

## Foodplant Preferences of *Pieris* Caterpillars (Lepidoptera)

Frances S. Chew

Department of Biology, Tufts University, Medford, Massachusetts 02155, USA

**Summary.** Larvae of five Nearctic *Pieris* butterflies accept a wide range of native and naturalized crucifers under laboratory test conditions. Preferences among crucifers are usually statistical rather than absolute. Caterpillars do not necessarily reject plants that do not support larval growth in favor of those that do. Preferences are not significantly altered by larval development or prior experience with specific foodplant species. Progeny of different females do not exhibit significantly different preferences. Retention of behavioral flexibility by *Pieris* may enable older larvae to exploit alternative resources not suitable for young larvae.

### Introduction

In phytophagous insects where the ovipositing adult chooses food for its progeny, the degree of larval discrimination among potential food resources may or may not relate to the precision with which adults select appropriate foodplants (e.g., Dethier 1959; Wiklund 1975). In *Pieris* butterflies, adults lay eggs and larvae feed only on plants whose tissues contain glucosinolates (mustard oil glucosides), a class of more than 70 compounds at least some of which are phagostimulatory to *Pieris* larvae (David and Gardiner 1966; Schoonhoven 1967). However, not all plants that contain glucosinolates support *Pieris* larval development (e.g., Bowden 1971; Chew 1975; Slansky and Feeny 1977); ovipositing *Pieris* sometimes select plants that contain glucosinolates but that are unsuitable for their progeny. Two types of oviposition "mistakes" have been documented in two native Nearctic *Pieris* species (Chew 1977). First, adults often lay eggs on naturalized plants that contain glucosinolates but do not support successful larval development. Second, adults often choose native plants that promote growth but which are too small to support complete development. These behaviors suggest the possibility that larvae whose mothers place them on qualitatively unsuitable or quantitatively insufficient plants may themselves distinguish among potential food resources.

This paper describes *Pieris* caterpillar choice among potential foodplant species in its habitats, observed under laboratory conditions, and examines factors which may influence development of larval feeding preference for specific foodplants. Several questions are of particular interest: 1) What type of sensory input – olfaction, contact, gustation – permits larvae to distinguish among potential foodplants? 2) What are the preferences of larvae of five Nearctic *Pieris*? 3) How do preferences change with successive larval instars and can preferences of mature larvae be influenced by previous experience with certain foodplants? 4) Do progeny of different

females exhibit different preferences? A companion paper (Chew, in preparation) examines larval mobility and ability to locate appropriate foodplants under laboratory and field conditions.

### Materials and Methods

#### 1. Biological Materials

Caterpillars of five *Pieris*<sup>1</sup> species were observed. *Pieris napi macdunnoughii* Remington and *P. rapae* L. were primary subjects. *P. n. macdunnoughii* is native to montane regions of the southern Rocky Mountains. *P. rapae*, introduced from Palearctic sources to the region near Quebec about 1860, is naturalized throughout much of North America. During its rapid spread from Quebec to other parts of North America (Scudder 1889), *P. rapae* probably chose its larval foodplants from among unfamiliar Nearctic Cruciferae as well as agricultural plantings and naturalized weeds. These larvae were observed for comparison with *P. n. macdunnoughii*, which has recently confronted the establishment of at least one naturalized crucifer in its habitat (Chew 1977). Limited numbers of three other *Pieris* species were observed viz., *P. occidentalis* Reakirt, native to montane regions of the Rocky Mountains, and *P. virginienensis* Edw. and *P. napi oleracea* Harris, native to eastern North America.

Larvae observed were either reared from eggs and larvae collected in the wild or were progeny of wild females from which eggs were collected in the laboratory. Females were caged with cultivated radish plants (*Raphanus sativus* cultivar Early Scarlet Globe, Ferry Morse Seed Co., Mountain View, CA) and placed in sunlight or under incandescent lights. Eggs were removed from plants with fine glass needles and placed on aluminum foil so they hatched in the absence of plant material. Upon hatching, larvae were transferred to crucifers for rearing or to choice-tests arenas to determine their preferences before exposure to plants.

