Acta Zoologica Academiae Scientiarum Hungaricae 48 (Suppl. 1), pp. 117–135, 2002

CONTRASTED FORAGING TACTICS IN TWO SPECIES OF POLYPHAGOUS CATERPILLARS

BERNAYS, E. A.* and M. SINGER

Department of Entomology, Forbes 410, University of Arizona, Tucson AZ 85721, USA
**E-mail: schistos@ag.arizona.edu*

Polyphagy can occur at the level of species, population or individual. We analyzed foraging by two polyphagous species of caterpillar in the field and laboratory in a first investigation of the differences between polyphagy at different levels. We sought to obtain details that would inform different regulatory mechanisms and different adaptive bases. The fast-growing noctuid, *Trichoplusia ni* is known to be polyphagous at the level of species and population, while the slower-growing arctiid, *Grammia geneura*, is additionally polyphagous at the level of the individual. *T. ni* individuals showed greater uniformity in time spent feeding, had longer but fewer feeding bouts, and moved very little, compared with *G. geneura*. While *T. ni* rested on the food, *G. geneura* more commonly rested off it. *T. ni* individuals rarely mixed food items but rather showed increased preference for the rearing food, while *G. geneura* individuals habitually took a mixture of food items. We relate the differences to several potential physiological and ecological factors that are contrasted, including the crypsis of *T. ni* which alters with the food plant, and to the probable aposematism of *G. geneura*.

Key words: foraging, generalist, food-mixing, Lepidoptera

INTRODUCTION

The term polyphagous, as applied to a species of herbivorous insect, does not necessarily imply that individual insects of that species are polyphagous. To begin with, polyphagous insect herbivore species may be made up of populations having relatively narrow host ranges (FOX & MORROW 1981, THOMPSON 1994), and a relatively polyphagous population of insects may be made up of specialist individuals (BERNAYS & MINKENBERG 1997). Among the major phytophagous orders of insects, examples of these different levels of polyphagy may be found but they vary in relative abundance. For example, among orthopterans studied, individuals of most species feed on multiple foods, while among lepidopterans, it is more common for individuals to feed on only one plant species. Here, larvae remain on the host chosen by their ovipositing mothers. In only a small minority of species do individuals habitually move from plant to plant (MERZ 1959, DETHIER 1988*a*, SINGER 2000).

Even among individuals of food-mixing taxa there are contrasts between those that mix little and move little on the one hand, and those that move continuously between different food plants and eat many species in the course of a day.

For example, individuals of some grasshopper species may feed on dozens of species in a day, while others, that may be equally polyphagous over their lifetime, feed on only two or three in a day (CHAMBERS *et al.* 1996). There is little known about the costs and benefits of these different strategies, although data on grasshoppers indicate that individuals mixing their food plants have a faster growth rate than those that do not, and thus benefit individually from taking the mixture (BERNAYS *et al.* 1994, BERNAYS & MINKENBERG 1997).

Among Lepidoptera mixtures tend not to be beneficial (BERNAYS & MINKENBERG 1997, HAGELE & ROWELL-RAHIER 1999, SINGER 2000) except over long time frames, where the normal food of first instar larvae is different from that of the later stages (GASTON *et al.* 1991). On the contrary, it is not uncommon for individuals to increase their fidelity to a plant that has been fed upon, the phenomenon of "induction of preference" (JERMY *et al.* 1968, JERMY 1987), and in some cases at least, individuals benefit physiologically from remaining with a single host species (KAROWE 1989). Thus, many species are relatively immobile and more or less restricted to the host plant chosen by the mother. A typically sedentary species is the noctuid, *Trichoplusia ni*. The mobility of some generalists is necessitated by other types of constraints. For example, armyworms (*Spodoptera* spp.) that feed mainly at night and must find shelter off the plant during the day, may move to different plants on different days. Also, restricted food patches may dictate movement, as with *Heliothis virescens* feeding on tobacco, where each flower (the preferred tissue) is too small to support much feeding, at least of the later stadia. In some cases large species that feed on small herbaceous plants finish individual plants and must then search for additional ones (JONES 1977). At high population densities, some species such as *Lymantria dispar* and *Spodoptera* spp. move extensively, while the most extreme strategy is found in a number of generalist arctiids that spend relatively long periods moving, especially in the later stadia, when they encounter and feed upon many different foods. They may eat parts of up to 20 different plant species in the course of a day. Such is the case with *Grammia geneura* (SINGER 2000).

This study is an experimental analysis of foraging by caterpillars of two species of polyphagous Lepidoptera that appear to be at the extremes of the possible foraging strategies, the noctuid *Trichoplusia ni*, and the woolly bear arctiid, *Grammia geneura*. Using field and laboratory observations we asked a) how do generalists at the species level differ in individual foraging tactics? b) does induction of preference play a role in the patterns observed? c) what physiological or ecological factors might influence such differences?

MATERIALS AND METHODS

The study organisms

Grammia geneura (STRECKER) (Arctiidae) is a species occurring in arid savanna of SW United States and Mexico. There are two generations each year in SE Arizona where we studied them. Adult females do not feed and have little flight ability. They lay large numbers of eggs in loose batches onto the substrate, which is sometimes simply the leaf litter. They do not place eggs on plants. Newly hatched larvae must find their food plants, and in some seasons they may have to wait for the germination of plants after rain. Larvae are dark, covered in long setae, and apparently distasteful, at least to some predators. Populations used for this study were from southern Arizona. They have one generation of larvae that develop over a period of several weeks on herbaceous plants available after the summer rains. A second generation of larvae begin their development in the fall, then, after sheltering during winter, they resume development on the herbaceous plants (mostly different species) that appear in spring.

Trichoplusia ni (HÜBNER) (Noctuidae, Plusiinae) is a worldwide pest of many vegetables and other plants. It is fast-growing, multivoltine and highly polyphagous on herbaceous plants (SUTHERLAND & GREEN 1984). Adult females are competent fliers and lay single eggs on many different plant species to which they are attracted; individuals readily lay on more than one plant species (LANDOLT & MOLINA 1996). Larvae initiate feeding beside the egg and typically remain on the same plant until pupation. They are green and apparently cryptic on their host plants and known to be palatable to numerous different predators. Populations used in this study were from southern Arizona. They have been found on vegetables in gardens and on numerous wild plants including several species of Asteraceae.

