

Do caterpillars disperse their damage?: larval foraging behaviour of two specialist herbivores, *Euphydryas phaeton* (Nymphalidae) and *Pieris rapae* (Pieridae)

RODNEY MAURICIO* and M. DEANE BOWERS

Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138, U.S.A.

Abstract. 1. To examine ecological and evolutionary aspects of caterpillar foraging behaviour, this study focused on observation of the individual foraging behaviour of two lepidopteran species, *Pieris rapae* L. and *Euphydryas phaeton* (Drury), on their respective host plants.

2. Periodic observations over the course of a day showed that the larvae move considerable distances, forage on the upper surfaces of leaves, and often immediately leave areas from which they have fed, leaving a pattern of dispersed herbivory.

3. Differences in foraging behaviour were not found between the two species, even though one species is aposematic and the other is cryptically coloured, but there were significant differences in the foraging patterns of *P. rapae* on the two host plants, broccoli and radish.

Key words. Caterpillar foraging, *Euphydryas phaeton*, *Pieris rapae*, Nymphalidae, Pieridae, predator avoidance, crypsis, warning coloration.

Introduction

Lepidopteran larvae directly translate food into adult fitness; there exists a strong positive correlation between the final pupal weight of a caterpillar and its adult fecundity (Scriber & Slansky, 1981). Given this relationship, it is not surprising that a number of models have attempted to predict 'optimal' patterns of foraging in insects (Hassell & Southwood, 1978). Observations of caterpillar foraging behaviour, however, rarely reveal behaviours which are consistent with the predictions of optimal for-

aging theory (Jones, 1977; Heinrich, 1979; Fitzgerald, 1980; Treacy *et al.*, 1987). Indeed, there seems to be much wasted time and effort: caterpillars crawl around more than they have to, skip leaves, eat only parts of leaves, and sit still for long periods of time (Heinrich, 1979; Stamp, 1984; Reynolds *et al.*, 1986; Bergelson & Lawton, 1988; Dethier, 1988).

Larval physiology may explain some of these deviations from optimal foraging. For example, basking in the sun may increase digestion rates by increasing body temperature, thereby increasing rates of development (Sherman & Watt, 1973; Casey, 1976). Much of the discussion, however, has centred on the relative importance of predator avoidance (Heinrich, 1979) versus within-plant allelochemical (Feeny, 1976; Rhoades & Cates, 1976; McKey, 1979) and nutritional (Mooney *et al.*, 1981; Mooney

* Present address: Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

Correspondence: Dr M. Deane Bowers, University of Colorado Museum and Department of E.P.O. Biology, Campus Box 334, University of Colorado, Boulder, CO 80309, U.S.A.

& Gulmon, 1982; Schultz, 1983) heterogeneity, as the most important factors determining larval feeding behaviour (Schultz, 1983). Supporting the importance of within-plant chemical heterogeneity, Edwards & Wratten (1983) postulated that localized, wound-induced chemical changes in leaf quality are critical in determining patterns of insect movement on plants by causing herbivores to disperse their damage.

Although studies of foraging behaviour of individual larvae on their host plants are increasing (Jones, 1977; Hansen *et al.*, 1982; Treacy *et al.*, 1987; Bergelson & Lawton, 1988; Dethier, 1988; Stamp & Bowers, 1988), they generally focus on gregarious, economically important species (Fitzgerald, 1980; Fitzgerald *et al.*, 1988; Lance, 1983; Schultz, 1983; Hansen *et al.*, 1982), or species that feed on trees (*op. cit.*; Stamp, 1984; Bergelson *et al.*, 1986; Bergelson & Lawton, 1988). Information about the foraging patterns of a variety of insect species on their natural hostplants, and especially those that forage on herbaceous plants, are needed. For example, although Edwards & Wratten (1983) suggested that localized induced defences caused insects to disperse their damage on the plant or leaf, their hypothesis was based on patterns of leaf damage of an undefined guild of herbivores, and not on observation of actual foraging behaviour of herbivores. The damage they observed could have been the result of other phenomena: herbivory on unexpanded leaves might result in what looked like dispersed damage; the observed damage could have been created by very early instar larvae that initiated small holes at the site of hatching; or the damage could have been caused by different individuals (of the same or different species).

We studied the foraging behaviour of two herb-feeding, specialist caterpillars, one of which was cryptic and the other warningly coloured and unpalatable. Larvae of the cabbage white, *Pieris rapae* L. (Pieridae), are green and cryptic and specialize on plants in the Brassicaceae. They are palatable to wasps (Gould & Jeanne, 1984) and birds (Jones, 1977). These larvae in our experiments were fed on two plant species, broccoli, *Brassica oleracea* var. *botrytis*, L. (Bailey, 1949), and common radish, *Raphanus sativus* L. The Baltimore checkerspot, *Euphydryas phaeton* (Drury) (Nymphalidae), is a warningly coloured special-

ist on plants containing iridoid glycosides (Bowers, 1983), and primarily feeds on turtlehead, *Chelone glabra* L. (Scrophulariaceae). These caterpillars may be unpalatable to birds (Bowers, 1980), but like many 'unpalatable' insects, degree of unpalatability depends on the hostplant (Bowers, 1980; Brower, 1984). Individual larvae of both species were followed to determine: (1) patterns of foraging activity and quiescence, (2) distances and patterns of travel during daily foraging bouts, (3) whether individual caterpillars dispersed their damage, (4) if the two species differed in their foraging patterns, and (5) whether foraging behaviour was hostplant-dependent.