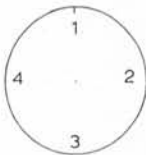
Except for larvae reared on specific plants to test the effect of experience with specific plants on mature larval preferences, *P. n. macdunnoughii* and *P. rapae* larvae were reared from wild-caught females on cultivated radish leaves. *P. n. macdunnoughii* females were collected near Gothic (Gunnison Co.), Colorado; *P. rapae* females were collected near New Haven (New Haven Co.), Connecticut. *P. occidentalis* larvae, from wild females caught near Gothic, were reared on *Descurainia richardsonii* Schulz (Sweet) leaves cut from wild plants. *P. virginienensis* larvae, from wild females caught near Washington (Litchfield Co.), Connecticut, were reared on *Dentaria diphylla* Michx., transplanted from this locality. *P. n. oleracea* larvae, from females caught near Craftsbury (Orleans Co.), Vermont, were reared on *D. diphylla* transplanted from this locality.

<sup>1</sup> Nomenclature follows Howe (1975). Higgins (1975) placed Palearctic *P. napi* and *P. rapae* in the genus *Artogeia*, and extended this designation to Nearctic representatives of these species; however, his revision did not include the Nearctic species *P. virginienensis* and *P. occidentalis* so their status in his scheme remains uncertain

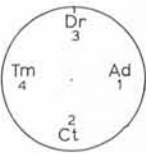
Plant species: Ad = 1  
 Ct = 2 (control)  
 Dr = 3  
 Tm = 4

Random sequence: 3124

Arena positions (clockwise)



Plants in arena



Larval choice Ad = position 2, plant sp. 1

**Fig. 1.** Randomization scheme for positions of plants in choice-test arenas. The plant species are each assigned an integer. For each arena, a random sequence containing these numbers determines the order in which these plant species will appear in the arena clockwise from an arbitrary mark. This scheme varies the positions of plants from arena to arena and permits differentiation between larval response to a directional bias and larval preference for certain plant species. *Ad*, *Arabis drummondii*; *Ct*, non-crucifer control; *Dr*, *Descurainia richardsonii*; *Tm*, *Thlaspi montanum*. A larva choosing a plant at position 2 would encounter *Arabis drummondii* (species 1) in this arena

Leaves offered to larvae were cut from plants grown from seed in the greenhouse, transplanted from natural populations, or found in the wild. *Thlaspi arvense* L. and cultivated radish were grown from seed hypodroponically using vermiculite and Hyponex "7-6-19" (total nitrogen, available phosphoric acid, potash). Sterilized soil was used for all other species grown from seed viz., *Arabis drummondii* Gray, *A. glabra* (L.) Bernhardt, *Cardamine cordifolia* Gray, *Draba aurea* Vahl, *Descurainia richardsonii*, *Sinapis alba* L. and *Thlaspi montanum* L. Thirteen species were transplanted or collected from field populations, viz., *Alliaria officinalis* Andr., *Barbarea vulgaris* R. Br., *Brassica rapa* L., *Capsella bursa-pastoris* (L.) Medic., *Descurainia sophia* (L.) Webb., *Erysimum asperum* (Nutt) DC., *E. cheiranthoides* L., *Lepidium campestre* (L.) R. Br., *L. densiflorum* Schrad., *L. virginicum* L., *Rorippa islandica* (Oed. ex. Murr.) Borb., *Thlaspi arvense*, and *T. montanum* L. Nomenclature of these plants follows Fernald (1950), Harrington (1954), Tutin et al. (1964), and Weber (1976).

## 2. Measurement of Larval Preferences

An experimental choice-test was designed to assess short term (over several hours) larval foodplant preferences. Larvae were tested individually to assure independence from possible influence by others. Females of these *Pieris* usually lay eggs singly in the field (e.g. Klots 1951; Remington 1952).

Arena choice-tests were conducted in 9.0 x 1.5 cm plastic petri dishes as described by Berube (1972). A moisture reservoir was prepared by filling one half of a plastic petri dish with plaster of paris (gypsum). This plaster was moistened and covered with filter paper (Whatman No. 1) marked with pencil to indicate the center of the circle and the peripheral positions for plant species to be offered to larvae. The other half of the petri dish was used as a cover to maintain humidity in the arena. Arenas were placed beneath fluorescent or incandescent lights with fans circulating air beneath the lights. Leaves of mature plants

(same life stages as are exploited by *Pieris* under field conditions) were cut into pieces approximately 0.5 x 0.5 cm. While no attempt was made to measure the amount of leaf material offered, pieces of comparable size were offered in individual arenas. These leaf pieces were placed in arenas on the moistened filter paper just prior to a test. As a control, a sample of a plant species containing no glucosinolates was included in each arena. To avoid position effects of adjacent offerings in the arena and possible directional stimuli, the positions of plant offerings were randomized by a method shown in Fig. 1. A maximum of six plant species (including the non-crucifer control) was offered simultaneously. While the group of species offered to larvae was arbitrary (often determined by availability of particular crucifer species), each crucifer offered to *P. n. macdunnoughii* and *P. rapae* was offered as a member of at least two different arrays.