Field observations

In this work we report on individuals observed in nature during daylight hours when most foraging occurs. Temperatures at foliage level varied from approximately 25 to 30°C. Eleven final stage larvae of *G. geneura* were continuously observed for periods of at least six hours. Most records of last stage *T. ni* indivuals were of two to three hours but these were supplemented with one six-hour observation, and intermittent observations on nine individuals over five days (four on *Ocimum basilicum*, three on *Mentha spicata*, one on *Lactuca sativa* and one on *Encelia farinosa*).

During continuous observations we recorded manually all feeding and locomotor events as well as plant species fed upon. Budgets were constructed for time spent feeding and walking. Survivorship analyses were used to examine the distribution of feeding bout lengths and interbout lengths (SIMPSON 1982). It was necessary to pool both of these for each species, to obtain sufficient numbers of each.

Laboratory observations of foraging patterns

Grammia geneura larvae were reared individually in plastic containers (8 cm high × 16 cm diameter) with screened ventilation holes. The bottom of each container was lined with filter paper. Three food plants were provided in symmetrically arranged vials of water in quantities such that caterpillars could feed *ad libidum*. The species were *Plantago insularis* (Plantaginaceae), *Malva parviflora* (Malvaceae) and *Tithonia fruticosa* (Asteraceae). One treatment had three vials with one of each plant species available, while the other treatments had three vials, each with a sprig of the same food. All plants were acceptable and supported development (SINGER 2000). Containers were kept in an environmental chamber with L:D cycle of 12:12 and temperatures of 28:24°C. Mean durations of development, from hatching to silking, were 39±2, 43±2 and 80±4 days respectively. The foods were replaced on alternate days but always refreshed prior to observations. A total of 10 or 11 individuals was observed in each of the four treatments for a period of four hours early in the final larval stadium when feeding is maximal. Fluorescent lights provided illumination and the temperature was kept at 26 to 28°C. We recorded feeding, movement and location using the Observer program (NOLDUS 1991) loaded onto a Dell laptop computer.

Trichoplusia ni larvae were reared in groups of twenty in plastic cups (7 cm high × 8 cm diameter) with cut sprigs of three foods available *ad libidum*. The food plants were *Mentha spicata* (Lamiaceae), *Lactuca sativa* (Asteraceae) and *Ocimum basilicum* (Lamiaceae). The foliage of the three species in the mixed-food treatment was intermingled to allow movement between foods, and though not placed in vials of water, it was repaced daily. Larvae have been found on all three foods in nature and these species are known to support quite rapid development (BERNAYS & MINKENBERG 1997). Containers were kept in an environmental chamber with L:D cycle of 12:12 and temperatures of 26:23°C. There were significant differences in development rates. Mean durations of development, from hatching to wandering, were 8±1, 10±1 and 9±1 days for *Mentha*, *Lactuca* and *Ocimum* respectively. On day two of the final larval stadium the insects were transferred to individual plastic boxes (11×11×4 cm) with screened ventilation holes. They were provided with a mixture of the same three foods, or only one. In either case, they were in three vials, one of each species, or all three of the same species, in three symmetrically arranged vials of water, again, *ad libidum*. Six individuals were observed for six hours on each of the four treatments. Fluorescent lights provided illumination and the temperature was kept at 27°C. We recorded all feeding, locomotion and resting positions using an HP hand-held computer programmed as an event recorder.

Experiment on induction of preference

The results clearly indicated that *G. geneura* could not be exhibiting any induced preference for previously eaten food because larvae moved between food plant species too frequently. However, to determine if there were restrictions in food acceptability due to experience in *T. ni*, the following experiment was carried out with the offspring of three adult females reared from field-collected larvae. Newly hatched larvae were separated into three groups of approximately 50 and reared in plastic containers (28 cm high × 15 cm diameter) with one of three foods, *Mentha spicata*, *Lactuca sativa* or *Ocimum basilicum*. An hour before the experiment food was removed from the rearing containers. Sixteen individual larvae of the same age (±2 d) from each treatment were placed singly in Petri dishes (8 cm diameter). These were lined on the bottom with damp filter paper on which was placed a single freshly cut disk of leaf (1 cm diameter) of each of the three foods, arranged symmetrically round the periphery. Caterpillars were taken singly from their rearing containers and each placed centrally in a test dish. Individuals took between five minutes and an hour to initiate movements. We recorded the first food contacted and the first food upon which the caterpillar fed continuously for 30 seconds or more.

Finally, first instar larvae from one female *T. ni* were placed on *Mentha*, *Ocimum* or *Encelia farinosa* in the field. There were approximately thirty of each. Most were lost, presumably due to predation, but one on *Mentha*, two on *Ocimum* and two on *Encelia farinosa* survived, and these were photographed to record morphological differences observed.

RESULTS

Field observations

There was a marked contrast in the foraging patterns of the two species of caterpillars in the field. Average percent of time spent walking was 0.4±0.1 in *T. ni* and 14±4 in *G. geneura*. Average percent of time spent feeding was 21±3 for *T. ni* and 15±2 for *G. geneura*. Of the nine individual *T. ni* followed for five days, none moved from the branch of the plant upon which it was first seen, and moves to new