Materials and Methods

Study organisms. *Euphydryas phaeton* is confined to the marshy habitats of its primary food plant, *C. glabra*. The larvae are warningly coloured orange with black stripes and spines. Larvae reared on *C. glabra* are unpalatable and emetic to birds (Bowers, 1980). *Chelone glabra* is a clonal perennial that grows to approximately 1 m in height and has lanceolate or ovate, toothed leaves on short petioles. The leaves are opposite and vary in length from 2 to 10 cm.

Pieris rapae feeds on plants in the Brassicaceae and occasionally on the Capparidaceae. The larvae are cryptically coloured pale green and smooth in texture. For our experiments with *P. rapae*, we used common radish and broccoli. Common radish is a widely distributed annual found in disturbed areas such as roadsides and old fields. The leaves, stalked and covered with sharp hairs, are approximately 10–15 cm long at maturity. Young plants have leaves in a rosette. Broccoli is a widely cultivated crucifer. The leaves are glabrous, thick, fleshy, obovate or oblong, and 15–50 cm in length.

Study site. The study was conducted from June to August 1987 in an experimental garden in Cambridge, Massachusetts. Twenty *C. glabra* plants had been transplanted from western Massachusetts into this plot 3–5 years earlier. The distance between plants was approximately 0.5 m on all sides.

Sixty young *B. oleracea* plants were planted in a 5 × 12 array on 27 May. Each plant was separated from its neighbour by 0.5 m. A second plot of twenty young *B. oleracea* plants was

planted in a 4 × 5 array (0.5 m between plants) on 1 July. On 28 July the second plot was covered by an enclosure (2 × 2 × 1.5 m) of aluminium screening built to protect foraging caterpillars from predatory wasps (*Polistes* sp.). Air flow and light within the enclosure did not seem to be significantly altered by the screening. Air temperatures were measured at various times during the day, both inside and outside the enclosure, and were not different.

Seventy-two plants of *R.sativus* were grown from seed. Seedlings were started in growth chambers and transplanted into the garden when 20 days old (15 cm height). The plants were arranged in a 6 × 12 array with each plant 0.5 m away from its neighbours.

Euphydryas phaeton larvae were collected in May in Leverett, Franklin Co., Mass., and reared on fresh leaves of *C.glabra*. *Pieris rapae* larvae were reared from eggs laid by females collected in June in Cambridge, Mass. Larvae were reared on *B.oleracea* or *R.sativus*, depending on the plant species to be used for observation. Pupae were collected and emerging adults were mated in net bags (0.5 × 0.5 × 0.7 m). Additional adults, both male and female, were periodically captured and introduced into the colony.

Larvae of both insect species were reared in a growth chamber at 25°C day:20°C night with a photoperiod of 16D:8N, until used for observations of foraging behaviour. *P.rapae* larvae were often brought into a cold room (15°C) in order to slow development and thus provide a continuous source of late instar larvae.

Observation procedure. All larvae used in this study were late instars (IV–VI). Early instar larvae were too small to follow in the field. Late instar caterpillars which were about to pupate were not used.

The day before observations, larvae had spots of fluorescent acrylic paint put on their backs, without apparent effect on the larvae (Hansen *et al.*, 1982; Cornell *et al.*, 1988). This allowed us to monitor individuals. Most foraging observations were completed on sunny, warm days although some observations were taken on overcast, warm days (Table 1). On the morning of observations, the larvae were starved for 1 h, then placed on the plant on the axis of a mid-level leaf. Larvae were left undisturbed for 30 min to acclimate.

At 15 min intervals, the following information

Table 1. Summary information for observation dates of foraging caterpillars. P. = partly.