Small larvae (first, second, third instars) were placed at the centers of circles of 1.5 cm radius. Plant pieces were placed on the periphery of the circles. Large larvae (fourth and fifth instars) were placed in circles of 4.0 cm radius. One larva was placed in each arena with a camel's hair brush or springsteel forceps. Larval behavior was recorded as *touching* (with head) a plant piece, *attacking* (actively feeding) or having *chosen* a plant (either the first plant piece consumed or the plant on which the larva spent the greatest proportion of its time and feeding activity). These behavioral categories correspond to three levels of information which may influence choice (Berube 1972). First, a larva may perceive olfactory cues from some distance, prior to contact. Second, upon touching the plant and receiving chemotactic stimuli, the larvae may attack (bite) the plant or leave if the stimuli are inappropriate (e.g. a non-crucifer). Finally, sustained feeding may occur in the presence of appropriate stimuli and the absence of feeding deterrents or adverse physiological reactions to feeding. Larval behavior was recorded at intervals of 15 to 30 s during the first 5 min when larvae would first touch or attack a plant; observations were then recorded at intervals of 15 to 30 min until 180-240 min had elapsed. For each larva the identities of the first plant touched, the first attacked, and the plant chosen were then determined.

Data were examined using G-tests for goodness of fit to an even distribution and heterogeneity of distributions (Sokal and Rohlf, 1969). Tests for goodness of fit to an even distribution were used to determine whether larvae selected or avoided certain plants. If larvae exhibit no choice, they should be evenly distributed over all species, including the non-crucifer control; if larvae exhibit no choice among crucifers but avoid non-crucifers (as might be expected), then the distribution of larvae should show significant deviation from even distribution when all plant species are considered, but no significant deviation when the non-crucifer control is excluded from the analysis. G-tests for heterogeneity of distributions were used to compare similarity of distributions obtained under different conditions on a specific array of plants, e.g. cut leaves vs. intact leaves, distribution of plants first touched vs. first attacked by larvae.

Tests on newly hatched first instar and early fourth instar larva showed that these closed arenas with cut leaves yield results that are statistically indistinguishable from open arenas in which whole leaves (with petioles extruding below the arena floor into water) are presented. For 48 *P. rapae* tested on an array of four species of intact leaves (including a non-crucifer control), and 45 *P. rapae* larvae tested on the same array of cut leaves, the distributions of larvae were not statistically significant: for the first plant touched,  $G_H = 0.973$  (df=3,  $P > 0.5$ ); for first plant attacked,  $G_H = 0.062$  (df=2,  $P > 0.9$ ); non-crucifers were never attacked; for plant chosen,  $G_H = 0.157$  (df=2,  $P > 0.9$ ). For 62 *P. n. macdunnoughii* larvae presented with four species (including non-crucifer control) of intact leaves and 46 larvae presented with the same array of cut leaves, further similar results were obtained:  $G_H = 4.309$  (df=3,  $P > 0.1$ ), 2.002 (df=2,  $P > 0.1$ ), and 3.202 (df=2,  $P > 0.1$ ). These results do not imply that *Pieris* larvae do not distinguish between leaves with cut surfaces (which may release some volatile products of glucosinolate enzymatic hydrolysis [e.g. Benn 1977; Mitchell and Richards 1978]) and intact leaves. Rather, they suggest that with respect to foodplant choice, larvae behave similarly under these two sets of circumstances. This similarity permitted use of cut leaves in subsequent trials to make best use of limited quantities of plant material.

### 3. Larvae Observed

Larvae of the five *Pieris* species, of various ages from newly hatched (within 10 h of hatching) to mature fifth instar, were offered a variety of crucifer species to determine whether they exhibit any preference among these species. These tests, repeated on the same cohorts of larvae as they developed, permitted comparison between larval behavior in successive instars.