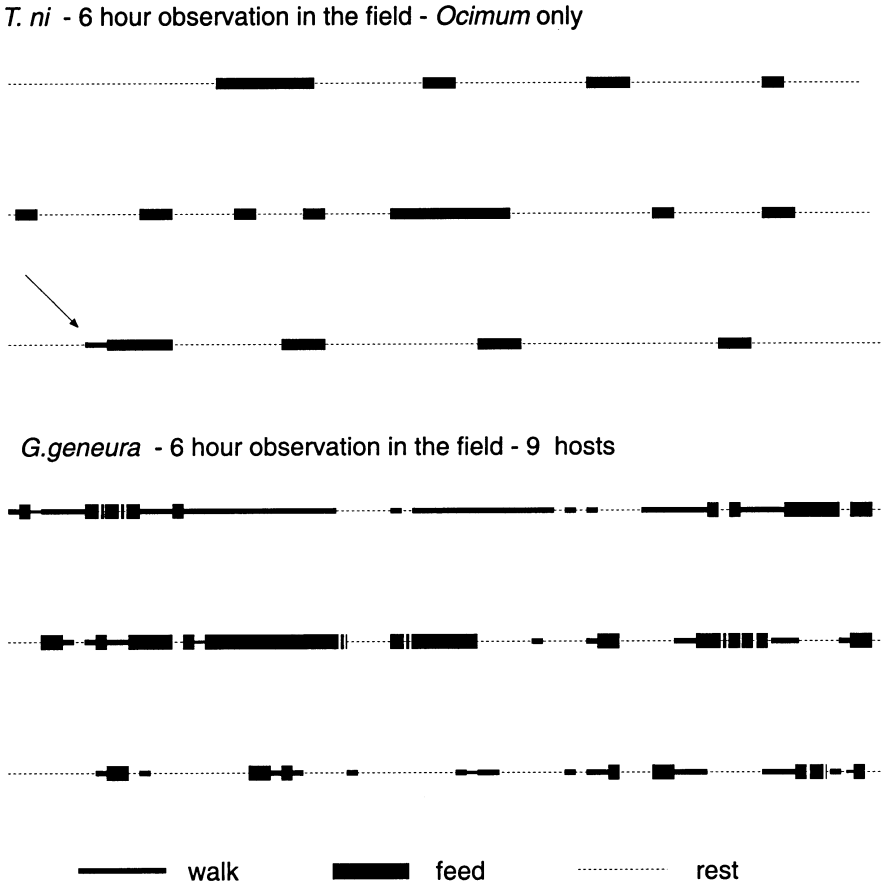


Fig. 1. Examples of data from field observation of last instar larvae of *Trichoplusia ni* and *Grammia geneura* demonstrate the contrast in patterns of foraging. Note the absence of locomotor activity in *T. ni* except for the small walk before a meal during hour five (arrow)

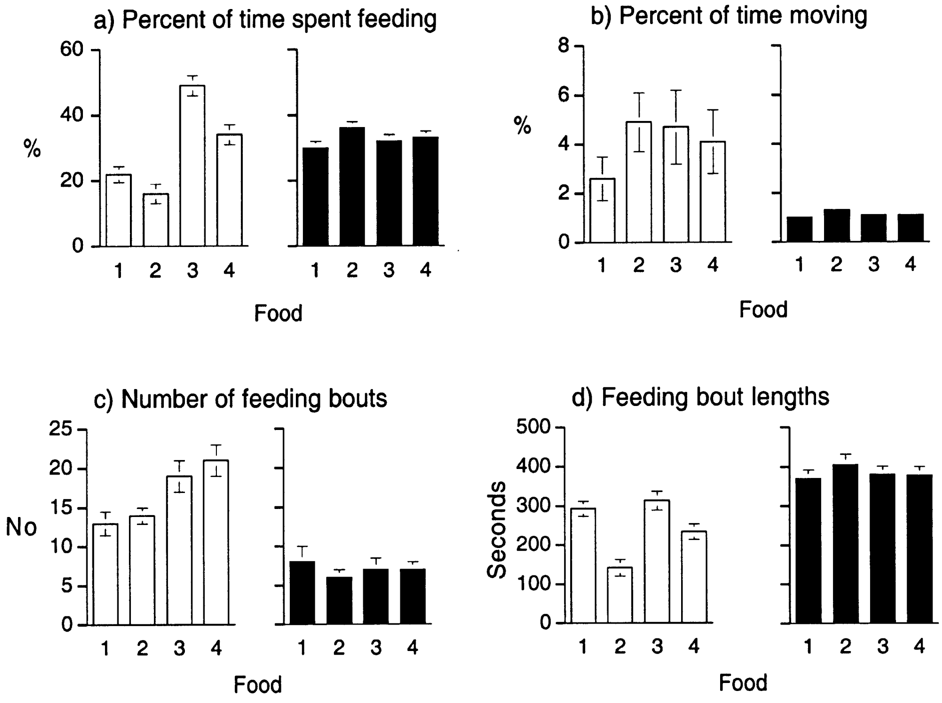
leaves were generally initiated when a leaf was completely eaten, apart from the petiole and parts of the midrib. This involved a maximum move of eight cm. On one occasion, a larva on *E. farinosa* moved to a new leaf after eating less than half of another. All individuals of *G. geneura* moved between plants with numbers of individual plants eaten in a six-hour period varying from eight to 41, and numbers of different species eaten varying from two to nine. In no case was a whole leaf eaten. Figure 1 gives the pattern of feeding, walking and resting in one individual early in the final larval instar of each species watched for six hours in the field. The *T. ni* larva remained on the host, *Ocimum*, feeding at intervals but without moving from the same leaf. There was one short interval of movement (arrow) when it crossed the mid vein and fed on the other side of the leaf. The *G. geneura* larva, by contrast, moved frequently and had many feeds on nine different plant species.

Field conditions are variable and the food plants of the two species differed in size and distribution so that it is difficult to determine the extent to which the different foraging patterns were truly intrinsic. Furthermore, the precise stage of development of individual caterpillars in the field was unknown. Laboratory observations carried out under very similar conditions for the two species and in similarly-sized containers with standard insects, indicate that the differences are maintained in large degree.

Laboratory observations

Proportion of time spent feeding was similar overall in the two species. However, larvae of *G. geneura* varied in the amount of time spent feeding on different plants, with *Plantago* being eaten for a much greater proportion of the time than either of the other single foods or the mixture (Fig. 2a). *G. geneura* individuals spent more time moving than *T. ni* (Fig. 2b), and had more feeding bouts (Fig. 2c) of shorter duration (Fig. 2d) on all three plants individually and in the mixture.

