



International Association for Ecology

Coexistence and Host Use by a Large Community of Pierid Butterflies: Habitat Is the Temple

Author(s): S. P. Courtney and F. S. Chew

Source: *Oecologia*, Vol. 71, No. 2 (Jan., 1987), pp. 210-220

Published by: [Springer](#) in cooperation with [International Association for Ecology](#)

Stable URL: <http://www.jstor.org/stable/4218147>

Accessed: 14/10/2010 16:10

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=springer>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to *Oecologia*.

<http://www.jstor.org>

Coexistence and host use by a large community of Pierid butterflies: habitat is the templet

S. P. Courtney¹ and F. S. Chew²

¹ Department of Biology, University of Oregon, Eugene, OR 97403, USA

² Department of Biology, Tufts University, Medford, MA 02155, USA

Summary. We report studies on the butterfly-hostplant communities in the species-rich area of west central Morocco. Pieridae feeding on Capparales form two distinct ecological guilds: inflorescence feeders and folivores. Several members of each guild may synchronously occur in sympatry. Substantial levels of cannibalism and inter-specific predation occur amongst the inflorescence feeders. No evidence was obtained for segregation of butterfly species on different hosts. Host plants included in the diet of specialists were also used by generalists. Despite substantial differences observed in laboratory trials of larval survivorship on different hostplants, results were congruent for all Pieridae, suggesting that little one-to-one insect-host coevolution has occurred. Host specialization was instead related to the year-to-year stability of host numbers in an area. High levels of pierid infestation occurred on host species with numerically stable populations. Host numerical stability was correlated with habitat type. There is little evidence for segregation of competing inflorescence feeders by host-plant species, but some evidence for segregation by habitat type (particularly by shading levels). We interpret our results as indicating that the hostplant affiliations of Moroccan Capparales-feeding Pieridae are subject to (at best) diffuse coevolutionary effects from hosts and competitors, and are strongly influenced by habitat characteristics.

Key words: Habitat use – Pieridae – Coevolution – Butterfly community

The choice of diet by phytophagous insects is intimately linked with their community structure. Biotic interactions with hostplants, competitors or predators may influence the pattern of host use within guilds (Slobodkin et al. 1967; Gilbert and Singer 1975; Smiley 1978; Thompson 1983) as also may abiotic effects (Courtney 1982b). However, the relative contributions of these interactions to the specificity of a particular herbivore population is difficult to assess. Observed patterns of host specificity may, for instance, be strongly influenced by historical interactions that can no longer be observed. Plant defences against herbivores could be the result of prior encounters with unknown herbivores or pathogens (Janzen 1968, 1973). Similarly, failure to detect present-day competition or predation (e.g.,

the general paucity of competitive interactions among folivores, Lawton and Strong 1981) does not necessarily exclude such interactions as significant evolutionary influences (Wiens 1977; Schoener 1983). Diffuse competition and coevolution (Fox 1981; Futuyma and Slatkin 1983) rather than tightly-coupled pairwise relationships, will further confound assessment of the relative importance of these processes to the evolution of host specificity. Despite these and other difficulties, comparative studies of host use and specialisation offer considerable power in understanding the evolutionary significance of herbivore-host interactions. We report here studies on a rich community of Capparales-feeding Pieridae. Our previous studies on host choice in similar, but much simpler, communities have emphasized the importance of biotic interactions favouring specialisation (Chew 1975; Courtney 1981), and the destabilising effects of abiotic variation (Chew 1977a; Courtney 1982b). We have undertaken the present study in an attempt to apply these emergent principles to a very large and complex set of species interactions. The central questions of the study address community structure: (1) Do communities of herbivores that exploit physiochemically-similar host plants occur as random association of species, each independently adapted to their environment (including their hosts), or are they structured associations that partition resources? (2) If resource partitioning occurs, what are the environmental variables of importance?

Previous work on non-agricultural populations of butterflies that feed on plants in the Capparales (Pieridae: Pierini and Euchloini) suggests that individuals in many populations attempt to oviposit and feed on almost every glucosinolate-containing species growing in those habitats where adults fly (Nearctic: Shapiro 1975, 1976; Chew 1975, 1977b, 1981; Opler 1974; Neotropical: Kellner and Shapiro 1983; Palaearctic: Wiklund and Ahrberg 1978; Ohsaki 1980; Yamamoto 1981; Courtney and Duggan 1983). Such patterns include introduced butterflies utilising native hosts (e.g., Chew 1981) and also native insects attacking naturalized plants (Shapiro 1975, 1976; Yamamoto 1981) even when some such plants prove lethal to larvae (Chew 1975, 1977b; Rodman and Chew 1980). Such communities typically contain relatively few native species of glucosinolate-containing plants, and often involve recently naturalized plants or herbivores (Kellner and Shapiro 1983; Chew 1981).

Broad diet widths observed in these regions (e.g., North and South America) may be due to the advantageous incor-

poration of new food resources by native species (e.g., Shapiro 1976). Alternatively, broad diet widths may be due to evolutionary inertia because of lack of sufficient time to refine utilisation patterns in pairwise coevolution (e.g., Chew 1977; Rodman and Chew 1980).

Notable exceptions to broad patterns of host generalization do occur: The Neotropical *Itaballia viardi* appears confined to a single species of host (Jordan 1981), as does *Pieris virginiensis* in eastern North America (Shapiro 1971; Cappucino and Kareiva 1985), and several *Pieris* species of Europe (Courtney 1982b). In at least three cases (*I. viardi*, *Pieris cheiranthi*, and *P. virginiensis*), host specialisation occurs in the presence of alternative hosts. In several other species, however (*P. bryoniae*, *P. krueperi*, *P. ergane*), specialisation is associated with use of extreme habitats (dense woodland or alpine areas) with reduced host diversity. These latter species may have evolved host specialisation following adaptation to their peculiar habitat characteristics. Courtney (1982b, 1986) has considered in detail the way that environmental uncertainty may select for host generalism in habitat specialists.

We examine here the association of Pierid butterflies with their hostplants (Capparales) in a community in western Morocco. The Mediterranean region is a centre for species diversity in the Capparales (Maire 1952–1967; Hedge 1976) as well as being an area where many species of Pieridae co-occur (Carcasson 1964; Higgins and Riley 1980). Further, because North Africa is an area of biogeographic mixing between Palaearctic and Ethiopian biota, it provides an opportunity to observe a natural experiment on adaptation to new hosts, and the introduction of new members to both the host and herbivore communities. We ask whether the butterfly species in these communities are adapted to each other's presence, or whether they represent independent entities. We focus on the following questions: 1. to what degree (if any) do the butterflies respond differentially to potential hostplants? 2. Given that there is broad overlap in geographic ranges of the insect species, on what basis (if any) are environmental resources partitioned among Pieridae? 3. Given that butterfly oviposition and larval feeding on Angiosperm inflorescences has evolved only a few times (Chew and Robbins 1984), what differences occur between species in the flower-feeding and folivorous guilds?

Materials and methods

Study sites and species

We studied butterflies and their hostplants in localities in western Morocco, ranging from the southern slopes of the High Atlas to the northern slopes of the Middle Atlas. Our study sites encompassed an elevational gradient from near sea-level to 2,600 m. Our data were collected from February–July 1981, April–May 1982, and April–June 1983. The work was centred in four areas: 1. in the vicinity of Taroudannt (elev. 200 m) in the Oued Souss river plain; 2. The Marakech Plain, and the foothills of the High Atlas Range near Asni (elev. 1,150 m, 45 km S of Marakech); 3. A high valley of the High Atlas near Oukaimeden (elev. 2,600 m) in the vicinity of Djebel Toubkal (4,165 m), about 55 km S of Marakech; 4. The area surrounding Ifrane (elev. 2,000 m) in the Middle Atlas range. These areas were chosen for the diversity of habitats in close proximity to each

other, and the richness of their pierid fauna (Powell 1931; Carcasson 1964; Wyatt 1956; Higgins and Riley 1980).

These areas included habitats with varying vegetational cover (in addition to members of the Capparales): exposed ridges and limestone outcrops, dry riverbeds, stone desert ('hammadah'), grain fields, roadsides, mesic alpine meadows, sclerophyllous shrubby areas (maquis), orchards, light woodland and cedar forest.