To examine the effect of early experience with specific foodplants on larval preference in later instars (the "conditioning" effect documented in a number of lepidopterous larvae (e.g. *Pieris brassicae* [e.g. Johansson, 1951]) 25 newly hatched larvae of *P. n. macdunnoughii* were reared individually on *Cardamine cordifolia*. Their sibs (25 larvae) were reared on an alternate foodplant, *Descurainia richardsonii*. These two plant species contain dissimilar arrays of glucosinolates (Chew, 1979; Rodman and Chew, 1980). Both groups were offered both crucifer species in several successive choice-tests. The choices of individual larvae in successive instars were recorded. A similar experiment was conducted on 50 larvae of *Pieris rapae*, using *Barbarea vulgaris* and cultivated radish as alternate foodplants. In addition, two related series of choice-tests were conducted. First, 50 larvae of *Pieris rapae* were reared individually on cultivated radish and tested in successive instars on *Barbarea vulgaris*, *Descurainia sophia*, and cultivated radish to examine the consistency of individual responses in successive instars. Second, choice tests were conducted in 153 early fifth instar larvae of *P. n. macdunnoughii*, collected as eggs in the wild and reared on the plants on which they were collected, viz., *Arabis drummondii*, *Descurainia richardsonii*, *Draba aurea*, and *Thlaspi montanum*. The larvae were offered these four plants in choice-tests.

To preliminarily investigate possible behavioral differences among progeny of different female butterflies, offspring of five *P. n. macdunnoughii* females were observed. These females, captured in the wild, were observed to oviposit one to three times just prior to capture: 1) successive ovipositions on *Thlaspi montanum* and *Draba aurea*; 2) two successive ovipositions on *Descurainia richardsonii*; 3) a single oviposition on *Thlaspi montanum*; 4) successive ovipositions on *Descurainia richardsonii* and *Arabis drummondii*, and 5) three successive ovipositions on *Thlaspi montanum*. Eggs were obtained from each female and the larvae were tested as first and fourth instars on these four crucifer species plus *Cardamine cordifolia*. In addition, the behavior of progeny of two other wild-caught females was observed.

## Results

### 1. Larval Reception of Plants

Data in Table 1 reveal certain characteristics of larval perception of plants and show that larva behave similarly in closed and open arenas. Larvae show limited ability to distinguish crucifers from non-crucifers in these choice-tests arenas prior to contact with the plant. The frequencies with which each plant species is first touched by larvae in arenas are often indistinguishable from an even distribution: of 80 groups of tests of all five *Pieris* species, 44 tests were not significantly different at the 0.05 level; in other cases, larvae avoided contact with control (non-crucifer) plants. Under both laboratory and field conditions, larvae wandering a few mm away from crucifers sometimes missed them, a finding reported for some other lepidopterous larvae and their foodplants (e.g. Dethier 1959; Ishikawa et al., 1969). Jones (1977) reported that fifth instar *P. rapae* larvae consistently turn towards crucifers from distances of several to a dozen cm. However, because larvae may respond to moisture gradients to locate plants over these distances (e.g. Meyer and Raffensperger 1974), and Jones' larvae were not offered alternative plants, it is uncertain whether the larvae observed by Jones respond over several cm to crucifers specifically, or toward vegetation in general.

**Table 1.** Larval perception of plants. Plants first touched, attacked, and chosen by *P. n. macdunnoughii* (instar IV) larvae in arenas with intact and cut leaves. Comparisons of larval response with intact and cut leaves yield the following: for plants touched,  $G_H=1.028$  (3 df,  $P>0.5$ ); for plants attacked,  $G_H=1.053$  (2 df,  $P>0.5$ ); for plants chosen,  $G_H=4.604$  (2 df,  $P>0.05$ ). See text for other results

Plants offered	Intact leaves			Cut leaves		
	Touched	Attacked	Chosen	Touched	Attacked	Chosen
Control	8	0	0	8	0	0
<i>Cardamine cordifolia</i>	14	16	16	17	18	13
<i>Descurainia richardsonii</i>	16	18	19	22	24	25
<i>Thlaspi arvense</i>	8	10	9	15	19	23

Larval unerringly distinguish crucifers from non-crucifers upon contact and gustation. They attacked only crucifers. Only twice during these tests did larvae appear to attack non-crucifers (control) plants. In many cases the plants first consumed (chosen) by larvae were the same as those first attacked. However, larvae sometimes attacked several plants before remaining on one or continuing to feed for an extended period (> 1 h). Although the frequencies of plant species first attacked and chosen by a group of larvae are often statistically indistinguishable from each other, older individual larvae sometimes first consumed (chose) a different crucifer from the one they initially attacked.