Survivorship analysis of the feeding bout lengths demonstrates differences in the pattern of bouts more fully (Fig. 3). On all host plants, *G. geneura* had larger proportions of shorter feeding bouts than *T. ni* (Fig. 3a) while the differences were much more extreme in the field (Fig. 3b). Here, more than 50% of bouts taken by *G. geneura* were of durations less than one minute, whereas most bouts of *T. ni* were of ten minutes duration or longer. In the survivorship analysis of the interbout lengths we found that *G. geneura* has a continuum of interbout intervals with no clear break between short and long intervals (Fig. 4). By contrast, with *T. ni* we found that there was a population of short interbouts and a population of longer interbouts (Fig. 4). This suggests that the feeding bouts in this species are grouped together to form meals. This was not an artifact of different behavior by different individuals or of different behavior on different foods, because all individuals showed similar patterns and appeared to do so on the different foods. However, data were too few to statistically compare behavior on the different foods.



Food	*Gg*	*Tn*
1	*Tithonia*	*Mentha*
2	*Malva*	*Lactuca*
3	*Plantago*	*Ocimum*
4	MIX	MIX

☐ *G. geneura* ■ *T. ni*

Fig. 2. Activity budgets of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in laboratory observations on various food plants. Mean and standard errors given. 2a. Percent of time spent feeding: *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.9$). 2b. Percent of time spent moving: no significant differences among treatments for either *G. geneura* or *T. ni* (Kruskal-Wallis tests, $P > 0.5$). 2c. Number of feeding bouts. *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.5$). 2d. Feeding bout lengths. *G. geneura* significantly different among treatments (Kruskal-Wallis test, $P < 0.01$); *T. ni* no significant differences (Kruskal-Wallis test, $P > 0.3$)

Four variables were used to demonstrate other major differences in foraging pattern by the two species in the laboratory. First, the likelihood of rejection of host plants that are encountered during locomotion. In all four treatments, *G. geneura* often rejected the available host(s), especially *Malva*, although this was highly

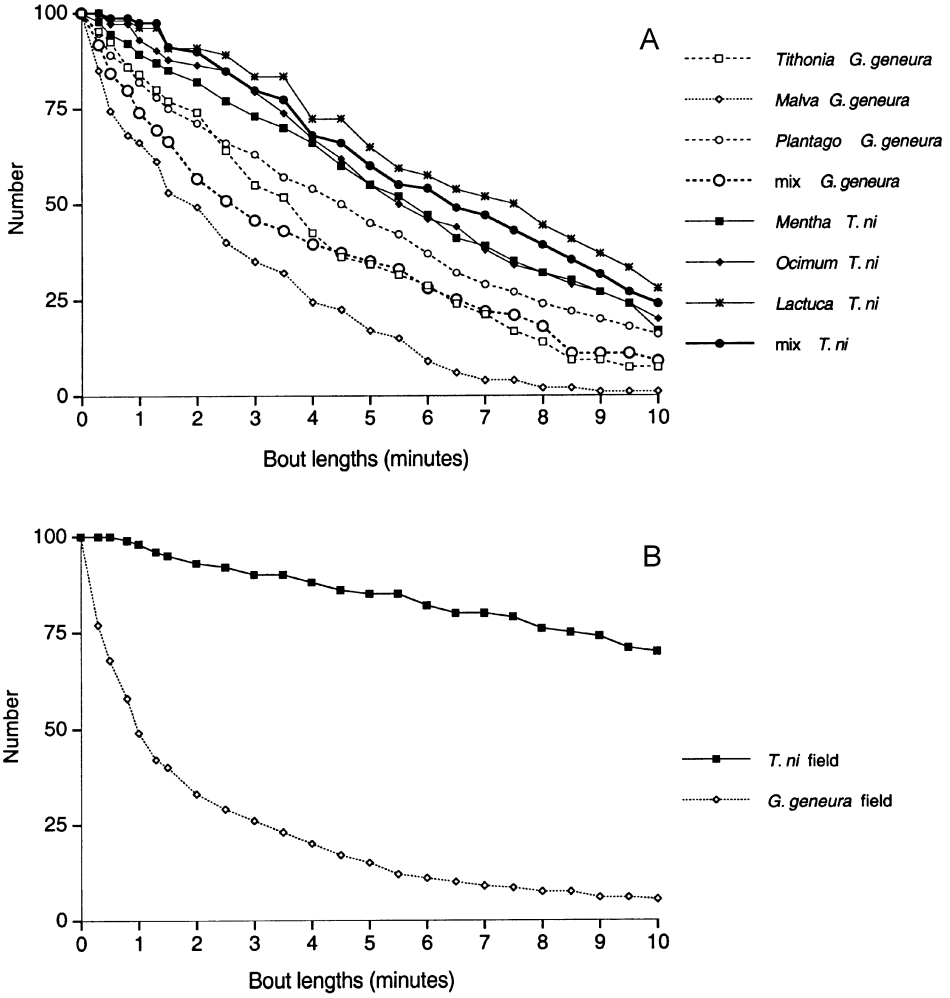


Fig. 3. Survivorship curves of feeding bout lengths of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in observations on various food plants. All values are presented as percentages so that treatments and species can be compared. 3a. Laboratory observations on three single plant species and a mixture for each species. 3b. Field observations with *T. ni* feeding on a single plant and *G. geneura* feeding on a mixture

suitable for development (SINGER 2000). By contrast, *T. ni* rarely rejected a plant encountered although encounters with new foods were relatively uncommon (Fig. 5a). This is demonstrated also by the number of switches between food eaten during observations (Fig. 5b). It reflects a generally higher level of activity and transitions between behavioral states (Fig. 5c). Interestingly, *G. geneura* caterpillars spent much of their resting time off the plants while *T. ni* caterpillars rested at their feeding sites (Fig. 5d).

T. ni caterpillars showed different host-related behaviors after being reared on single hosts, showing a preference for the rearing plant. Those reared on any one of the three test plants oriented toward, and made contact first with the rearing host when given a choice (Fig. 6a). Some individuals moved after an initial encounter, so that the first feeding bout was on a different plant, but in most cases, the first feeding bout of 30 seconds or more was on the rearing plant (Fig. 6b).