We studied nine Pierid butterfly species in detail in this region; flight records from our data and Higgins and Riley (1980): *Anthocharis belia* L. (April–May); *Elphinstonia charlonia* Donzel (March–April); *Euchloe ausonia* Hubner (April–May); *Euchloe belemia* Esper (February–May); *Pontia daplidice* L. (February–July and later); *Pieris rapae* L. (March–July and later); *Pieris brassicae* L. (April–July); *Zegris eupheme* Lederer (April–June); *Colotis evagore* Lucas (late May onwards). Some information was also noted on *Euchloe falloui* Allard (February–April) and *Pieris napi segonzaci* LeCerf (May–July). These two species were not successfully reared, and occupied extreme habitats (arid stone desert in the Sahara, and alpine streamside areas, respectively) and they were not studied in detail.

Nearly all of the above species are representatives of genera of Palaearctic distribution (Higgins and Riley 1980). *C. evagore* is a widespread African species which penetrates the Palaearctic, where it is the only representative of a large genus centred in the Ethiopian region. *Anthocharis*, *Euchloe*, *Elphinstonia*, *Zegris* and *Colotis* are members of Eulichoini; *Pieris* and *Pontia* are Pierini. The larvae of *Pieris*, *Colotis*, and *Elphinstonia* are folivores; the other genera are here inflorescence and seed feeders.

Morocco is a centre of diversity for two families in the Capparales: Brassicaceae (=Cruciferae) and Resedaceae (Maire 1952–1976). Of the many Capparales species in this region (we collected some 100 species), nearly 30 were abundant in the Asni area. Dr. I. Al-Shebaz of the Gray Herbarium, Harvard University, made or confirmed most species identifications, and voucher specimens are deposited in the Phippen-LaCroix Herbarium, Tufts University. Nomenclature follows Maire (1952–1976), Polunin and Smythies (1973), and Tutin et al. (1964).

Field observations

To determine what host plant species would support growth of each butterfly species, caterpillars were reared on the appropriate tissues (inflorescence or leaf) of the abundant species of Capparales during 1981 and 1983. Eggs were obtained from female butterflies by eliciting oviposition in captivity or by following females ovipositing in the wild and collecting their eggs. Ten to twenty-five individuals of each species were reared at ambient temperatures in the field laboratory on each plant species tested. The following responses were observed: 1. Did newly hatched caterpillars eat the plants offered to them? 2. Did they moult and survive to the second instar? 3. What percentage survived to the third instar and beyond? Early instar larvae are particularly vulnerable, and death due to unpalatable or unsuitable food occurs before the third instar (Chew 1975; Courtney 1981, 1986). Because environmental conditions in the field laboratory could not be controlled, no attempt was made to record responses that would have permitted more detailed analysis of host plant suitability (e.g., development

time, feeding rates, pupal weight, gross assimilation efficiencies; see Scriber and Slansky 1981).

Field observations of butterfly interactions with plant species included ovipositions and the occurrence and survival of eggs and larvae on plants. Although neither type of data is necessarily a reliable indicator of hostplant suitability (e.g., Gilbert and Singer 1975; Chew 1975; Courtney 1981, 1982a; Chew and Robbins 1984; Singer 1984), these data indicate the range of plants utilised by each butterfly species, and allow identification of those hosts on which intra- and inter-specific encounters might occur. Some observations were also made on parasitism by several braconid and pteromalid parasitoids; in general, levels of parasitism were low (exceptions being *Apanteles* spp. attack of *Z. eupheme* and *E. ausonia* at Ifrane) and we found no indications that parasitoids or other natural enemies were important mediators of the interaction between pierid species, or between pierids and their hostplants.

Field abundances of adult butterflies were estimated at 49 study sites (each usually corresponding to a single habitat type). We recorded the numbers of adult butterflies at each site throughout their flight season, and at each visit to the site. Equal effort could not be given to captures at different places and times, due to variation in weather conditions and observer numbers. Each visit-record approximates 1–1/2 observer h.

Field abundances of Capparales hostplants were assessed by transect and quadrat methods, to yield estimates of the densities of the various species. Transects were selected at random, and the numbers of crucifers of each species present were recorded for 100 m² of habitat, or (in the case of heterogeneous habitats) until the whole study site was traversed (up to 1,000 m² of data collected). The degree of shading in a study site was measured, as a variable known to affect Pierid habitat selection (Petersen 1958; Shapiro 1975; Chew 1981; Yamamoto 1983). The procedure followed was to take a series of hemispherical photographs using a fish eye-lens. The proportion of sky which is obscured by vegetation or rocks in them is an indicator of shading (see Warren 1985, for a further description of this technique).

Results

Ecological overlap of Pierid species

Figure 1 shows the frequency of co-occurrence of Pierid species, considering all species together (except *E. falloui*), or as their composite leaf- and inflorescence-feeding guilds. The coexistence of two or more species within a guild is frequent, occurring at the majority of study sites. Although there is some evidence of over-dispersion, the study sites were not chosen randomly and cannot be viewed as a statistically valid sample for examining segregation of species. *E. falloui* was found at only one locality (not included in the above 49), where it flew in its typical habitat, open stone desert, where no other pierid, and few hostplants occur.

Substantial overlap in host use occurred, as shown by our records of oviposition and immatures (Table 1). Little evidence of host specialisation was noted (Fig. 2), although *Zegris eupheme* concentrated oviposition on the most visually conspicuous *Isatis tinctoria* (see Courtney 1982a, 1983, for a discussion of host use by *Z. eupheme*); *A. belia*

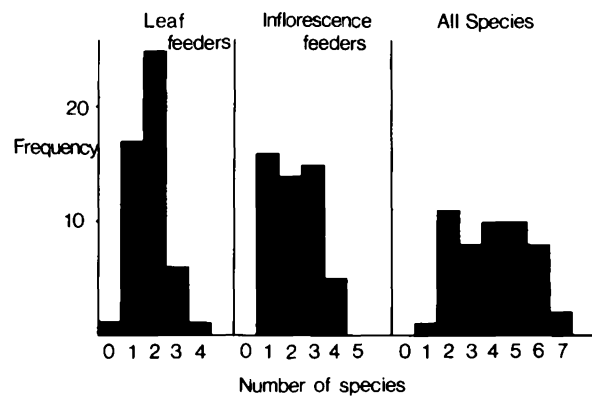


Fig. 1. Species richness on study sites. Shown are the frequencies of species number in the leaf- and inflorescence-feeding guilds, and for all species combined, at 49 study sites in western Morocco, 1981–1983. For leaf-feeders, maximum possible species number is 4 (mean = 1.78, variance = 0.57). For inflorescence-feeders, maximum is 5 (mean = 2.18, variance = 0.99). For all species, maximum is 9 (mean = 3.98, variance = 2.42). The observed variance: mean ratios suggest overdispersion.

and *P. daplidice* also exhibited conditional preferences, with some hosts being used only when preferred species were not abundant (Courtney and Forsberg, unpublished work). As a result of host generalism and some habitat overlap, larvae and eggs of two or more species may often co-occur on the same individual host. The probability of such interaction depends on the level of infestation by the insects – interaction occurred most frequently between *A. belia*, *E. ausonia* and *E. belemia*, all feeding on small inflorescences. Cannibalism and inter-specific predation was observed in the field in all the inflorescence-feeding species, but not in the five folivores (*P. rapae*, *P. napi*, *P. brassicae*, *C. evagore* and *E. charlonia*); neither was there any evidence of cannibalism between guilds. Only rarely will folivorous larvae commence feeding on flowers or seeds, or an inflorescence feeder on leaves: There appears to be little interaction between guilds. However, within the inflorescence-feeding guild, cannibalism was an important cause of death (Fig. 3), as in several other inflorescence-feeders worldwide (Courtney and Duggan 1983; Karban and Courtney unpublished work). Note that the tendency, exhibited by many Pierids, of ovipositing on isolated, individual hostplants (Courtney and Courtney 1982; Chew and Robbins 1984) results in a positive aggregation of immatures of the various species, greatly increasing the potential for inter-specific egg predation and competition, as also noted for American Pierinae (Shapiro 1975). Given the substantial levels of predation which may occur, resource segregation by host species or habitat type (Courtney 1982b) would result in reduced mortality of offspring.