Date	No. of observations	No. larvae observed	Weather
<i>Euphydryas phaeton</i> on <i>Chelone glabra</i>			
6/3/87	14	10	Sunny, 21°C
6/5/87	18	10	Cloudy, 21°C
6/9/87	22	8	Sunny, 22°C
6/10/87	20	12	Sunny, 24°C
<i>Pieris rapae</i> on <i>Brassica oleracea</i>			
6/29/87	20	15	Sunny, 27°C
6/30/87	21	11	Sunny, 27°C
7/30/87	25	20	Cloudy, 25°C
7/31/87	28	18	Sunny, 27°C
8/4/87	26	18	Sunny, 32°C
8/6/87	25	20	Sunny, 29°C
8/7/87	28	20	Sunny, 29°C
<i>Pieris rapae</i> on <i>Raphanus sativus</i>			
8/11/87	21	10	Sunny, 28°C
8/12/87	23	10	Sunny, 26°C
8/13/87	24	10	P. sunny, 27°C
8/14/87	24	10	Sunny, 28°C

was recorded for each individual caterpillar: whether the larva was feeding, in the sun or shade, moving or not, its change in position from the last observation, its mapped position on the leaf, and comments on damage and behaviour. Meteorological data were also recorded. Observations were generally made from 09.00 to 16.00 hours (EST). All but the first two observation dates of *P.rapae* on broccoli were done under the enclosure. Observations of the *P.rapae* on *R.sativus* were done under aluminium screens which covered individual plants. At the end of the day the larvae were returned to the growth chambers in the laboratory. Lost larvae were replaced so that there was continual turnover of larvae. On two occasions larvae were left outside overnight. When larvae were not left outside overnight, the position of the larva at the end of the day was marked with coloured tape so that it could be returned to that same position the next day.

Distance travelled was summed for each caterpillar over the observation day. In the time activity budgets, all percentages reported are the ratio of the number of observations in which the action occurred to the total observations for the day.

Proportions were arcsine transformed for analysis. All parameters were tested for homogeneity of variance using a Bartlett's test. Data were compared using one-way analyses of variance (ANOVAs) with single degree of freedom comparisons to test the *a priori* hypotheses that (1) there would be interspecific differences in the foraging behaviour of *E.phaeton* and *P.rapae*, as representative of warningly coloured and cryptic larvae, respectively; and (2) that *P.rapae* would behave similarly on *B.oleracea* and *R.sativus*.

Results

Individual larvae do move considerable distances on their host plants (Fig. 1). The range of mean distances travelled in 1 day by *Euphydryas phaeton* was 24.8–50.0 cm (Fig. 1a). Considering that a typical leaf length of *Chelone glabra* is no more than 10 cm and the typical length of a sixth instar caterpillar of *E.phaeton* is 4 cm, a significant amount of moving was done by the larvae.

The range of distances travelled in 1 day by late instar *Pieris rapae* larvae was 23.3–83.2 cm (Figs 1b, c). Late instar *P.rapae* larvae average 2.5 cm in length, and forage on leaves averaging 15 cm in length.

There was no significant difference in the mean distance travelled by *E.phaeton* (36.4 cm) and the mean distance moved by *P.rapae* on its two host plants (weighted mean = 44.8 cm) (Table 2). However, *P.rapae* larvae on *Raphanus sativus* moved significantly greater distances (60.6 cm) than did those on *Brassica oleracea* (35.8 cm) (Table 2).

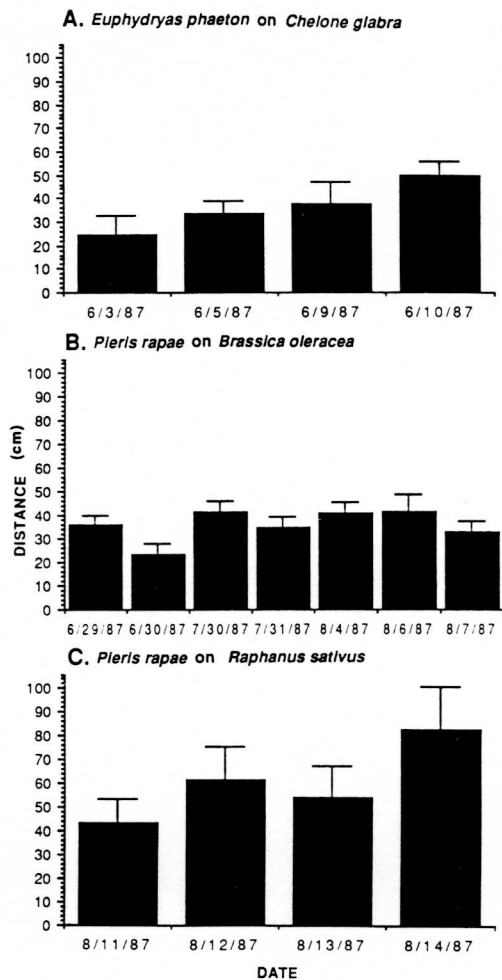


Fig. 1. Mean distance travelled by larvae of *E.phaeton* and *P.rapae* in 1 day, on the observation dates. The vertical bars are standard errors.

Table 2. Results of single degree of freedom comparisons of *E.phaeton* and *P.rapae*, and *P.rapae* on its two hostplants, *B.oleracea* and *R.sativus*.