There was a marked difference in appearance of full grown *T. ni* caterpillars reared on different hosts. On the very bright green *Ocimum*, individuals were of the same bright green hue and rested lengthwise along the leaf; on the dark green *Mentha*, they were closely matched to the colour of veins along which they rested; on the grey *Encelia*, caterpillars were also grey, and rested in looped fashion on the leaf surface (see Fig. 7). The most extreme, on *Ocimum* and *Encelia farinosa,* are shown in Fig. 7. Clearly, the individuals are more cryptic on their rearing hosts, but would not be on the other host.

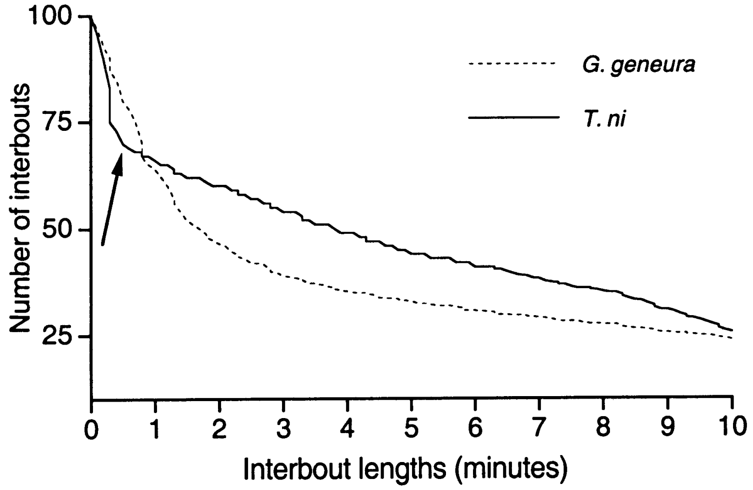
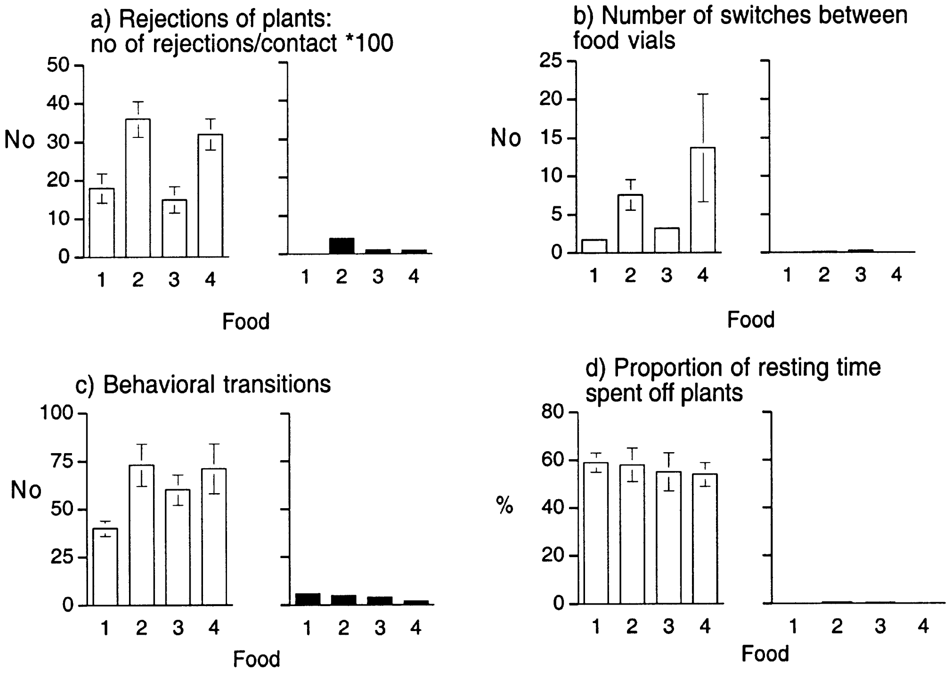


Fig. 4. Survivorship curves of interbout lengths of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in observations on various food plants in the laboratory. All values are presented as percentages so that species can be compared. Note that there is a break (arrow) in the curve for *T. ni* indicating two populations of interbouts, shorter ones that are within a meal and longer ones between meals

DISCUSSION

We have shown that caterpillars of two generalist species of Lepidoptera have highly contrasted foraging patterns in nature; one with great mobility and short feeding bouts on sequences of different foods, the other with restricted mobility, and clear fidelity to a single food. All of the behavioral parameters measured emphasize the marked difference in foraging strategy of these caterpillars, such



Food	*Gg*	*Tn*
1	*Tithonia*	*Mentha*
2	*Malva*	*Lactuca*
3	*Plantago*	*Ocimum*
4	MIX	MIX

□ *G. geneura* ■ *T. ni*

Fig. 5. Foraging details of last instar larvae of *Trichoplusia ni* and *Grammia geneura* in laboratory observations on various food plants. Mean and standard errors given. 5a. Rejections of host plants. 5b. Switches between food vials. 5c. Behavioral transitions: between feeding, walking and resting. 5d. Resting time on or off food plants

that the two cannot be considered together in foraging models, even though both are polyphagous species.

Of the three foods tested singly in the laboratory, *G. geneura* fed for very different periods on each one, with the time spent feeding on *Plantago* being three times that spent feeding on *Malva*. Growth and development of *G. geneura* is similar on these two plant species (SINGER 2000), and amounts eaten per unit time are similar (BERNAYS & SINGER 1998), suggesting that differences in feeding time reflect nutritional compensatory behavior. By contrast, *T. ni* spent similar amounts of time feeding (about 30%) on all three plant species tested although *Mentha* supported a significantly faster growth rate than either *Lactuca* or *Ocimum* (BERNAYS