Foodplant suitabilities and associations

Caterpillars from nearly all Pierid species responded similarly to potential hostplants (Fig. 4). Based on responses of the caterpillars to a range of Capparales, these potential hostplants can be placed into four groups representing differential suitabilities of the hostplants for each butterfly species: 1. Plant that are not eaten, even by starving caterpillars; 2. Plants that are eaten, but on which all larvae die in the first instar; 3. Plants on which some larvae survive

Table 1. Capparales frequently encountered in western Morocco, and Pierinae recorded as ovipositing on them. Ab *Anthocharis belia*; Ea *Euchloe ausonia*; Eb *E. belemia*; Ec *Elphinstonia charlonia*; Ze *Zegris eupheme*; Ce *Colotis evagore*; Pd *Pontia daplidice*; Pb *Pieris brassicae*; Pn *Pieris napi segonzaci*; Pr *P. rapae*. Plant nomenclature follows Maire (1952–1976), Tutin et al. (1963) and Polunin and Smythies (1974)

Species	Affiliation	Associated butterflies
<i>Capparis spinosa</i> L.	Capparaceae	Ce Pb Pr
<i>Reseda alba</i> L.	Resedaceae	Pd
<i>R. attenuata</i> Ball	Resedaceae	
<i>R. phyteuma</i> L.	Resedaceae	Pd
<i>R. lutea</i> L.	Resedaceae	Pd
<i>Alyssum minus</i> (L.) Rothm.	Cruciferae: Alysseae	
<i>A. minutum</i> Schlecht, exDC	Cruciferae: Alysseae	
<i>A. atlanticum</i> Desf.	Cruciferae: Alysseae	
<i>A. serpyllifolium</i> Desf.	Cruciferae: Alysseae	
<i>Lobularia libyca</i> (Viv.) Webb	Cruciferae: Alysseae	
<i>Cheiranthus cheiri</i> L.	Cruciferae: Hesperidae	
<i>Matthiola parviflora</i> (Sch.) R. Br.	Cruciferae: Hesperidae	
<i>M. longipetala</i> (Vent.) D.C.	Cruciferae: Hesperidae	
<i>Malcolmia patula</i> (Lag.) D.C.	Cruciferae: Hesperidae	
<i>Capsella bursa-pastoris</i> (L.) Medic	Cruciferae: Lepidieae	
<i>Cardaria draba</i> (L.) Desv.	Cruciferae: Lepidieae	Ea Pr
<i>Biscutella didyma</i> L.	Cruciferae: Lepidieae	Ab Ea Eb Pd
<i>B. laevigata</i> L.	Cruciferae: Lepidieae	Ab Ea
<i>Iberis amara</i> L.	Cruciferae: Lepidieae	
<i>Descurainia sophia</i> (L.) Webb ex Prantl	Cruciferae: Sisymbrieae	Pr
<i>Moricandia arvensis</i> (L.) DC	Cruciferae: Sisymbrieae	Ea Pb
<i>M. foleyi</i> Batt.	Cruciferae: Sisymbrieae	Ea
<i>Isatis tinctoria</i> L.	Cruciferae: Sisymbrieae	Ea Ze Pd Pb Pr
<i>Neslia paniculata</i> (L.) Desv.	Cruciferae: Sisymbrieae	Ea Pr
<i>Sisymbrium officinale</i> (L.) Scop.	Cruciferae: Sisymbrieae	Ea Pb Pr
<i>S. irio</i> L.	Cruciferae: Sisymbrieae	Ab Ea
<i>S. erysimoides</i> Desf.	Cruciferae: Sisymbrieae	Ab Ea Eb Pb Pr
<i>Diplotaxis tenuisiliqua</i> Del.	Cruciferae: Sisymbrieae	Ab Ea Eb Ec Pd Pb Pr
<i>D. virgata</i> D.C.	Cruciferae: Sisymbrieae	Eb Pr
<i>D. catholica</i> (L.) DC	Cruciferae: Sisymbrieae	Eb Pr
<i>D. tenuifolia</i> (L.) DC	Cruciferae: Sisymbrieae	Ea Eb Pr
<i>Alliaria petiolata</i> (Beb.) C & G	Cruciferae: Sisymbrieae	
<i>Nasturtium officinale</i>	Cruciferae: Arabideae	Pn Pr
<i>Arabis parvula</i> L.	Cruciferae: Arabideae	
<i>A. verna</i> (L.) R.Br.	Cruciferae: Arabideae	
<i>Trachystoma balli</i> O.E. Schulz	Cruciferae: Brassiceae	Ea Pr
<i>Crambe hispanica</i> L.	Cruciferae: Brassiceae	Pb Pr
<i>Hirschfeldia incana</i> (L.) L-F	Cruciferae: Brassiceae	Ea Ze Pd Pb Pr
<i>Brassica rapa</i> L.	Cruciferae: Brassiceae	Ab Ea Pb Pr
<i>Sinapis arvensis</i> L.	Cruciferae: Brassiceae	Ab Ea Eb Pr
<i>S. alba</i> L.	Cruciferae: Brassiceae	Ea Pr
<i>Erucastrum laevigatum</i> (L.) O.E. Schulz	Cruciferae: Brassiceae	Ab Ea Eb Ec Pd Pr

the first instar, but less than 50% survive through the third instar; 4. Plants on which more than 50% survive through the third instar. Figure 4 shows that for 7 of the 8 butterfly species we reared, the ordering of hostplant suitabilities is the same for each butterfly, despite the lack of close taxonomic relations of the species to each other (Higgins 1975) and the presumed long evolutionary opportunity for host affiliation in this unglaciated area (note, however, that there is currently no acceptable phylogeny for Pieridae). Caterpillars of the same 7 species all refused to eat plants listed at the left of the figure, and responded favourably to nearly all plants at the right. Although some butterflies are more polyphagous than others (e.g., *Pontia daplidice*, which feeds on Resedaceae that other caterpillars refuse or do poorly on), these species also survived well on those plants suitable

for more stenophagous species. Hence, the specific plants placed in each category for each butterfly species differ primarily in number rather than identity – There is general ‘agreement’ between butterfly species on the suitability of hostplants.

Responses of *Colotis evagore* differ from those of the other Pierids. This butterfly is unable to utilise crucifers which support the growth of the other butterflies. Its phenology (adults fly from late May onwards) makes it ecologically monophagous (*sensu* Smiley 1978), since few or no Capparales other than *C. spinosa* can grow during the Moroccan summer. Of Ethiopian origin, *C. evagore* has not adapted to using Palaearctic hostplants.

By contrast, some Palaearctic Pierini (*P. rapae* and *P. brassicae*) readily use *C. spinosa*, although *Capparis* is