### 2. Preferences Among Crucifers

Larvae of the five *Pieris* species accepted most of the crucifers offered in choice-test arenas. As shown in Table 2, one species of larvae consistently preferred one crucifer (the preference is statistical rather than absolute), unconditionally rejected a few, and did not consistently distinguish among the rest. Other species rejected a few crucifers and similarly exhibited no consistent preferences.

In a majority of cases, larval responses to plants corresponded closely with adult oviposition behavior and with what is known about suitability of the plant for larval growth in that particular *Pieris* species. *P. n. macdunnoughii* larvae unconditionally rejected both *Erysimum asperum* and *E. cheiranthoides*. Other *Erysimum* species contain cardenolides (Hegnauer 1964) but the effects of these compounds on these *Pieris* have not been examined. Adults may nectar at flowers of these plants (Chew 1974) but do not lay eggs on them (Chew 1977), a situation reminiscent of the behavior of montane legume-feeding *Colias alexandra* towards one of the abundant legume species growing in its habitat (Watt et al. 1974). *P. n. macdunnoughii* prefer *Descurainia richardsonii*, on which they develop rapidly (Chew 1975). They did not, however, exhibit preference for *Thlaspi arvense*, whose glucosinolate profile shares a major compound with that of *D. richardsonii* (Chew 1979; Rodman and Chew 1980). Nor did they or larvae of *P. occidentalis* consistently avoid this plant, which is lethal to young larvae of both species. Both *P. n. macdunnoughii* and *P. occidentalis* females lay eggs on *T. arvense*; for *P. occidentalis* at least, females lay proportionately fewer eggs on *T. arvense* than expected on the basis of its relative abundance (Chew 1977), but the avoidance is statistical rather than absolute.

**Table 2.** Preferences of *Pieris* larvae for leaves of various crucifer species. Data from which this table was compiled are of the form of Table 1, and original data are available in Chew (1974 and unpublished)

<i>Pieris</i> species	Plant species offered	N (larvae tested)	Preference hierarchy
<i>P. napi macdunnoughii</i>	<i>Arabis drummondii</i> (Ad)	1365	Dr... > > Ea, Ec
	<i>Cardamine cordifolia</i> (Cc)		
	<i>Descurainia richardsonii</i> (Dr)		
	<i>Draba aurea</i> (Da)		
	<i>Erysimum asperum</i> (Ea)		
	<i>E. cheiranthoides</i> (Ec)		
	<i>Barbarea vulgaris</i> (Bv)		
	<i>Lepidium densiflorum</i> (Ld)		
	<i>Rorippa islandica</i> (Ri)		
	cultivated radish (Rc)		
	<i>Thlaspi arvense</i> (Ta)		
	<i>Thlaspi montanum</i> (Tm)		
<i>P. rapae</i>	<i>Alliaria officinalis</i> (Ao)	590	none... > Cb
	<i>Barbarea vulgaris</i> (Bv)		
	<i>Arabis drummondii</i> (Ad)		
	<i>Capsella bursaPastoris</i> (Cb)		
	<i>Draba aurea</i> (Da)		
	<i>Dentaria diphylla</i> (Dd)		
	<i>Descurainia sophia</i> (Ds)		
	<i>Lepidium campestre</i> (Lc)		
	<i>L. virginicum</i> (Lv)		
	<i>Thlaspi arvense</i> (Ta)		
	<i>T. montanum</i> (Tm)		
	cultivated radish (Rc)		
<i>P. virginiensis</i>	<i>Dentaria diphylla</i> (Dd)	109	none
	<i>Barbarea vulgaris</i> (Bv)		
	<i>Lepidium campestre</i> (Lc)		
	<i>Thlaspi montanum</i> (Tm)		
<i>P. napi oleracea</i>	<i>Barbarea vulgaris</i> (Bv)	108	none
	<i>Brassica rapa</i> (Br)		
	<i>Dentaria diphylla</i> (Dd)		
	<i>Sinapis alba</i> (Sa)		
<i>P. occidentalis</i>	<i>Arabis drummondii</i> (Ad)	76	none
	<i>Arabis glabra</i> (Ag)		
	<i>Descurainia richardsonii</i> (Dr)		
	<i>Lepidium densiflorum</i> (Ld)		
	<i>Thlaspi arvense</i> (Ta)		

*Pieris rapae* larvae avoid *Capsella bursa-pastoris* but did not consistently prefer any crucifer among those offered. *P. rapae* feeds on a wide variety of crucifers which support a large range of larval growth rates (e.g. Slansky and Feeny 1977).