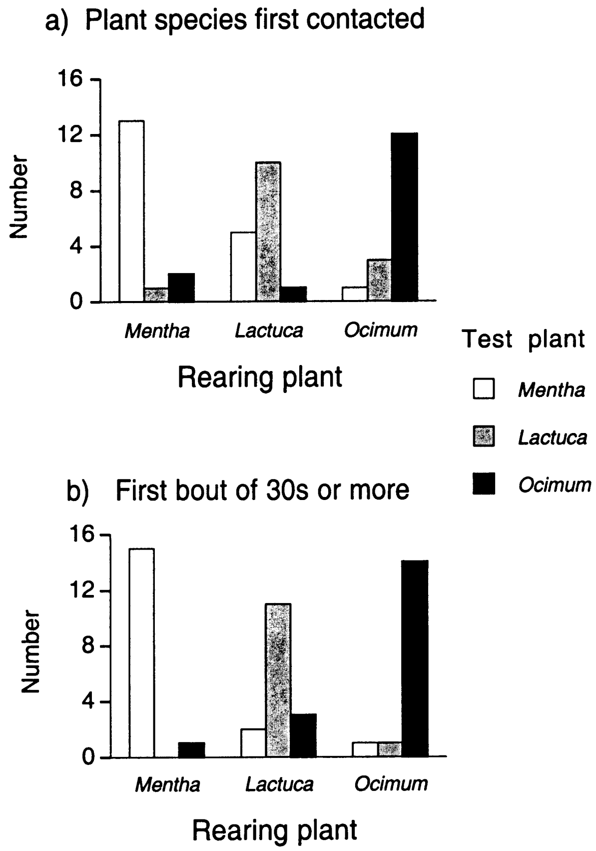


Fig. 6. Induction of preference in *Trichoplusia ni*: a = Plant species first contacted after rearing on *Mentha*, *Lactuca* or *Ocimum* and then given a choice of all three; b = Plant species upon which the first feeding bout is at least 30 seconds after rearing on *Mentha*, *Lactuca* or *Ocimum* and then given a choice of all three

& MINKENBERG 1997). Rates of food intake were not measured but all three plants are soft and eaten with apparent ease. There could be differences in rate of intake, however, relating to differences in palatability. Alternatively, this species may eat all acceptable foods maximally, optimizing intake rate rather than balancing specific nutrient requirements. Perhaps with its rapid development rate, obtaining sufficient nutrition for growth is generally a limiting factor, so that any foods that are of reduced nutrient value cannot be eaten in quantities that allow optimum development rate.

On the mixture of foods, both caterpillar species fed for 30% of the time in the laboratory. *G. geneura* individuals mixed the foods eaten and 30% is actually similar to the mean of the different individual values obtained with the three treatments in which single plant species were provided. *T. ni* caterpillars fed almost entirely on a single food, even when offered the mixture, and the time spent feeding was not different from that found with each of the treatments with a single food plant species.

Percent of time spent moving in laboratory experiments was also relatively high (at about 4% of time) in *G. geneura*, although much less than in the field. It was somewhat less on *Tithonia*, at least during the period of observation. Growth rates are relatively low on *Tithonia* (SINGER 2000) and it is possible that feeding on this plant also reduced activity for some reason. The limited time spent feeding on *Tithonia* was due to relatively few feeding bouts. The small proportion of time spent feeding on *Malva* however, was due to both few feeding bouts as well as their shorter duration. Since *Malva* contains high levels of protein (SINGER unpubl.), the reduced time spent feeding is further support for the idea that *G. geneura* limits intake when need is satisfied. Number of feeding bouts and the average lengths of feeding bouts were similar across foods, including the mix for *T. ni*, although protein levels varied (single measurements on pooled plant material gave approximate values of 4, 3 and 2% fresh weight for *Mentha* and *Ocimum* and *Lactuca* respec-

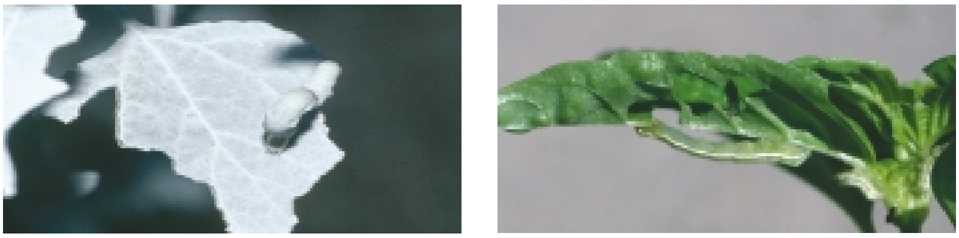


Fig. 7. Photographs of *Trichoplusia ni* reared in the field on either *Mentha* (left) or *Encelia* (right)

tively, BERNAYS unpubl.). The similarity in behavior on the three foods is consistent with a strategy of maximizing food intake irrespective of protein content.

On all foods tested in the lab *T. ni* bout lengths were longer than those of *G. geneura*, but the difference between the species is considerably greater when bout lengths in the field are examined. The reasons for this are not known, but several factors may contribute. Individuals reared in the laboratory experienced none of the disturbances from environmental change or presence of potential natural enemies that might enhance adaptive patterns of risk avoidance such as selective attention to food (causing longer bouts) in the case of *T. ni* (BERNAYS 2001) or movement away from damaged plants (causing shorter bouts) in the case of *G. geneura* (SINGER 2000). It is also possible that the state of the plants (cut vs growing) had an effect, for example if cut plants become less palatable to *T. ni* and more palatable to *G. geneura.* Finally, the arrangement of the foods may have contributed to the differences. In nature, we found *T. ni* on food resources of substantial size, where perhaps there is little else to perceive, whereas in the lab experiments, the bouquets of food were small. By contrast, in nature, *G. geneura* commonly feeds upon very small food items such as young seedlings or plants stunted under arid conditions, while the bouquets of food in the laboratory were often larger. What ever the reason, it demonstrates the importance of using field data as well as laboratory data in any study of foraging tactics.

With respect to interbout lengths there was a major difference between the two species. *T. ni* larvae showed a clustering of feeding bouts with small interbouts between them, as well as many longer interbouts. This distinction is shown by the survivorship analysis of interbout lengths, in which there is a marked break in the curve providing a criterion for describing two populations of interbout lengths, and thus meals, made up of more than one feeding bout. No such criterion was found for *G. geneura*. The differing patterns were brought about by the fact that most *T. ni* caterpillars often had one or more small interbouts following a long feeding bout. Thus a meal often consisted of a long bout followed by a short interbout and another short bout. The underlying cause of such a pattern may be the declining level of excitation during a meal as has been described for grasshoppers and various other animals (SIMPSON *et al.* 1988). The reason for not seeing this in *G. geneura* may relate to the overall pattern of short bouts and the related effects of relatively high levels of locomotor activity.