Behaviour	<i>E.phaeton</i> v. <i>P.rapae</i>			<i>P.rapae</i> on <i>B.oleracea</i> v. <i>R.sativus</i>		
	df	F	P	df	F	P
Distance travelled	1, 12	3.326	NS	1, 12	12.933	<0.005
Time in sun (%)	1, 12	13.625	<0.005	1, 12	0.093	NS
Time feeding (%)	1, 12	1.823	NS	1, 12	11.770	<0.005
Time moving (%)	1, 12	0.728	NS	1, 12	28.108	<0.001
Time stationary (%)	1, 12	0.728	NS	1, 12	28.108	<0.001

On two occasions, *P. rapae* larvae were left out overnight and distance travelled over night was measured in order to determine the extent of nocturnal foraging. On the first night, the larvae ($N = 18$) moved a mean length of 3.4 cm (SE = 1.4) and on the second night, the larvae ($N = 20$) moved a mean length of 12.7 cm (SE = 2.8). Many larvae had not moved at all.

Individual larvae of both species spent more time in the sun than in the shade (Fig. 2). *Euphydryas phaeton* larvae were in the sun an average of 91.6% of the observations, while *P. rapae* spent an average of 74.8% of the obser-

ations in the sun. *Euphydryas phaeton* spent significantly more time in the sun than *P. rapae* (Table 2). There was no significant difference between *P. rapae* on its two host plants with regard to time spent in the sun (Table 2).

Of the time the larvae spent in the shade, only part of the time was spent on the undersides of leaves (Fig. 2). Of the 8.4% of the time *E. phaeton* spent in the shade, about half of that time was spent on the undersides of leaves. In addition, *E. phaeton* spent an average of 10.0% of its time on emergent leaves. Of the 25.2% of the time *P. rapae* spent in the shade, only 4.5% of that time was spent on the undersides of the leaves.

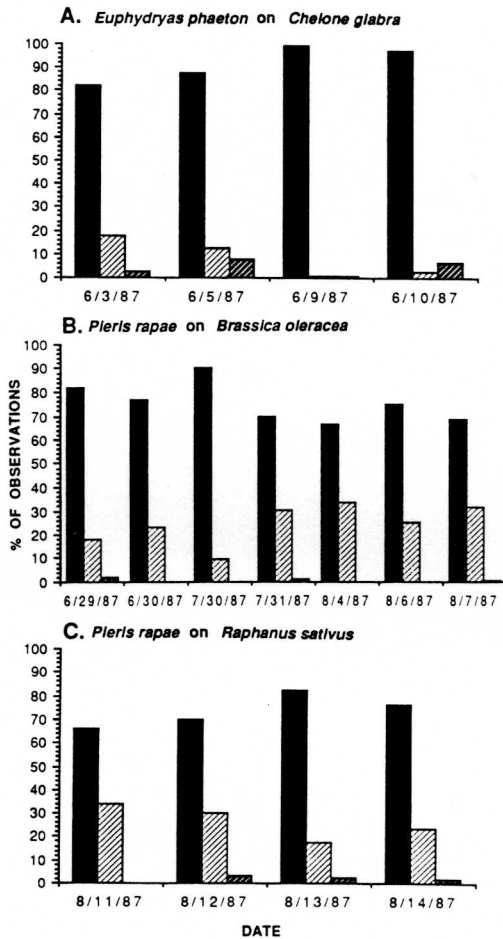


Fig. 2. Mean percentage of observations of larvae of *E. phaeton* and *P. rapae* found in a particular location: sun (solid columns), shade (lightly hatched columns), or on the undersides of leaves (heavily hatched columns). Larvae were considered in the shade if they were not in direct sunlight.

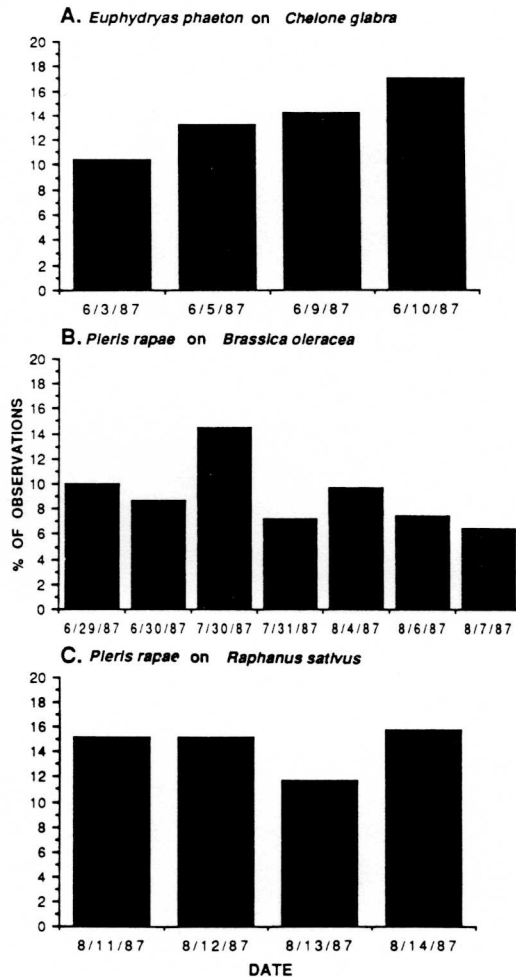


Fig. 3. Mean percentage of observations of larvae of *E. phaeton* and *P. rapae* that were feeding.

