 0.0267$; Fig. 4) was not significant after Bonferroni correction. A nearly significant butterfly species × host age interaction ($P = 0.0567$) suggests that *P. bryoniae* might be at a relative disadvantage on senescing plants (Fig. 5). This observation requires independent verification, but is mentioned here because it suggests a possible adaptive difference across the hybrid zone. The combination of factors in Table 4 did not have sufficient degrees of freedom to test for remaining interactions, and separate ANOVAs did not show additional significant interactions ($P > 0.25$).

Discussion

Larval survivorship on different hosts does not appear to be a major factor under strong differential selection on opposite sides of the *Pieris napi/bryoniae* hybrid zone, even though few

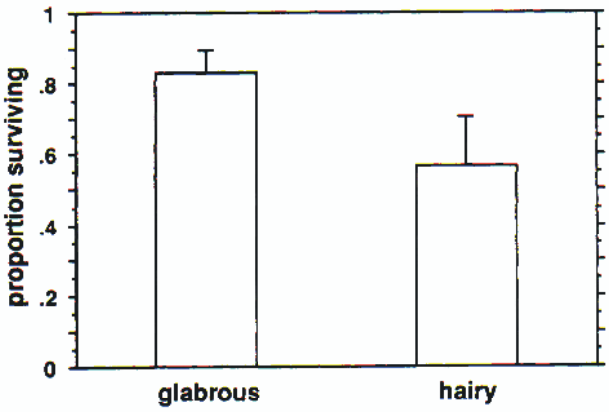

Fig. 3. Main effect of leaf hairiness on survivorship (95% CI).

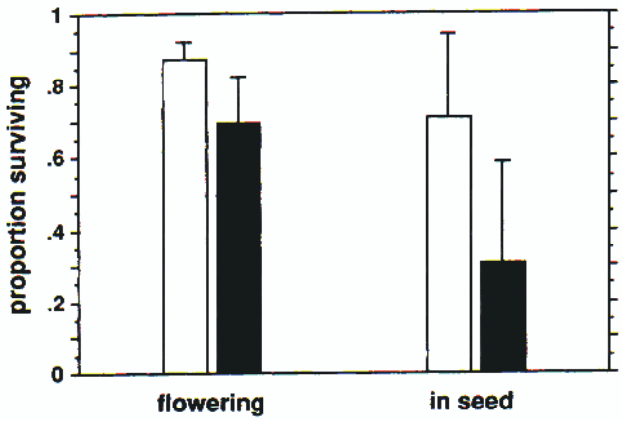

Fig. 4. Effect of interaction between plant hairiness and host age on larval survivorship (95% CI). White, glabrous leaves; black, hairy leaves.

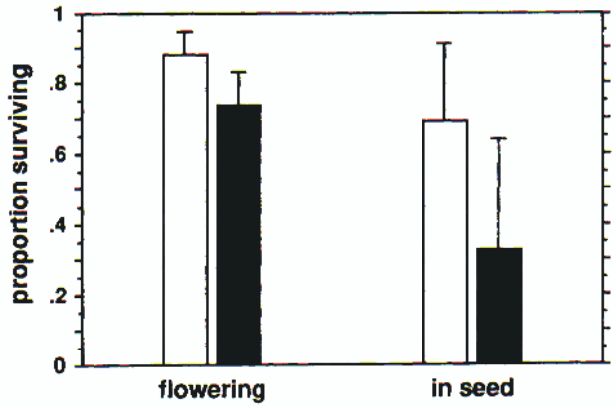

Fig. 5. Effect of interaction between butterfly species and host age on larval survivorship (95% CI). White: *Pieris napi*; black: *P. bryoniae*. The main effect of host age is significant ($P = 0.000005$), and the interaction is almost significant ($P < 0.06$) before Bonferroni corrections are applied.

suitable hosts occupy the habitats of both butterfly taxa. *Pieris napi* and *P. bryoniae* have relatively large and overlapping host ranges, with hosts being either qualitatively acceptable or unacceptable to larvae of both. Varga's (1967) supposition that *P. napi* and *P. bryoniae* are locally specialized to use different hosts was not supported in this study.

The host range in this laboratory study is probably indicative of broad host use in the field, even though realized host range is determined also by female oviposition behaviour. The primary evidence is that eggs and larvae were found naturally on half of the potential hosts found to be acceptable. Clearly further field observations combined with choice experiments on oviposition, such as those of Huang & Renwick (1993), are required to verify the remainder. Two exceptions might be the alpine mat-forming crucifer *Draba aizoides* and the tiny rock-dwelling *Kernera saxatilis*, which even in large stands are probably too small to support growth of even a single larva to pupation. On the other hand, *Pieris* larvae may often be forced to search for a second plant to complete development (Cappuccino & Kareiva, 1985), and the inclusion of such a small plant as *Draba aizoides* in the host range may be related to this (Chew, 1975, 1977). Perhaps more likely is that these small species are phytochemically similar to the larger species occurring in the Alps; this similarity in the Brassicaceae has been implicated in the broad host range of other *Pieris* (Renwick & Chew, 1994). Several females were also observed testing and rejecting *Arabis ciliata* for oviposition. These plants are usually small and typically occur among larger, more acceptable crucifer species such as *Biscutella*, the species that attracts most of the oviposition at higher elevations.