Larvae of *T. ni* rarely rejected a food after mouthpart contact, or switched to a new food when alternatives were available. When resting they stayed at or near the feeding site. By contrast, *G. geneura* commonly rejected plants, even those that were highly favorable and that led to relatively fast development when presented alone. Furthermore, *G. geneura* generally rested away from the food after a postprandial walk. The physiological bases for these differences are unknown, but perhaps involve variation in levels of, or sensitivity to, octopamine (ROEDER 1999). An ultradian rhythm in activity appears to be important in the postprandial locomotion of *G. geneura* (BERNAYS & SINGER 1998). The functional aspects of the differences can also only be speculated upon, but it is clear that *T. ni*, being cryptic on its food, would be better served to move little and feed decisively. The defensive strategies of *G. geneura* appear to involve chemical defenses (and possible aposematism – M. S. SINGER unpubl. results) and active movement away from plants they have recently fed upon.

Finally, *T. ni* exhibited strong induction of preference. That is, there was clear evidence that the rearing plant was strongly preferred over other acceptable alternatives. Previous work on this species is equivocal; LEE (1990) found evidence of induction while M. WEISS (unpubl. data) found none. In the present study induction was very clearly demonstrated by both orientation activity in the presence of a choice and acceptability after contact. The behavior of *G. geneura* precludes induction of this sort and the question remains, why does *T. ni* show induction? There is no clear answer and JERMY (1987) has even questioned the adaptive value of the phenomenon in general.

Many have suspected that induction is a phenomenon whose function is explained physiologically. Thus, if detoxification enzymes or specific proteases are induced by experience of certain metabolites or proteins, it is surely safer and more economical to remain with one host plant species. Although such enzymic induction is well known (YU 1986), its adaptive value is still uncertain. Growth may be improved by staying with the rearing host (e.g., KAROWE 1989), or it may not (e.g.,ESCADOR 1993). Certainly, induction of specific detoxification enzymes caused by ingestion of a particular toxin may then allow a food containing the toxin to be eaten with impunity (GLENDINNING & SLANSKY 1995, SNYDER & GLENDINNING 1996), and this alone may be the functional value of induced enzyme production.

Other aspects of the biology of the insect may be relevant however, though a survey of the literature on induction provided little help: among the species where it has been reported as absent, weakly present, or strong, we found no correlates with respect to phylogeny, diet breadth, egg clustering, or crypsis [the analysis involved the species reported in JERMY (1987) and all references found since, see appendix 1]. However, among the reports available it seems that most lepidopteran species tested show it to some extent, at least in some populations. In the behavior of *G. geneura* and other food-mixing species we have reason to believe that induction of food preference does not occur. It is possible that sequestering the larvae with single high quality foods may induce an increased preference for that food, but in nature such restriction does not occur. Analyses of bout lenghts in the field also shows that these decline on a food that is eaten for several bouts, but that longer bouts occur following a switch to a new food (SINGER 2000). This further implies an absence of induced preference for the experienced food.

We suggest that induction has some general value in focusing of attention on foods currently available (BERNAYS 2001) but that, in the case of *G. geneura*, where the problem of predation is apparently low, other factors mitigate against induction. For example, mixing may be important for reducing the risk of ingesting high levels of a toxin or of feeding extensively on a plant with a nutrient imbalance. Such factors may be important in an exceedingly diverse plant community with great chemical variability among species (SINGER 2000).

Caterpillars are extremely vulnerable to predation and parasitism (e.g., HEINRICH 1993, MONTLLOR & BERNAYS 1993, WESELOH 1993, BERNAYS 1997) with mortality levels that may exceed 99.5% (e.g., MIRA & BERNAYS 2002), and the relationship between caterpillars and their host plants is surely influenced by higher trophic levels (e.g., BERNAYS 1988, BOWERS 1993, STAMP & WILKINS 1993, DYER & FLOYD 1993, SINGER 2000). It is important therefore to consider the foraging strategies in the light of risk from natural enemies, and the tactics used by the caterpillar species for avoidance of predation and parasitism.

Grammia geneura and *Trichoplusia ni* provide a marked contrast in their adaptations for avoiding predation, which are probably not unrelated to foraging strategy. *G. geneura* is a member of the subfamily Arctiinae in which species are often aposematic, and larvae are all hirsute. We have no information on chemical defenses of *G. geneura*, although there are indications of unpalatability (SINGER 2000). In addition, some secondary metabolites stimulate the same taste cell as sugars and amino acids (BERNAYS *et al.* 2000), suggesting that they are of particular value. Larvae are often aggregated and conspicuous to humans. From these characters we believe that *G. geneura* is aposematic and that this allows it to be conspicuously mobile and protected from much predator attack.

In contrast, *T. ni* typifies many species of cryptic caterpillar with its smooth cuticle and general green coloration. Its behavior appears to be cryptic also. On larger leaves with a conspicuous main vein, such as *Ocimum*, it commonly rests along the vein; on plants with smaller leaves with a network of veins, such as *Mentha,* it more often rests in the looped position. It is acceptable to many predators (BERNAYS 1988, BERNAYS & CORNELIUS 1989) and parasitoids (FLINT 1987) so that its only defense is to be inconspicuous. For this to be effective, mobility must be restricted (HEINRICH 1993) and feeding should be both rapid and efficient (BERNAYS 1997). Food mixing is not compatible with these constraints.

Restricted acceptability of potential foods is thought to improve decisiveness, and thus improve feeding efficiency and crypsis in specialists (BERNAYS 1996, 1998). A similar benefit may accrue to generalists that show an induction of preference. In addition, if feeding on different plant species can lead to morphological changes that enhance crypsis, as we found here, one would expect selection for behavior that improves fidelity to the plant already experienced. Such morphological plasticity has been reported in other contexts (POULTON 1885, GRAYSON & EDMONDS 1989, GREENE 1989), but it would be interesting to examine its occurrence in relation to the occurrence of induced preference in other species. As well as visual crypsis, chemical crypsis has been demonstrated (ESPELIE & BROWN 1990) and it is known that the chemistry of the caterpillar cuticle varies with its food in *Manduca sexta* (ESPELIE & BERNAYS 1989, CORNELIUS & BERNAYS 1995). Recently, this has been demonstrated to be important in predator avoidance (PORTUGAL 2000). There is thus the possibility that induced preference for a particular food plant may be accompanied by chemical crypsis.