Itemized time activity budgets show that *E.phaeton* larvae spent an average of 13.8% of the observations feeding, 17.8% moving and 82.2% stationary (Figs 3a, 4a). *P.rapae* spent an average of 11.0% of the observations feeding, 14.7% moving and 85.3% stationary (Figs 3b, 3c, 4b, 4c). In each activity there was no significant difference between *E.phaeton* and *P.rapae* (Table 2). However, there were significant differences between the means of per cent observations feeding, moving, or not moving in the comparison of *P.rapae* on *B.oleracea* (feeding: 9.1%; moving: 9.9%; stationary: 90.1%)

and *P.rapae* on *R.sativus* (feeding: 14.4%; moving: 23.0%; stationary: 77%) (Table 2).

In *E.phaeton* an average of 54% of feeding bouts were immediately followed by a change in position (Fig. 5a). A change in position was any movement away from the previous location of more than 1 cm. 57% of the feeding bouts of *P.rapae* on *B.oleracea* and 74.9% of the feeding bouts of *P.rapae* on *R.sativus* were immediately followed by changes in position (Figs 5b, c).

Feeding observations of *E.phaeton* confirm that the larvae rarely eat more than 50% of the area of a single leaf of *C.glabra* (Fig. 6). In fact,

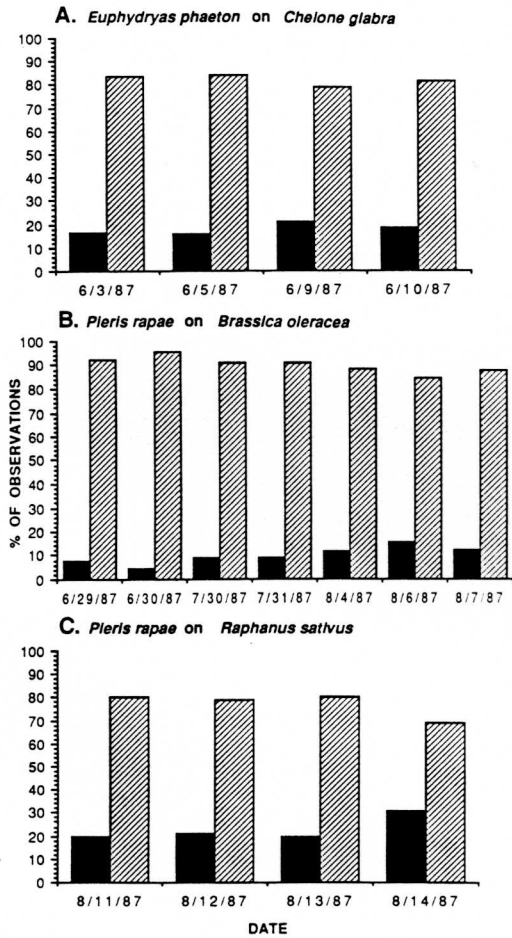


Fig. 4. Mean percentage of observations of larvae of *E.phaeton* and *P.rapae* found either moving (solid columns) or stationary (hatched columns). Since larvae were engaged in either one activity or the other, the two activities are presented together and sum to 100%.

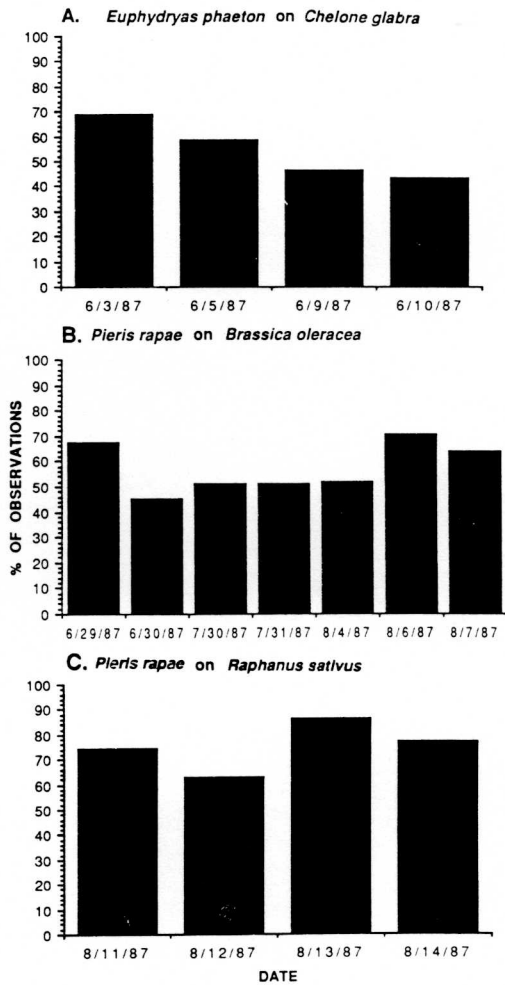


Fig. 5. Mean percentage of observations of feeding of *E.phaeton* and *P.rapae* followed in the next observation by movement or a change in position.