Limited observations on *Pieris virginiensis*, whose larvae feed on *Dentaria* spp. in their rich woodland habitats (Klots 1951; Howe 1975) suggest that larvae do not prefer *Dentaria* to other crucifers. *P. virginiensis* adults, like those of some other *Pieris* species, lay eggs only on crucifers growing in certain habitats (e.g. Petersen 1954; Cromartie 1975; Chew 1977); since very few crucifer species grow in these woodland habitats, larvae are confined to *Dentaria*. At Washington, Connecticut, *P. virginiensis* uses *D. diphylla*, the only species growing abundantly there; near New Haven, Connecticut, both *D. diphylla* and *D. laciniata* are used. Glucosinolate analyses of leaves of the two species near New Haven reveal similar profiles (J. E. Rodman personal communication).

*Pieris napi oleracea* did not exhibit preference among the several crucifers growing in its habitat. Nor did these larvae avoid

*Barbarea vulgaris*, which does not support complete development (Chew 1978).

These data suggest that larvae do not always distinguish behaviorally among plants whose glucosinolate profiles are similar (Chew 1979; Rodman and Chew 1980) even though larvae can probably perceive these differences at the level of chemosensory receptors (Dethier and Kuch 1971; Dethier 1978).

### 3. Effects of Development and Experience with Foodplants

Newly hatched and older larvae show similar behavioral responses towards an array of crucifers (Table 3). However, preferences of third and fourth instar larvae are sometimes more pronounced than those of earlier or later instars. Berube (1972) suggests that fifth instar of *Colias*, which ingest most of the food assimilated by the larva (e.g. Waldbauer 1968), may be too hungry to reject acceptable foodplant species in favor of preferred species.

**Table 3.** Plants chosen by young and mature larvae. *P. n. macdunnoughii* larvae were offered *Arabis drummondii*, *Cardamine cordifolia*, *Descurainia richardsonii*, *Draba aurea*, and *Thlaspi montanum*. *P. rapae* larvae were offered cultivated radish, *Barbarea vulgaris*, *C. cordifolia*, and *Lepidium campestre*. Original data of the form of Table 1 are from Chew (1974)

Instar	N	G <sup>a</sup>	df <sup>b</sup>	P	G <sub>H</sub>
<i>P. n. macdunnoughii</i>					
unfed I	152	1.689	4	> 0.5	16.297
(fed) I	62	25.971	4	< 0.005 <sup>c</sup>	(20 df,
II	105	58.331	4	< 0.005 <sup>c</sup>	P > 0.5)
III	64	58.892	4	< 0.005 <sup>c</sup>	
IV	54	67.216	4	< 0.005 <sup>c</sup>	
V	73	28.901	4	< 0.005 <sup>c</sup>	
<i>P. rapae</i>					
unfed I	30	7.253	3	> 0.05	21.551
II	58	8.011	3	> 0.025 <sup>d</sup>	(12 df,
III	32	6.492	3	> 0.05	P > 0.025)
IV	29	9.948	3	> 0.01 <sup>d</sup>	
V	28	2.943	3	> 0.1	

<sup>a</sup> G-test is for goodness of fit to even distribution

<sup>b</sup> Non-crucifer control was excluded from analysis

<sup>c</sup> In these cases, larvae preferred *Descurainia richardsonii*

<sup>d</sup> In these cases, larvae preferred cultivated radish

Preferences of mature larvae are not significantly influenced by exposure to different crucifer species. Although there is evidence for induction of larval preferences in other Lepidoptera (e.g. Jermy et al. 1968; Hanson 1976) and *Pieris brassicae* L. (Johansson 1951; David and Gardiner 1966), previous work on *Pieris rapae* L. has yielded inconsistent results (Hovanitz and Chang 1965; cf. Takata 1961; Chew 1974). Comparison of plants chosen by two groups of *P. n. macdunnoughii* larvae (reared on *Cardamine cordifolia* and *Descurainia richardsonii* and offered these plants) yielded the following results: for newly hatched first instar larvae (before any contact with plants)  $G_H=0.325$  (1 df,  $P>0.5$ ); for second instars,  $G_H=1.717$  (1 df,  $P>0.1$ ); for third instars,  $G_H=1.711$  (1 df,  $P>0.1$ ); for fourth instars,  $G_H=0.208$  (1 df,  $P>0.5$ ). All but three individuals chose the alternate crucifers species at least once: two larvae reared on *D. richardsonii* and one larva reared on *C. cordifolia* consistently chose *D. richardsonii*.