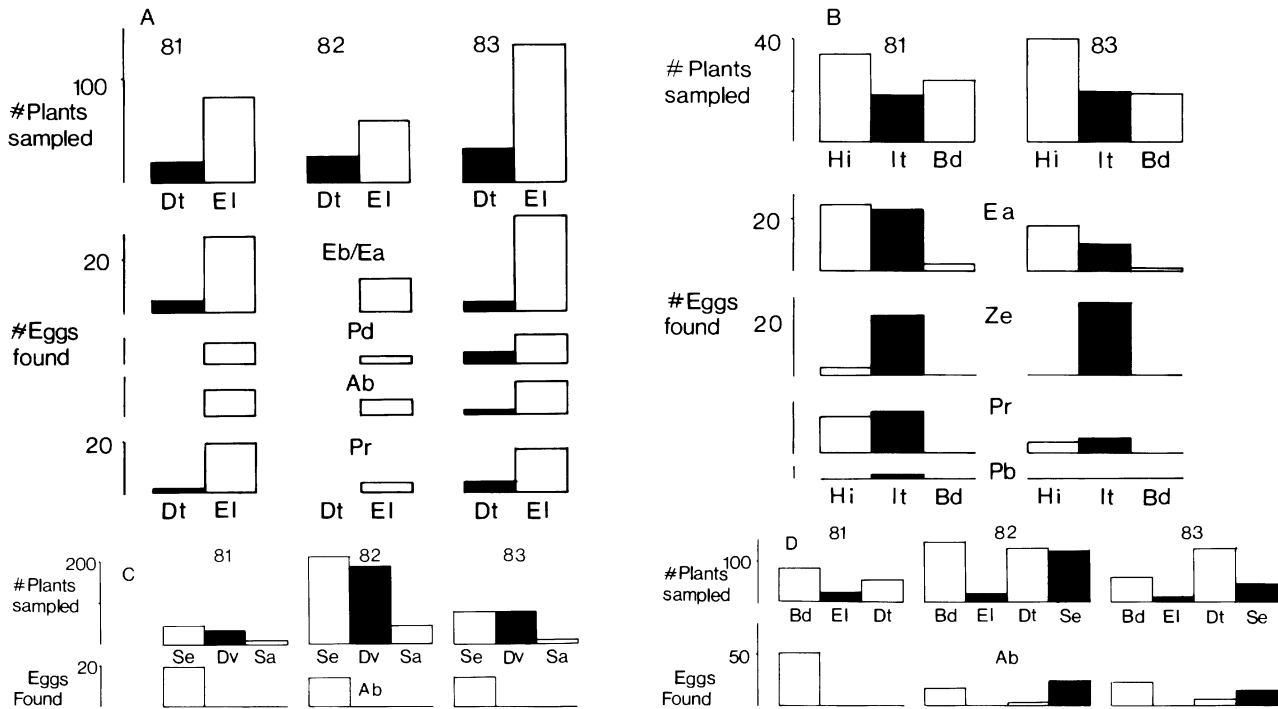


Fig. 2A–D. Selected data to illustrate patterns of host use. **A** Five butterfly species show no evidence of segregation by hosts, and use two hosts in approximate proportion to their abundance. **B** Overlapping host use. One visually inconspicuous host (*Bd*) is not widely used. One butterfly (*Ze*) concentrates nearly all oviposition on one host (*It*). **C, D** Conditional host use by one butterfly (*Ab*). Preferred hosts (*Bd, Se*) are used more often than less preferred hosts (*Dt*). Note that in 2D, the butterfly does not use a plant (*El*) which is a host elsewhere (**A**). Similarly, in 2C another host (*Sa*) is ignored, although it was a host at Asni
Abbreviations: Site A = 10 km S of Marakech, roadside habitat, 1981 to 1983. Site B = Vicinity of Ifrane, 1981 and 1983. Site C = Vicinity of Taroudannt, 1981 to 1983. Site D = 'Roller Site', 1 km east of Moulay Brahim, Asni Region, 1981 to 1983
Ab = *Anthocharis belia*; *Ea* = *Euchloe ausonia*; *Eb* = *E. belemia*; *Ze* = *Zegris eupheme*; *Pd* = *Pontia daplidice*; *Pb* = *Pieris brassicae*; *Pr* = *P. rapae*; *Dt* = *Diplotaxis tenuisiliqua*; *Dv* = *D. virgata*; *El* = *Erucastrium laevigatum*; *Hi* = *Hirschfeldia incana*; *It* = *Isatis tinctoria*; *Bd* = *Biscutella didyma*; *Se* = *Sisymbrium erysimoides*; *Sa* = *Sinapis arvensis*

largely a genus of Ethiopian and Neotropical regions. *C. spinosa*, a large perennial, is a major host for both folivores at several study sites. Inflorescence feeders do not lay eggs on the plant, an unsurprising fact in view of the large bee-pollinated flower which bears little resemblance to a crucifer or *Reseda* flowerhead.

Breadth of diet of a particular butterfly species was related to the magnitude of year-to-year changes in densities of the chosen hostplant species (Fig. 5). Variance in host numbers is calculated from the change in densities [$\log(\text{number of plants}/1,000 \text{ m}^2 \text{ of habitat}) + 1$] in successive years, disregarding the sign of the change. A single variance value is calculable for all populations of a particular host species, and for all host species used by a particular butterfly species. We included in Fig. 5 all data on those host species which were the major host in at least two populations of the particular butterfly. Species with relatively narrow diet (*C. evagore*, *Z. eupheme*, *A. belia*) used hosts of high numerical stability from one year to the next. Associated with this trend is the degree of infestation of a butterfly upon its hostplants (Fig. 6): more stenophagous species occur at high densities on their preferred hosts. These observations, combined with data on hostplant utilisation in the field (Fig. 2), and laboratory-derived results on overlap in host suitability (Fig. 4) indicate that inter-specific encounters are more likely to occur on some plants than others. Of 33 species of potential hosts, for which host records are reasonably complete, most had no or several asso-

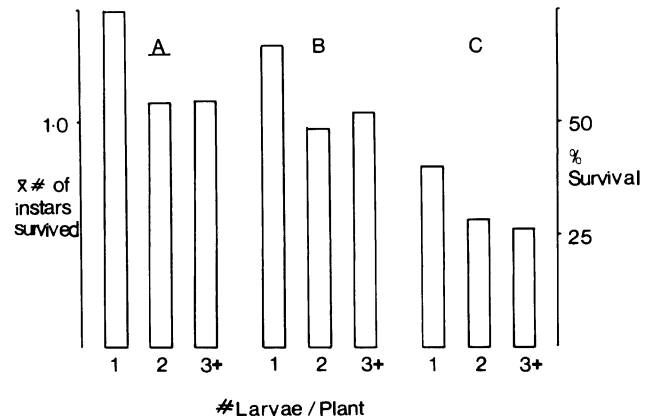


Fig. 3A–C. Survival in the field of eggs and larvae of the inflorescence-feeding guild in relation to density of immatures on a plant. Shown are (**A**) The mean number of instars survived (animals dying in the egg stage count zero; animals surviving beyond the third instar count four – see Karban and Courtney, 1987 for rationale), and the percentage of immatures surviving the (**B**) egg or (**C**) first instar stages. Data from areas of extensive agricultural or grazing activity are excluded, since mortality was very high in such areas. Data were all collected in the Marakech-Asnregion during 1981 and 1983. 211 records refer to *A. belia* immatures, the remainder (171) to *Euchloe* and *Pontia*. Initial cohort sizes: solitary individuals = 309; two individuals = 50; three or more = 23. Comparison of the numbers dying or surviving when alone or with at least one other Pierid yield χ^2 values of 7.91 $P < 0.01$, and 0.19, n.s. (at 1 d.f.) for egg and first instar mortality, respectively

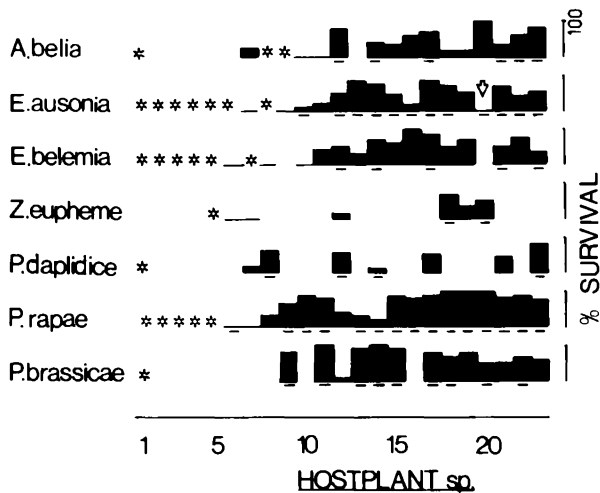


Fig. 4. Survival of larvae of seven Pierid species in laboratory trials with different hostplants. The percentage of larvae surviving to the third instar are shown (most hostplant induced mortality of Pierids occurs in the early instars — see text). A starred symbol indicates that all larvae refused to eat the hostplant and subsequently starved. When at least one larva attempted to feed, the percentage survival is shown, even if no larva survived. A blank entry indicates that pairing of host and butterfly species was not investigated. An underlined figure indicates that this was a butterfly-host association which had been observed in the field. In one case (arrowed) we are assured that our laboratory result of low survival is artefactual — *Euchloe ausonia* feeds well on host no 20 (*Hirschfeldia incana*) in the field, and is strongly associated with it at Ifrane. Efforts were made to compare survivorships on the hosts most frequently occurring in a particular species habitat. Additional data, not shown, indicate survivorships: of 100% and 100% for *E. ausonia*, and 80% and 67% for *P. rapae* on *Cardaria draba* and *Neslia paniculata*, respectively; of 36% and 67% for *P. daplidice* on *Reseda phyteuma* and *R. attenuata*; of 50% and 0% for *E. ausonia* and *E. belemia* on *Arabis parvula*; of 0% for *A. belia* on *Arabis verna*. Additionally, *Z. eupheme* larvae refused to eat *Reseda alba*, and *E. ausonia* refused *R. attenuata*. *Colotis evagore* larvae refused *Sisymbrium irio*, *Sinapsis arvensis* and *Erucastrum laevigatum* foliage, but survived well on *Capparis spinosa*, the natural host. Hostplant species in the Fig. 1. *Alyssum minus*; 2. *A. minutum*; 3. *A. atlanticum*; 4. *Cheiranthus cheiri*; 5. *Matthiola parviflora*; 6. *Descurainia sophia*; 7. *Capsella bursa-pastoris*; 8. *Reseda lutea*; 9. *Capparis spinosa*; 10. *Trachystoma balli*; 11. *Crambe hispanica*; 12. *Biscutella didyma*; 13. *Moricandia arvensis*; 14. *Diplotaxis tenuisiliqua*; 15. *Sisymbrium officinale*; 16. *S. irio*; 17. *S. erysimoides*; 18. *Isatis tinctoria*; 19. *Nasturtium officinale*; 20. *Hirschfeldia incana*; 21. *Sinapsis arvensis*; 22. *Brassica rapa*; 23. *Erucastrum laevigatum*