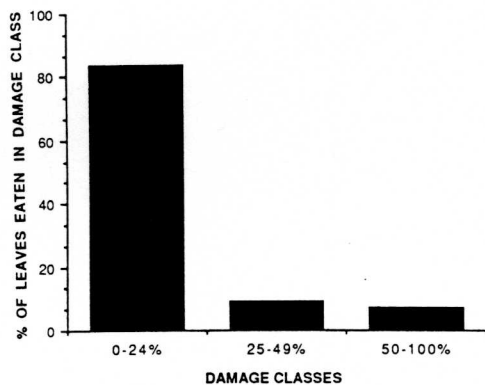


Fig. 6. Percentage of leaves of *C. glabra* eaten by *E. phaeton*, which fall into three damage categories, <25%, 25–49%, 50–100%. Total number of leaves was fifty-five.

83.6% of leaves eaten had less than 25% of the leaf area of a single leaf removed, 9.1% of the eaten leaves had between 25% and 49% leaf area lost and only 7.3% of the eaten leaves had more than 50% of their leaf area removed. The total number of leaves damaged by all *E. phaeton* larvae during these observations was fifty-five.

Discussion

Our observations of the foraging behaviour of individual larvae of two species with coloration indicating very different strategies of predator avoidance (cryptic versus warningly coloured) show that individual larvae of both species move considerable distances while foraging on their host plants. We also found that larvae spend a rather large portion of their time moving or feeding compared to other caterpillar species that have been studied (Bergelson & Lawton, 1988; Dethier, 1988). The consequences to the plant of such a foraging pattern is a dispersed pattern of damage, confirming the observations of Edwards & Wratten (1983). Two observations are particularly compelling in this regard: First, in the majority of cases, a feeding bout was immediately followed by a change in position, either to a new leaf or to another part of the same leaf (Fig. 5). Second, in *Chelone glabra*, only 17.4% of the leaves that had been fed upon had greater than 25% of the leaf area removed (Fig. 6).

Two hypotheses have been offered to explain herbivore foraging patterns. The first suggests that plant heterogeneity at the leaf and plant scale explains foraging patterns in herbivores (Schultz, 1983; Edwards & Wratten, 1983). Thus herbivores move in order to eat the highest quality foliage they can find. Schultz (1983) predicted that herbivores would move over the leaf and the entire plant searching for foliage which is high in nutrients and water and low in allelochemicals. Superimposed on this heterogeneity, however, herbivory can alter the quality of the host plant (Ryan & Green, 1974; Haukioja & Niemala, 1976, 1977; Niemala *et al.*, 1979; Carroll & Hoffmann, 1980), which may in turn modify the foraging patterns of herbivores (Edwards & Wratten, 1983). Heinrich (1979) suggested a second explanation for the observed foraging patterns of insect herbivores: predator avoidance. Heinrich (1979) predicted that the foraging patterns of palatable and unpalatable caterpillars would differ. He suggested that palatable, cryptic caterpillars avoided predation by at least one of the following: foraging on the undersides of leaves, foraging at night, 'commuting' to and from the feeding area, clipping off partially eaten leaves, and moving away from an unfinished leaf so as not to remain near an area which might attract visually cued predators. In contrast, unpalatable caterpillars did none of these and often rested exposed on leaf surfaces (Heinrich, 1979; Heinrich & Collins, 1983).

Our study compared the foraging patterns of larvae of a cryptic species, *P. rapae*, and a warningly coloured species, *E. phaeton*. Comparisons of total distance travelled in a day, distance travelled per observation, and percentage of time spent feeding, moving and stationary showed that both species, whether aposematic or cryptic, foraged similarly. Although *E. phaeton* spent significantly more time in the sun than did *P. rapae*, both species remained in the sun for the majority of the time they were observed. In addition, *P. rapae* larvae did not seem to move or feed at night and spent most of their time on the upper surfaces of leaves in the sun. Our data, therefore, do not support Heinrich's (1979) prediction that palatable, cryptically coloured larvae would restrict foraging to night-time and to the undersides of leaves. *P. rapae* larvae did disperse their damage, but so did larvae of *E. phaeton*. Heinrich

(1979) considered cryptic tree-feeding caterpillars, which may have different habits from cryptic larvae, such as *P.rapae*, that feed on herbs.