The experiment on *P. rapae* larvae reared on radish and *Barbarea vulgaris* yielded similar results. Comparison of plants chosen by larvae reared on and offered these crucifers yielded the following results: for newly hatched larvae,  $G_H=0.642$  (1 df,  $P>0.1$ ); for second instars,  $G_H=0.418$  (1 df,  $P>0.5$ ); for third instars,  $G_H=1.325$  (1 df,  $P>0.1$ ); for fourth instars,  $G_H=0.058$  (1 df,  $P>0.9$ ); for fifth instars,  $G_H=0.144$  (1 df,  $P>0.5$ ). All but two individuals chose the alternate crucifer at least once: one individual reared on cultivated radish and one reared on *Barbarea vulgaris* consistently chose radish. These results do not exclude the existence of individuals which specialize on one crucifer species but exposure to certain foodplants does not appear to induce such specificity.

Most of the *P. n. macdunnoughii* larvae collected on crucifers in the field did not prefer crucifers on which they were collected and reared to alternative foodplants (Table 4). The group of larvae collected (as eggs) and reared on *Descurainia richardsonii* preferred *D. richardsonii*, but when results of this group are compared with those from other larvae, they are not significantly different ( $G_H=5.283$ , 9 df,  $P>0.5$ ). Given the previously demonstrated preference of *P. n. macdunnoughii* for *D. richardsonii*, these results suggest

**Table 4.** Plants chosen by *P. n. macdunnoughii* larvae collected on crucifers. Individuals were collected from crucifers in the field as eggs and young larvae, reared on these foodplants, and tested during fifth instar. Original data from Chew (1974). Comparison of the four groups yields  $G_H=5.283$  (9 df,  $P>0.5$ )

Source of eggs	N	G	df	P
<i>Arabis drummondii</i>	30	3.040	3	> 0.5
<i>Descurainia richardsonii</i>	45	7.821	3	< 0.025 <sup>a</sup>
<i>Draba aurea</i>	27	1.272	3	> 0.5
<i>Thlaspi montanum</i>	51	2.655	3	> 0.5

<sup>a</sup> These larvae preferred *D. richardsonii*

that the range of potential foodplants accepted by larvae remains the same throughout larval development and that this range – at least among foodplants that are found in the butterfly's native habitat – is not significantly altered by exposure to a particular plant species.

#### 4. Differences between Progeny of Different Females

Comparison of plants chosen by offspring of five females which were observed ovipositing prior to capture, and offspring of two additional wild-caught females showed no significant heterogeneity (Table 4). For first instar larvae of these females,  $G_H=25.751$  (24 df: 7 females, 5 crucifers offered;  $P>0.5$ ); for fourth instars,  $G_H=29.370$  (24 df,  $P>0.5$ ). While these results do not exclude the possibility variation among progeny of different females, they suggest that such differences are likely to be statistical rather than absolute.

#### Discussion

Many specialized insect herbivores choose as food resources plants which contain specific plant secondary compounds. For *Pieris* butterflies only plants which contain glucosinolates are recognized as potential food. These glucosinolates, and related compounds (e.g. isothiocyanates) may render crucifers more conspicuous to *Pieris* (and other crucivorous insects) than their phenology and relative abundance in plant communities might indicate (Feeny 1975). However, these indicators of suitable resources may occasionally mislead ovipositing adult insects. In some cases, where butterflies encounter introduced plants, they lay eggs even if these plants do not support larval development (e.g. Straatman 1962; Sevastopulo 1964). In other cases, butterflies lay eggs on very small plants that support only the initial stages of larvae growth (e.g. Dethier 1959; Douwes 1968; White 1974). In the *Pieris* butterflies observed by Chew (1977), substantial numbers (in some cases, a majority) of caterpillars must complete their development of plants other than those on which their mothers placed them (as eggs). *Pieris* females effectively place on many larvae the burden of choosing the bulk of food resources which contribute to their development.