ciated Pieridae using them in the field (10 host species had no Pieridae; only 4 spp. [mostly *Reseda* spp.] had 1 pierid; The numbers of species with 2, 3, 4 or 5 pierids were: 8, 3, 2, 4, respectively; one especially common hostplant, *Erucastrum laevigatum* (L.), was host to six species of pierid, while the widespread *Diplotaxis tenuisiliqua* hosted seven Pieridae).

Habitats occupied by Pierid butterflies

To examine patterns of adult occupation of Pierid habitats, we ordered data on adult abundance at study sites on a single horizontal axis based on one of two alternative criteria: 1. Similarity of the array of Capparalean species present at that site (the host community was clustered using

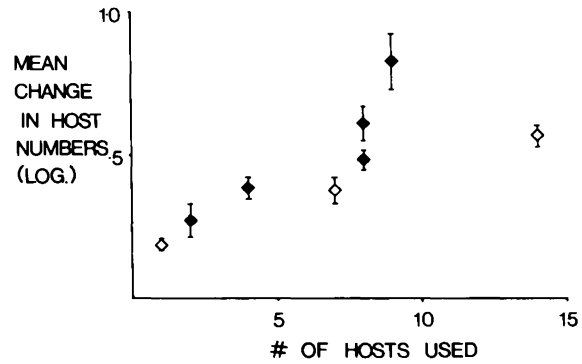


Fig. 5. The relationship between diet width and hostplant numerical variability. Each datum refers to a single butterfly species, and shows the number of hostplants which are frequently used for oviposition, and the average change in numbers (expressed as a log, ± 2 S.E.) that these hostplants exhibit in 49 study sites over 3 years. Average change in numbers is calculated from the value: $\log(\text{density in 2nd year} + 1 / \text{density in 1st year} + 1)$ (sign ignored) for each host at each site. Folivores (open symbols) and Inflorescence-feeders (closed symbols) may show slightly different relationships

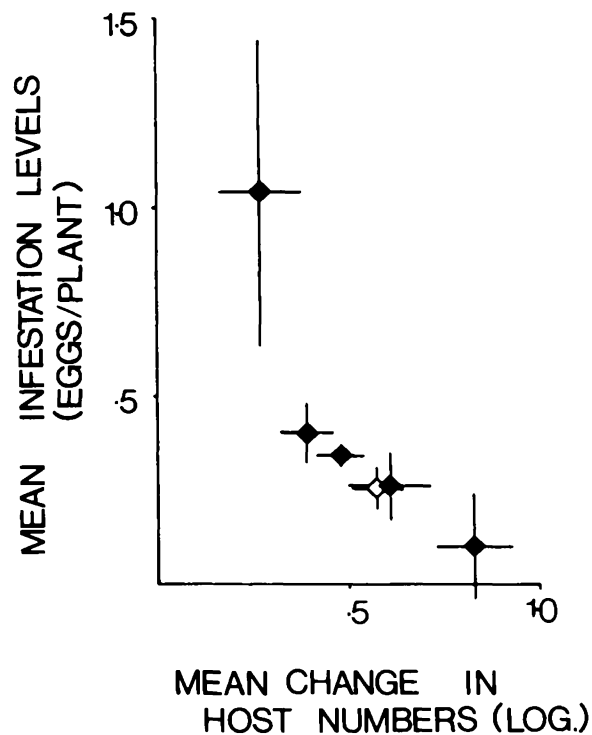


Fig. 6. The relationship between average infestation levels of a butterfly species on its hosts, and the numerical variability of those hosts. Mean infestation levels (± 2 S.E) are averaged across all host populations, as are data for average change in host numbers (sign of change ignored) (± 2 S.E). Data, for five inflorescence-feeding species (closed symbols) and the folivore *P. rapae* (open symbol), are shown

the procedures of Braun-Blanquet phytosociological analysis, so that sites adjacent to each other on the horizontal axis are most similar to each other in the identity and relative abundance of hostplants occupying them); 2. In order of measured shading levels, from least to most shading (i.e., from deserts and fields to rocky outcrops, orchards and

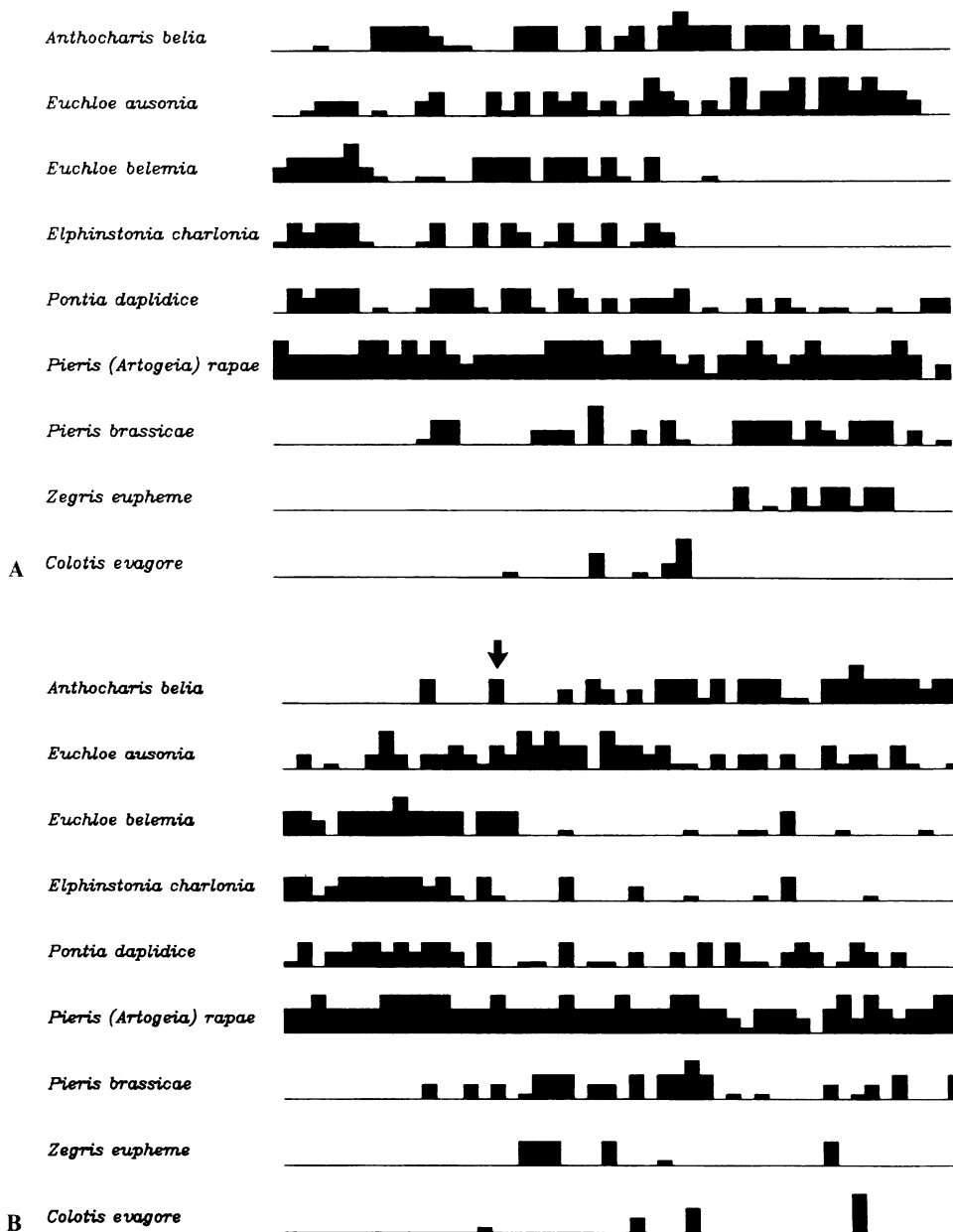


Fig. 7A, B. Frequency of occurrence of adult butterflies on 49 study sites (visited bi-weekly during spring seasons of 1981–1983), when study sites are grouped by: **A** hostplant associations **B** habitat type. Height of each column is based on five rankings of butterfly abundance and frequency: absent; 5 or less adults captured during 3 years; occurred on 33% or more of visits; occurred on 67% or more of visits; highly abundant (100 or more captures) and occurring on 90% of visits). The arrow in the lower figure refers to one site where *A. belia*, *E. ausonia* and *E. belemia* co-occurred in some numbers

woodlands). Figure 7A, B show the relative abundances of adult butterflies at each site, when sites were ordered by these two criteria, respectively.