Both caterpillar species we studied are oligophagous: *E.phaeton* feeds on plants in four families containing iridoid glycosides (Bowers, 1980, 1983), while *P.rapae* feeds on crucifers which contain mustard oil glycosides (Chew, 1975). Iridoid glycosides and mustard oil glycosides may serve as larval feeding stimulants for specialist insects (Bowers, 1983; Feeny, 1976). Larvae of one specialist on plants containing iridoid glycosides (*Junonia coenia* Hübner, Nymphalidae) performed better on diets with higher levels of these compounds (Bowers & Puttick, 1989), and females preferred to lay their eggs on substrates with more iridoid glycosides (Pereyra & Bowers, 1988). Therefore, if induction and elevation of allelochemical levels is occurring in either of these systems, then we would predict that larvae would be attracted to sites of damage, rather than deserting them, and might perform better on damaged foliage. We have not tested this second prediction, but regarding the first prediction, our data show that the two specialists that we studied are not attracted to damaged sites, but leave them.

Our data suggest that differences between host plant species may be very important factors in determining patterns of caterpillar foraging behaviour. Although we found no difference in foraging between *E.phaeton* and *P.rapae*, there was a consistent difference in foraging between *P.rapae* on *B.oleracea* and *R.sativus*. The reasons for the differences in larval foraging on the two hostplants are unknown. They may be due to differences in the induction, or lack thereof, of chemical defences, to nutritional differences, or to physical differences between the two hostplants such as the presence of hairs on *R.sativus* leaves.

Thus, caterpillar foraging behaviour may not be predictable solely on the basis of optimal foraging, predator avoidance or plant chemical and physical attributes, but on a combination of these parameters. Elucidating the factors determining foraging patterns in several plant-insect systems will provide the information necessary to help understand the evolution of insect foraging patterns, and the importance of both host-plant characteristics and natural enemies in shaping those patterns.

Acknowledgments

We thank K. Hoy Burgess, S. Collinge, E. Fajer and J. Lawton for comments on the manuscript. F. Chew provided information on rearing *P.rapae*, and N. Ellstrand provided seeds of *R.sativus*. This work was supported by the NSF Research Experience for Undergraduates program grant BBS 8712624, and a Ford Foundation grant for undergraduate research from Harvard University.

References

- Bailey, L.H. (1949) *Manual of Cultivated Plants*. MacMillan, New York.
- Bergelson, J., Fowler, S. & Hartley, S. (1986) The effects of foliage damage on casebearing moth larvae, *Coleophora serratella*, feeding on birch. *Ecological Entomology*, **11**, 241–250.
- Bergelson, J.M. & Lawton, J.H. (1988) Does foliage damage influence predation on the insect herbivores of birch? *Ecology*, **69**, 434–445.
- Bowers, M.D. (1980) Unpalatability as a defense strategy of *Euphydryas phaeton* (Lepidoptera: Nymphalidae). *Evolution*, **34**, 586–600.
- Bowers, M.D. (1983) The role of iridoid glycosides in host-plant specificity of checkerspot butterflies. *Journal of Chemical Ecology*, **9**, 475–493.
- Bowers, M.D. & Puttick, G.M. (1989) Iridoid glycosides and insect feeding preferences: gypsy moths (*Lymantria dispar*, Lymantriidae) and buckeyes (*Junonia coenia*, Nymphalidae). *Ecological Entomology*, **14**, 247–256.
- Brower, L.P. (1984) Chemical defense in butterflies. *The Biology of Butterflies* (ed. by R. Vane-Wright and P. Ackery), pp. 109–134. Academic Press, New York.
- Carroll, C.R. & Hoffmann, C.A. (1980) Chemical deterrent mobilized in response to insect herbivory and counteradaptation by *Epilachna tredecimnotata*. *Science*, **209**, 414–416.
- Casey, T.M. (1976) Activity patterns, body temperatures and thermal ecology in two desert caterpillars (Lepidoptera: Sphingidae). *Ecology*, **57**, 485–497.
- Chew, F.S. (1975) Coevolution of pierid butterflies and their cruciferous food plants. I. The relative quality of available resources. *Oecologia (Berlin)*, **20**, 117–127.
- Cornell, J.C., Stamp, N.E. & Bowers, M.D. (1988) Developmental change in leadership and activity patterns in the gregarious larvae of the buckmoth, *Hemileuca lucina* (Saturniidae). *Psyche*, **95**, 45–57.
- Dethier, V.G. (1988) The feeding behavior of a polyphagous caterpillar (*Diacrisia virginica*) in its natu-