Among acceptable hosts, those yielding lower survivorship tended to have hairy leaves (Table 5, $P = 0.00002$), and some of the mortality in these broods was due to disease. David *et al.* (1972) showed that resistance to pathogens is correlated with host quality, and incidence of disease would increase if leaf hairs do reduce host quality. Another possibility is that leaf hairs may be more likely to trap viral and bacterial pathogens splashed from the soil during rain. It was difficult to wash the more hirsute plant species, especially those with small rosettes, and Cappuccino & Kareiva (1985) found a higher incidence of disease in *Pieris virginiensis* when they soiled the leaves experimentally. Susceptibility to disease is not the entire story, however, because approximately half of the larvae throughout the experiment that died did so without any external sign of disease or injury, often in the fourth or fifth instar. It may seem odd that butterflies would use hosts of lower quality when better plants are available. Courtney (1982, 1986) has shown that selection to avoid less palatable plants is countered by constraints on the time available for searching by females.

The age class of the host plant had an important effect on caterpillar survivorship (Table 5, $P = 0.000005$), with older plants being less palatable. It was observed that cuttings of older plants began to turn yellow more quickly than those from young plants, suggesting that plant quality was lower in the older plants. There was also weak indication of a butterfly species × host age interaction that suggests a possible underlying physiological adaptation: *P. bryoniae*, denizen of the cooler mountains, rarely encounters senescing plants, whereas *P. napi*, denizen of hotter, low-elevation habitats, is more likely to encounter plant senescence and thus may have evolved a

greater larval tolerance. This interaction, if it is verified, has the potential to contribute to the overall selection difference driving the *P. napi/bryoniae* hybrid zone, and should be investigated in a study controlling age within the same plant species. However, plants that remain in good quality throughout the season are not unusual even at low elevation (e.g. *Alliaria*). An effective selection difference of $s = 0.65$ has been measured across the hybrid zone (A. H. Porter *et al.*, unpublished data), and larval adaptation to plant senescence is unlikely to be strong enough, by itself, to play a major role in the hybrid zone's dynamics.

This study yields conflicting results concerning the effect of butterfly species on larval survivorship (Fig. 2). This effect is not significant in Table 2 (after Bonferroni correction), where brood effects are included and host effects are considered globally. The butterfly species effect is highly significant in Table 5, where brood effects are not considered and host effects are broken down. A weak effect of butterfly species is suspected, but requires confirmation. This effect, if verified, would make a contribution to the overall selection differential across the *P. napi/bryoniae* hybrid zone. The question remains, why should *P. napi* show consistently better survivorship than *P. bryoniae*, even on plants restricted to the alpine, *P. bryoniae* habitat? The hybrid zone would not be likely to stop gene flow of traits favourable on both sides of the zone (Barton & Bengtsson, 1986), and, indeed, allozyme data suggest that gene flow is extensive between *P. napi* and *P. bryoniae* (Porter & Geiger, 1995). Certainly any genetic component for *P. napi*'s general superiority in survivorship should cross the hybrid zone and spread rapidly into *P. bryoniae*. In the same vein, it is difficult to understand why these butterflies should perform so well on plants that are not in their habitats. It may be due to a lack of variability in the defences of the plants themselves (Rodman & Chew, 1980). This is consistent with the observation that several pierines in North and South America have successfully included many introduced crucifers in their diets (Shapiro, 1975, 1976; Kellner & Shapiro, 1983). However, North American *Pieris* show low survivorship on other introduced crucifer species, including *Alliaria* (Courant *et al.*, 1994), presumably because these butterflies have evolved their host ranges in the absence of these plants. One might expect a similar effect between lowland and alpine habitats in Europe. If gene flow has spread diet-breadth adaptations from *P. bryoniae* into *P. napi*, it is then difficult to see why this has not also occurred in the other direction.

The relative importance of selection for larval survivorship on different host species varies among butterfly hybrid zones. Lindroth *et al.* (1988a,b) studied relative growth rates of *Papilio glaucus* and *P. canadensis* on plants from either side of their hybrid zone in eastern North America. Like *Pieris*, *Papilio glaucus* and *P. canadensis* are oligophagous, and like the biogeography of the *P. napi/bryoniae* zone, the ranges of host plants correspond to the boundary of the *Papilio* hybrid zone. But unlike *Pieris*, *Papilio glaucus* has limited survival and slow growth on aspen (*Populus tremuloides*), the preferred host of *P. canadensis*, whereas *P. canadensis* has similar deficiencies on *Liriodendron*, a frequent host of *P. glaucus*. Even in plants permitting survival of both *Papilio* species, the growth rates may differ so much that a strong selection differential is likely to be produced across the hybrid zone. Other factors are also probably under differential selection across the *Papilio glaucus/canadensis* hybrid zone, including the propensity to enter diapause (Rockey *et al.*, 1987) (as it seems to be in the *Pieris napi/bryoniae* hybrid zone), and intrinsic selective factors also occur, manifested in the skewed sex ratio of F_1 broods (Hagen *et al.*, 1991). The adaptive significance of larval growth rates and ultimate body size of *P. napi* and *P. bryoniae* on different hosts await experiments controlling host age and the thermal environment. However, preliminary observations suggest larval growth rates may differ among plant species by up to several days at room temperatures – also shown for *A. cardamines* by Courtney (1981) – but rates appear to differ only weakly, if at all, between butterfly taxa. Such differences would be small compared to the effect of temperature on growth rate (Sherman & Watt, 1973). In the transect used in this experiment, where the geography is steep and complex, phenologies of populations of even the same plant species may differ by as much as a month, and temperatures in these microhabitats provide another dimension of variability. In practice, females place eggs on plants in a variety of phenological stages and microhabitats (Ohsaki, 1980; P. Benninger, unpublished data). For the role of larval performance in the maintenance of the hybrid zone, the important consideration is relative differences among *P. napi* and *P. bryoniae* larvae, and these would have to be considerable not to be overwhelmed by residual genetic and environmental variance. The implication is that it seems unlikely that selection for larval growth rates on different hosts is an important factor driving the dynamics of the *Pieris napi/bryoniae* hybrid zone, although it too may play a minor role.

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