Adult butterfly species do not partition environments by host plant associations. The data in Fig. 7 substantiate the overlap in field utilisation patterns seen in Table 1 and Figs. 2 and 4. With respect to hostplant associations (Fig. 7A), the number of sites at which adults fly is correlated with the degree of euryophagy or stenophagy, rather than with exclusive occupation of specific hostplant species. Stenophagous species such as *Z. eupheme* and *C. evagore* are found in just a few sites where the hosts *I. tinctoria* and *C. spinosa* occur, but these sites are also occupied by several other pierids, which utilize these and other hosts. The pattern resembles a series of “included niches” rather than partitioning of resources.

Ordering by habitat types (Fig. 7B) offers some additional resolution, particularly for the three most interactive

species, the inflorescence feeders *A. belia*, *E. ausonia*, *E. belemia*. These species assort by habitat type most clearly. In the one site where each co-occurs in some abundance (arrow Fig. 7B), they fly in different parts of this site which encompasses several diverse habitat types. Overall, the three species tend not to occur at the same study site (a comparison of expected and observed co-occurrence of any 2 species (summing cells from a $2 \times 2 \times 2$ analysis) yields $\chi^2 = 4.28$ $P < 0.05$ at 1 d.f.). No other species shows such segregation, although four differ in peculiar niche characteristics, viz. *Pontia daplidice* (a vagrant occurring everywhere but at low density), *Elphinstonia charlonia* (a rosette feeder with early phenology), *Colotis evagore* (late phenology) and *P. brassicae* (the only species laying batches of eggs). Examination of the captures of adults in various habitats over the three years (Table 2, Fig. 8) confirms these patterns.

Habitat type and hostplant numerical stability (magnitude of year-to-year changes in density) were strikingly re-

Table 2. The numbers of adult Pierinae captured on study sites of different habitat types (data 1981 to 1983 combined). Open habitats include desert, open grassland and riverbeds. Mixed areas are those study sites which contain more than one of the other habitat types. Outcrops include all rocky areas including ridge-tops. Also shown is the average change (on a log scale) of potential hostplants on quadrats in the study sites

	Open	Fields	Mixed	Or- chards	Woods	Out- crops
No. of Sites	7	13	8	5	12	4
<i>A. belia</i>	—	3	124	88	160	82
<i>E. ausonia</i>	14	223	83	9	67	18
<i>E. belemia</i>	175	95	133	4	1	—
<i>P. daplidice</i>	66	34	89	5	62	18
<i>Z. eupheme</i>	—	63	—	—	9	—
<i>E. charlonia</i>	111	48	51	3	1	10
<i>P. rapae</i>	256	640	545	202	207	74
<i>P. brassicae</i>	1	44	127	1	77	17
<i>C. evagore</i>	—	3	42	—	2	46
\bar{X} Variability of Hosts	0.840	0.895	0.658	0.552	0.550	0.564

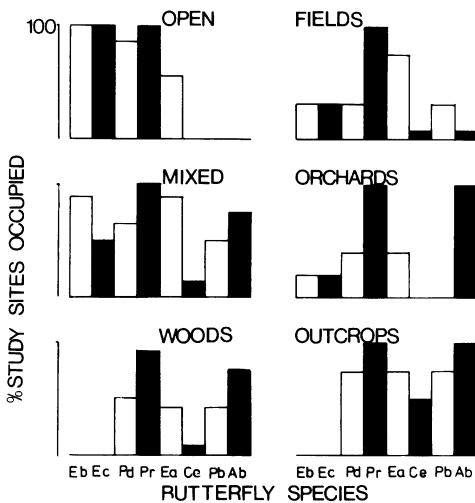


Fig. 8. The percentage of study sites in different habitat categories occupied by 8 Pieridae. A study site is regarded as containing particular Pierid if the species was seen there more than once during 1981–1983. Classification of habitats as in Table 2. Butterfly species key: as in Table 1

lated. Generally, study sites with high degrees of shading tended to contain hostplants of high numerical stability (Fig. 9). When study sites were clustered together (Table 2), it is clear that certain habitat types, such as desert and other open areas, offer a hostplant array which is highly unpredictable in abundance from year to year; other areas, such as alpine meadows, may contain more perennials, whose population densities are more stable.

Discussion

Several general results emerge from this work. First, responses of caterpillars of different species to host species (offered in the laboratory) are similar — few differences

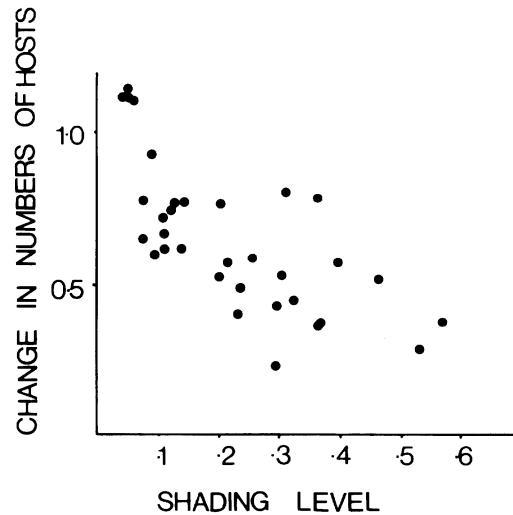


Fig. 9. The relationship between shading levels of a study site (indexed by hemispherical photography — % of sky obscured by vegetation or rocks) and the average changes in numbers of all Capparales occurring at that study site. $r = -0.672$, $P < 0.01$ at 31 d.f.

between butterfly species were observed. Second, there is extensive overlap in the hostplants utilised in the field, and in the habitats occupied by adults. Third, there is some evidence for competition via cannibalism of eggs and larvae, but only among inflorescence-feeding species; only these species show any evidence of segregation. Fourth, hostplant communities are not good predictors of the occurrence or abundance of adult butterflies, but habitat type does predict adult numbers for some species. Fifth, habitat type affects the numerical stability of hosts, which in turn affects the degree of stenophagy, the levels of infestation and the probability of intra- and inter-specific encounters by the different Pierid species. These results suggest that the inflorescence feeders, the most interactive guild, may avoid competition with each other for the limited resources of small inflorescences, by assortment of habitats. The rest of the pierid community appears to be an assortment of species whose host affiliations would not be altered by the disappearance of any other species.

Figure 10 is a scheme for the host and habitat affiliations of the Pierinae of western Morocco. By this means we emphasise the extensive ecological overlap among many of the species, but the distinctness of the leaf- and inflorescence-feeding guilds. Note that tribal identity does not assort with guild membership: Pierini and Euchloini appear in both guilds, suggesting that evolution towards a particular mode of life is not determined phylogenetically at this level (although lack of an adequate phylogeny for Pierinae urges cautious interpretation (see Robbins and Henson, in press)). Similar patterns occur in related groups elsewhere in the Palaearctic and the Nearctic, but not in the Andean Neotropical, where no guild organisation occurs. In the Andes, *Tatochila* and *Hypsochila* species indiscriminately use both inflorescences and leaves of Cruciferae (Kellner and Shapiro 1983; Courtney and Shapiro 1986). Andean Pierinae may represent a very old offshoot from ancestral Pierid stocks (Geiger and Shapiro, unpublished work), suggesting that specialised leaf or flower-feeding are derived characteristics.