- ral habitat. *Canadian Journal of Zoology*, **66**, 1280–1288.
- Edwards, P.J. & Wratten, S.D. (1983) Wound induced defenses in plants and their consequences for patterns of insect grazing. *Oecologia (Berlin)*, **59**, 88–93.
- Feeny, P. (1976) Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, **10**, 1–40.
- Fitzgerald, T.D. (1980) An analysis of daily foraging patterns of laboratory colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae), recorded photoelectrically. *Canadian Entomologist*, **112**, 731–735.
- Fitzgerald, T.D., Casey, T. & Joos, B. (1988) Daily foraging schedule of field colonies of the eastern tent caterpillar *Malacosoma americanum*. *Oecologia (Berlin)*, **76**, 574–578.
- Gould, W.P. & Jeanne, R.L. (1984) *Polistes* wasps (Hymenoptera: Vespidae) as control agents for lepidopterous cabbage pests. *Environmental Entomology*, **13**, 150–155.
- Hansen, J.D., Ludwig, J.A., Owens, J.C. & Huddleston, E.W. (1982) Movement of late instars of the range caterpillar *Hemileuca oliviae* (Lepidoptera: Saturniidae). *Journal of the Georgia Entomological Society*, **17**, 76–87.
- Hassell, M.P. & Southwood, T.R.E. (1978) Foraging strategies of insects. *Annual Review of Ecology and Systematics*, **9**, 75–98.
- Haukioja, E. & Niemala, P. (1976) Does birch defend itself against herbivory? *Reports from the Kevo Subarctic Research Station*, **13**, 44–47.
- Haukioja, E. & Niemala, P. (1977) Retarded growth of a geometrid larva after mechanical damage to the leaves of its host tree. *Annales Zoologici Fennici*, **14**, 45–52.
- Heinrich, B. (1979) Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia (Berlin)*, **42**, 325–337.
- Heinrich, B. & Collins, S.L. (1983) Caterpillar leaf damage and the game of hide and seek with birds. *Ecology*, **64**, 592–602.
- Jones, J.E. (1977) Search behaviour: a study of three caterpillar species. *Behaviour*, **3–4**, 237–259.
- Lance, D.R. (1983) Host-seeking behavior of the gypsy moth: the influence of polyphagy and highly apparent hostplants. *Herbivorous Insects* (ed. by S. Ahmad), pp. 201–224. Academic Press, New York.
- McKey, D. (1979) The distribution of secondary compounds within plants. *Herbivores: Their Interaction with Secondary Plant Metabolites* (ed. by G. A. Rosenthal and D. H. Janzen), pp. 55–133. Academic Press, London.
- Mooney, H.A., Field, C., Gulmon, S.L. & Bazzaz, F.A. (1981) Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. *Oecologia (Berlin)*, **50**, 109–112.
- Mooney, H.A. & Gulmon, S.L. (1982) Constraints on leaf structure and function in reference to herbivory. *Bioscience*, **32**, 198–206.
- Niemala, P., Aro, E.M. & Haukioja, E. (1979) Birch leaves as a resource for herbivores. Damage-induced increase in leaf phenols with trypsin-inhibiting effects. *Reports from the Kevo Subarctic Research Station*, **15**, 37–40.
- Pereyra, P.C. & Bowers, M.D. (1988) Iridoid glycosides as oviposition stimulants for the buckeye, *Junonia coenia* (Nymphalidae). *Journal of Chemical Ecology*, **14**, 917–928.
- Reynolds, S.E., Yeomans, M.R. & Timmins, W.A. (1986) The feeding behaviour of caterpillars (*Manduca sexta*) on tobacco and artificial diet. *Physiological Entomology*, **11**, 39–51.
- Rhoades, D.F. & Cates, R.G. (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry*, **10**, 168–213.
- Ryan, C.A. & Green, T.R. (1974) Proteinase inhibitors in natural plant protection. *Recent Advances in Phytochemistry*, Vol. 8. *Metabolism of Secondary Plant Products* (ed. by V. C. Runeckles and E. E. Conn), pp. 123–140. Academic Press, New York.
- Schultz, J.C. (1983) Habitat selection and foraging tactics of caterpillars in heterogeneous trees. *Variable Plants and Herbivores in Natural and Managed Systems* (ed. by R. F. Denno and M. S. McClure), pp. 61–90. Academic Press, New York.
- Scriber, J.M. & Slansky, F., Jr (1981) The nutritional ecology of immature insects. *Annual Review of Entomology*, **26**, 183–211.
- Sherman, P.W. & Watt, W.B. (1973) The thermal ecology of some *Colias* butterflies. *Journal of Comparative Physiology*, **83**, 25–40.
- Stamp, N.E. (1984) Foraging behavior of tawny emperor caterpillars (Nymphalidae: *Asterocampa clyton*). *Journal of the Lepidopterists' Society*, **38**, 186–191.
- Stamp, N.E. & Bowers, M.D. (1988) Direct and indirect effects of predatory wasps (*Polistes* spp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia (Berlin)*, **75**, 619–624.
- Treacy, M.F., Benedict, J.H., Schmidt, K.M., Anderson, R.M. & Wagner, T.L. (1987) Behavior and spatial distribution patterns of tobacco budworm (Lepidoptera: Noctuidae) larvae on chloroform-treated cotton plants. *Journal of Economic Entomology*, **80**, 1149–1151.