Results of this study suggest two characteristics of *Pieris* behavior toward potential foodplants which facilitate larval exploitation of alternative food resources. First, larvae of all five species accept most glucosinolate-containing plants; this acceptance extends even to larvae of *P. virginensis*, which are normally confined to plants of a single genus or species. This observation is consistent with

behavioral and electrophysiological evidence that individual glucosinolates (and/or their hydrolysis products) stimulate feeding *Pieris* (e.g. Verschaffelt 1911; Schoonhoven 1967) and oviposition behavior in *Pieris* adults (e.g. Ma and Schoonhoven 1973; Lundgren 1975). Such acceptance of previously unencountered plants provides potential for successful larval exploitation of new plants encountered and chosen by ovipositing females, or new plants encountered by wandering larvae. The apparent statistical (but not absolute) hierarchy of preference according to suitability may maximize (for individual larvae) larval exploitation of *D. richardsonii* when it is available, without jeopardizing larval ability to exploit alternative resources.

The exceptions to larval acceptance of crucifers and the apparent maladaptive acceptance of *Thlaspi arvense* (a lethal plant) by young *P. n. macdunnoughii* and *P. occidentalis* larvae (and *Barbarea vulgaris* by larvae of *P. n. oleracea*) suggest that glucosinolates may be necessary but not sufficient indicators of suitable foodplants. The unconditional rejection of some crucifers, e.g. *Erysimum asperum* (which may contain cardenolides: Hegnauer 1962) by *P. n. macdunnoughii* larvae suggests that the chemical determinant(s) of palatability are complex (Schoonhoven 1977; Dethier 1980), a conclusion reached by several authors for *Pieris rapae* and other crucifer specialists (e.g. Feeny, Paauwe, and Demong 1970; Slansky and Feeny 1977; Nielson 1978). The failure of *P. n. macdunnoughii* and *P. occidentalis* larvae to reject *Thlaspi arvense* also suggests that crucifers which support larval development poorly or not at all do not necessarily possess intrinsic (e.g. biochemical or morphological) properties which render them unpalatable to larvae. Thus plants which are lethal to these *Pieris* caterpillars fall into two categories: 1) those which are rejected by larvae before larvae feed; and 2) those which are behaviorally accepted, but prove physiologically unacceptable (cf. Wiklund 1973). In the case of *T. arvense*, small larvae refusing to eat this plant would starve because they cannot generally successfully locate other crucifers at distances approximating those found between crucifers in field populations (see Chew 1977). However, because larger larvae may successfully complete development on *T. arvense* (Chew 1975), the statistical rather than absolute avoidance of *T. arvense* in favour of the phytochemically similar native foodplant *D. richardsonii* may permit older larvae to exploit a food resource which is not suitable for younger larvae and which ovipositing females should thus avoid.

Second, failures to observe any correlation of larval preferences with the oviposition choices of mothers, the plants on which they were reared, or the age of larvae suggest that in these Nearctic *Pieris*, larval preferences remain constant during the course of a single generation (cf. Wiklund 1975; Claridge and Wilson 1978): the range of foods accepted by the population of larvae should approximate the range that is acceptable to an individual. Differences between individuals should be statistical rather than absolute. This retention of behavioral flexibility permits larvae to choose among resources that are available at the time alternative foodplants are needed (i.e., some weeks after oviposition choices are made, cf. Shapiro 1975) and suggests that there may be selection for larvae whose locomotory prowess enables them to effectively locate crucifers.

These characteristics of larval behavior suggest a further prediction about the responses of these Nearctic *Pieris* to crucifers, viz., that the ranges of foodplants that are behaviorally acceptable (but not necessarily suitable for growth) to larvae of each species may be quite similar. Although larval acceptance of potential foodplants has not been exhaustively tested, there is no evidence that the range of foodplants accepted by the normally restricted

*P. virginensis* is likely to be significantly smaller than the ranges accepted by *P. napi* or *P. rapae*. Thus, in *Pieris* populations confronted by previously unencountered crucifers which do not support larval development (as seems to be the case for a number of Nearctic *Pieris* confronted by weeds of Palearctic origin), discrepancy between plant species chosen by ovipositing females and those which support larval development will be resolved by selection against females which make inappropriate choices (Wiklund 1975; Chew 1977), or selection for larvae which both accept and develop on the newly encountered plant (Chew 1977), at least until they develop sufficient size and mobility to choose their own food resources.

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