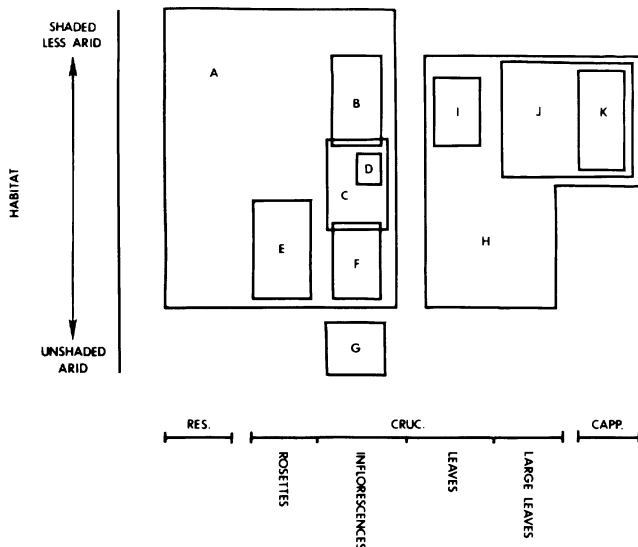


Fig. 10. Diagrammatic scheme for host and habitat use by west Moroccan Pierinae. Two axes are shown: habitat (ranging from open arid to shaded moister areas) and host affiliation and part used (Resedaceae, Cruciferae, Capparaceae; rosette, inflorescence, leaves, large leaves). Folivores and inflorescence feeders are distinct, but extensive overlap occurs within guilds. *A Pontia daplidice*, *B Anthocharis belia*, *C Euchloe ausonia*, *D Zegris eupheme*, *E Elphinstonia charlonia*, *G Euchloe belemia*, *H Pieris rapae*, *I P. napi segozaci*, *J P. brassicae*, *K Colotis evagore*

Figure 10 dramatises that the niches of several species are included within those of others: all inflorescence-feeders interact with *P. daplidice*, while *P. rapae* co-occurs with all other folivores. This ecological overlap is reflected in the broadly similar responses of very different herbivores to the same hostplant species (Table 1, Figs. 2 and 4). Exactly analogous results are found in other communities, such as Neotropical Capparales-feeding Pierids (Jordan 1981), *Aristolochia*-feeding Papilionids (Brown et al. 1981) and *Pasiflora*-feeding Heliconids (Smiley 1978; Gilbert 1979). It is a general prediction of theory that populations within inclusive niches may suffer asymmetric competition. Interestingly, the behaviour of two of our included-niche species suggests abilities to withstand competitive interactions: *Z. eupheme* (a near-specialist on *I. tinctoria* where it encounters 4 other Pierinae) is the most voraciously cannibalistic and predaceous of our species; *P. brassicae* is the only species studied which lays clutches of eggs — the larvae feed gregariously and rapidly defoliate individual hosts. Jordan (1981) describes a similar example to *P. brassicae*, when the specialist *Itaballia viardi* is able to pre-empt foliage of *Capparis frondosa*, the preferred host of all 5 generalist competitors.

Considerable attention has been paid to the deterrent effects of Pierid eggs upon further oviposition by females (e.g., Rothschild and Schoonhoven 1977; Wiklund and Åhrberg 1978; Shapiro 1981b; Hayes 1985). We did not test this proposition in our community. Shapiro (1981a) has particularly focussed attention on the bright red colouration of the eggs of inflorescence feeders, which are easily detected by humans; he suggests that red colouration has evolved to signal occupancy of the small resource (inflorescence). Evolution of red eggs in several Moroccan inflorescence-feeding taxa (*Pontia* and *Euchloini*) supports this

view, but the presence of red eggs in the *Euchloine* folivore (*Colotis evagore* (which never defoliates its host) suggests that red eggs may be a primitive character in these lineages (see Hayes 1985 for further discussion on this topic).

Two species (one host, one butterfly) are natural introductions into this community, as a result of mixing of the biota of different biogeographic regions. Some Palearctic butterflies have readily incorporated the Ethiopian food-plant into their host ranges, despite the plant's distinct growth form and (presumably) unusual array of phytochemical constituents (Chew 1986, for further discussion). Other butterflies (the inflorescence-feeders) have not done so presumably because the flower morphology does not present the necessary cues for oviposition. Larvae of these species performed poorly on this plant in laboratory trials. The Ethiopian butterfly has not adapted to use of Palearctic hosts, probably because of phenological isolation of the butterfly. These results suggest that incorporation of hosts into an insect's diet is not predictable, and that ecological factors (flower-type, phenology) that affect the insect's exposure to the plant may determine the result as much as does host chemistry.

We conclude by de-emphasising the role of pairwise insect-host relationships, and of host-insect relationships mediated by hostplant chemistry. Southwood (1982) has argued that habitat variance is a preeminent factor in the evolution of life-history traits. Our results (Figs. 5, 6, and 10) are in concurrence with this view. Generally, environmental unpredictability should select for generalist patterns of host use (Wiklund 1975; Chew 1977a; Jaenike 1978; Wiens 1977; Strong et al. 1984). Our observed correlations of environmental and host predictability with the specificity of host associations (Fig. 5) and infestation levels (Fig. 6) are in agreement with these predictions. Our results also show that habitat type determines the variance in host abundance experienced (Fig. 10, Table 2). A general theme in the evolution of Pierinae appears to be that populations become adapted to the Capparales available in their habitats, evolving host specialisation most readily only when hosts are species-poor in a chosen habitat. Pairwise interactions between Pierids and their hosts *do* occur: Lorkovic (1968) describes how larval colouration of the monophagous *Pieris ergane* matches the bluish leaves of *Aethionema*; Shapiro (1981b) suggests that some *Streptanthus* hosts of Pierinae have evolved egg-mimics to deter ovipositing females.

Such pairwise interactions are probably rare: coevolution (if it occurs at all) will occur between guilds of herbivores and hosts. Our results also argue against any prevalence of coevolution between competing herbivores, although segregation of habitats by three inflorescence feeders *may* represent the evolutionary outcome of past competition. The results reported here are most consistent with Pierid communities being independently assembled groups of species, with little evidence that host choice by one herbivore affects that of another. Note that the Pierid community of Morocco closely resembles that in the Levant, at the other end of the Mediterranean. The disjunct distributions of both *E. charlonia* and *Z. eupheme* overlap in both areas (sub-specific distinction is accorded local populations of both species), as do most of the other Pierinae recorded here. But species do not co-occur elsewhere: *E. belemia* and *E. falloui* are primarily North African species; *A. belia* and *E. ausonia* are primarily European (Higgins and Riley

1980). Host and habitat affiliations of these species persist when in isolation from each other. All our observations suggest that the interactions of Pierinae with their habitats, and the associated foodplants, are more important determinants of both community structure and host affiliation, than are pairwise interactions between species.

Acknowledgements. Much of the fieldwork reported here was carried out during an expedition to Morocco. Participants were: J. Binge, Sarah Courtney, A. Duggan, B. Eversham, J. Forsberg, I. Heller, C. Hill, R. Jefferson, A. Meyer, C. West. We are grateful to all for their help, labour, and good humour. J. Burns, P. Opler, C. Remington, C. Wiklund aided in preparation of the expedition. I. Al-Shebaz kindly identified some of our plant specimens. J. Forsberg, R. Robbins, A.M. Shapiro, and C. Wiklund contributed by way of discussion. We acknowledge support from the National Geographic Society (81-2305) and Tufts University (Marshall Fund) to FSC, and from the British Council and the University of Liverpool to SPC. SPC was in receipt of a National Environmental Research Council Fellowship during part of this study.

References

- Brown KS, Damman AJ, Feeny P (1981) Troidine relationships in southeastern Brazil: natural history and foodplant relationships. *J Res Lep* 19: 199–226
- Cappucino N, Kareiva PM (1985) Coping with a capricious environment: a population study of a rare pierid butterfly. *Ecology* 66: 152–161
- Carcasson RH (1964) A preliminary study of the zoogeography of african butterflies. *East Afr Wildl J* 2: 122–157
- Chew FS (1975) Coevolution of pierid butterflies and their cruciferous foodplants. I. The relative quality of available resources *Oecologia* (Berlin) 20: 117–127
- Chew FS (1977a) II The distribution of eggs on potential foodplants. *Evolution* 31: 568–579
- Chew FS (1977b) The effects of introduced mustards (Cruciferae) on some native north american cabbage butterflies (Lep. Pieridae). *Atala* 5: 13–19
- Chew FS (1981) Coexistence and local extinction in two pierid butterflies. *Am Nat* 118: 665–672
- Chew FS (1986) Searching for chemical defense in the cruciferae, in *Biochemical Coevolution* (ed. KC Spencer), Pergamon Press (in press)
- Chew FS, Robbins (1984) Egg-laying in butterflies. *Symp R Ent Soc* 11: 65–80
- Courtney SP (1981) Coevolution of pierid butterflies and their cruciferous foodplants III. *Anthocharis cardamines* survival, development and oviposition. *Oecologia* (Berlin) 51: 91–96
- Courtney SP (1982a) IV. Hostplant apparency and *Anthocharis cardamines* oviposition *Oecologia* 52: 258–265
- Courtney SP (1982b) V. Habitat selection, community structure and speciation. *Oecologia* (Berlin) 54: 101–107
- Courtney SP (1983) Notes on the biology of *Zegris eupheme* Led in Morocco. *J Lep Soc* 36: 132–136
- Courtney SP (1986) The ecology of pierid butterflies: dynamics and interactions. *Adv Ecol Res* 15: 51–131
- Courtney SP, Courtney S (1982) The 'Edge-Effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. *Ecol Entomol* 7: 131–137
- Courtney SP, Duggan AE (1983) The population biology of the orange-tip butterfly, *Anthocharis cardamines* in Britain. *Ecol Entomol* 8: 271–281
- Courtney SP, Shapiro AM (1986) The life history, ecology and behavior of a scarce andean butterfly *Hypsochila wagenknechti* (Pieridae). *Stud Neotrop Fauna Evt* (in press)
- Fox LR (1981) Defense and dynamics in plant herbivore systems *Am Zool* 21: 853–864
- Futuyma DJ, Slatkin M (eds) (1983) "Coevolution" Sinauer, Mass.
- Gilbert LE (1979) Development of theory in the analysis of insect-plant interactions. In: *Analysis of Ecological Systems*. Horn DJ, Mitchell RD, Stairs AR (eds), Columbus pp 117–154
- Gilbert LE, Singer MC (1975) Butterfly ecology. *Ann Rev Ecol Syst* 6: 365–397
- Hayes JL (1985) Egg distribution and survivorship in the pierid butterfly *Colias alexandra*. *Oecologia* (Berlin) 66: 495–498
- Hedge IC (1976) A systematic and geographical survey of the old world cruciferae. In: *The Biology and Chemistry of the Cruciferae*. Vaughan JG, MacLeod AJ, Jones BMG (eds) London: Academic pp 1–45
- Higgins LA (1975) *The Classification of European Butterflies* London
- Higgins LA, Riley ND (1980) *A Field Guide to the Butterflies of Britain and Europe* London
- Jaenike J (1978) On optimal oviposition behavior in phytophagous insects *Theor Popul Biol* 14: 350–356
- Janzen DH (1968) Hostplants as islands in evolutionary and contemporary time. *Am Nat* 102: 592–595
- Janzen DH (1973) Hostplants as islands II. Competition in evolutionary and contemporary time. *Am Nat* 107: 786–790
- Jordan CT (1981) Population biology and hostplant ecology of caper-feeding pierid butterflies in northeastern Mexico Ph.D. Dissertation, University of Texas, Austin p 163
- Karban R, Courtney SP (1987) Intraspecific host plant choice: lack of consequences for *Streptanthus tortuosus* (Cruciferae) and *Euchloe hyantis* (Lepidoptera: Pieridae). *Oikos* (in press)
- Kellner CV, Shapiro AM (1983) Ecological interactions of *Pieris brassicae* L. (Lep. Pieridae) and native pierinae in Chile *Stud Neot Fauna Evt* 18: 53–64
- Lawton JH, Strong DR (1981) Community patterns and competition in folivorous insects *Am Nat* 118: 317–338
- Lorkovic Z (1968) Systematisch-genetische und ökologische Besonderheiten von *Pieris ergane* Hbn (Lepidoptera Pieridae). *Mitt Schweiz Ent Ges* 41: 233–244
- Maire R (1952–1976) *Flore de l'Afrique de nord* Lechevalier, Paris
- Ohsaki R (1980) Comparative population dynamics of three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi* living in the same area II. Utilization of patchy habitats by adults through migratory and non-migratory movements *Res Popul Ecol* 22: 163–183
- Opler PA (1974) Studies on nearctic *Euchloe* pt. 7: comparative life histories, hosts and the morphology of immature stages *J Res Lep* 13: 1–20
- Peterson B (1954) Egg-laying and habitat selection in some *Pieris* species *Entomol Tidskr* 74: 194–203
- Polunin O, Smythies BE (1973) *Flowers of Southwest Europe* Oxford University Press
- Powell H (1932) Pupation of *Zegris eupheme meridionalis* Led *Proc Entomol Soc* 6: 52–54
- Robbins RD, Henson PM (1986) Why *Pieris rapae* is a better name than *Artogeia rapae* (Pieridae). *J Lepid Soc* (in press)
- Rodman JE, Chew FS (1980) Phytochemical correlates of herbivory in a community of native and naturalized cruciferae *Biochem Syst Ecol* 8: 43–50
- Rothschild M, Schoonhoven LM (1977) Assessment of egg-load by *Pieris brassicae* (Lepidoptera: Pieridae) *Nature* 266: 352–355
- Schoener TW (1983) Field experiments on interspecific competition *Am Nat* 122: 240–285
- Scriber JM, Slansky F (1981) The nutritional ecology for immature insects *Ann Rev Ent* 26: 183–211
- Shapiro AM (1971) Occurrence of a latent polyphenism in *Pieris virginiensis* (Lep. Pieridae) *Entomol News* 82: 13–16
- Shapiro AM (1975) Ecological and behavioral aspects of coexistence in six crucifer-feeding pierid butterflies in the central Sierra Nevada. *Am Midl Nat* 93: 424–433
- Shapiro AM (1976) The role of watercress (*Nasturtium officinale*) as a host of native and introduced Pierid butterflies in California. *J Res Lep* 14: 158–168
- Shapiro AM (1981a) The pierid red-egg syndrome. *Am Nat* 117: 276–294

- Shapiro AM (1981 b) Egg mimics of *Streptanthus* (Cruciferae) deter oviposition by *Pieris sisymbrii* (Lep. Pieridae). *Oecologia* (Berlin) 48:142–143
- Singer MC (1984) Butterfly-hostplant relationships: host quality, adult choice and larval success. *Symp R Entomol Soc* 11:81–88
- Slobodkin LB, Smith FE, Hairston NG (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. *Am Nat* 101:109–124
- Smiley JT (1978) Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* 201:745–747
- Southwood TRE (1977) Habitat, the templet for ecological strategies. *J Anim Ecol* 46:337–365
- Strong DR, Lawton JH, Southwood TRE (1984) *Insects on plants* Oxford: Blackwell Science Publications
- Thompson JN (1983) *Interaction and Coevolution* Wiley Interscience
- Tutin TA (1964) *Flora Europaea* Cambridge: Cambridge University Press
- Warren M (1985) The biology and status of the wood shite butterfly, *Leptidea sinapis* L. (Lep. Pieridae) in the British Isles *Ent Gaz*
- Wiens JA (1977) On competition and variable environments. *Am Sci* 65:590–597
- Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* (Berlin) 18:185–197
- Wiklund C, Ahrberg C (1978) Hostplants, nectar and source plants and habitat selection of males and females of *Anthocharis cardamines* L. (Lepidoptera). *Oikos* 31:169–183
- Wyatt C (1956) Lepidoptera collecting in the atlas mountains of Morocco. *Lepid News* 10:214–222
- Yamamoto M (1981) Comparison of population dynamics of two pierid butterflies, *Pieris rapae crucivora* and *P. napi nesis* living in the same area and feeding on the same plant in Sapporo, Northern Japan *J Fac Sci Hokkaido University* 22:202–249
- Yamamoto M (1983) Microhabitat segregation in two closely related pierid butterflies *Jap J Ecol* 33:263–270

Received June 18, 1986