In conclusion, we emphasize a major contrast in foraging strategies of the caterpillars of two generalist species of Lepidoptera, including the propensity for induction of preference. The contrast suggests a relationship with several aspects of the biology of the two species, including growth rates and detoxification needs on the one hand, and divergent strategies for avoiding risk of attack from natural enemies on the other. Whether the two species fit into two clear alternative categories will require studies on a range of other polyphagous species.

REFERENCES

BERNAYS, E. A. (1988) Host specificity in phytophagous insects: selection pressure from generalist predators. *Entomol. Exp. Appl.* **49**: 131–140.

BERNAYS, E. A. (1996) Selective attention and host-plant specialization. *Entomol. Exp. Appl.* **80**: 125–131.

BERNAYS, E. A. (1997) Feeding by caterpillars is dangerous. *Ecol. Entomol.* **22**: 121–123.

BERNAYS, E. A. (1998) The value of being a resource specialist: behavioral support for a neural hypothesis. *Amer. Nat.* **151**: 451–464.

BERNAYS, E. A. (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *Annu. Rev. Entomol.* **46**: 703–727.

BERNAYS, E. A. & CORNELIUS, M. L. (1989) Generalist caterpillar prey are more palatable than specialists for the generalist predator Iridomyrmex humilis. *Oecologia* **79**: 427–430.

BERNAYS, E. A. & MINKENBERG, O. P. J. M. (1997) Insect herbivores: different reasons for being a generalist. *Ecology* **78**: 1157–1169.

BERNAYS, E. A. & SINGER, M. S. (1998) A rhythm structuring foraging behavior in a polyphagous caterpillar. *Physiol. Entomol.* **23**: 295–302.

BERNAYS, E. A., BRIGHT, K. L., GONZALEZ, N. & ANGEL, J. (1994) Dietary mixing in grasshoppers: tests of two hypotheses. *Ecology* **75**: 1997–2006.

BERNAYS, E. A., CHAPMAN, R. F. & SINGER, M. S. (2000) Sensitivity to chemically diverse phagostimulants in a single gustatory neuron of a polyphagous caterpillar. *J. Comp. Physiol.* **186**: 13–19.

BOWERS, M. D. (1993) Aposematic caterpillars: life-styles of the warningly colored and unpalatable. Pp. 331–371. *In* STAMP, N. E. & CASEY, T. M. (eds) *Caterpillars: Ecological and evolutionary constraints on foraging*, Chapman and Hall, New York.

CHAMBERS, P. G., SWORD, G., ANGEL, J. E., BEHMER, S. & BERNAYS, E. A. (1996) Foraging by generalist grasshoppers: two different strategies. *Anim. Behav.* **52**: 155–165.

CORNELIUS, M. L. & BERNAYS, E. A. (1995) The effect of plant chemistry on the acceptability of caterpillar prey to a predatory ant, Iridomyrmex humilis. *J. Insect Behav.* **8**: 579–594.

DETHIER, V. G. (1988) The feeding behavior of a polyphagous caterpillar (Diacrisia virginica) in its natural habitat. *Can. J. Zool.* **66**: 1280–1288.

DYER, L. A. & FLOYD, T. (1993) Determinants of predation on phytophagous insects: the importance of diet breadth. *Oecologia* **96**: 575–582.

ESPELIE, K. E. & BERNAYS, E. A. (1989) Diet-related differences in the cuticular lipids of Manduca sexta larvae. *J. Chem. Ecol.* **15**: 2003–2018.

ESPELIE, K. E. & BROWN, J. J. (1990) Cuticular hydrocarbons of species which interact on four trophic levels: apple, Malus pumila; codling moth, Cydia pomonella; a parasitoid, Ascogaster quadridentata; and a hyperparasite, Perilampus fulvicornis. *Comp. Biochem. Physiol.* **95B**: 131–136.

FLINT, M. L. (1987) *Integrated pest management for cole crops and lettuce*. University of California Division of Agriculture and Natural Resources Publication 3307.

FOX, L. R. & MORROW, P. A. (1981) Specialization: species property or local phenomenon? *Science* **211**: 887–893.

GASTON, K. J., REAVEY, D. & VALLADARES, G. R. (1991) Changes in feeding habit as caterpillars grow. *Ecol. Entomol.* **16**: 339–344.

GLENDINNING, J. I. & SLANSKY, F. (1995) Consumption of a toxic food by caterpillars increases with dietary exposure: support for a role of induced detoxification enzymes. *J. Comp. Physiol. A* **176**: 337–345

GRAYSON, L. & EDMONDS, M. (1989) The causes of colour and colour change in caterpillars of the poplar and eyed hawk moths [Lathoe populi and Smerinthus ocellata]. *Biol. J. Linn. Soc.* **37**: 263–279.

GREENE, E. (1989) A diet-induced larval polymorphism in a caterpillar. *Science* **243**: 643–646.

HAGELE, B. F. & ROWELL-RAHIER, M. (1999) Dietary mixing in three species of generalist herbivores: nutrient complementation or toxin dilution. *Oecologia* **119**: 521–533.

HEINRICH, B. (1993) How avian predators constrain caterpillar foraging. Pp. 224–247. *In* STAMP, N. E. & CASEY, T. M. (eds) *Caterpillars; Ecological and evolutionary constraints on foraging.* Chapman and Hall, New York.

JERMY, T. (1987) The role of experience in host-plant selection by phytophagous insects. Pp. 142–158. *In* CHAPMAN, R. F., BERNAYS, E. A. & STOFFOLANO, J. G. (eds) *Perspectives in chemoreception and behavior.* Springer-Verlag, New York.

JERMY, T., HANSON, F. E. & DETHIER, V. G. (1968) Induction of specific food preference in lepidopterous larvae. *Entomol. Exp. Appl.* **11**: 211–223.

JONES, R. E. (1977) Search behaviour: a study of three caterpillar species. *Behaviour* **60**: 237–259.

LANDOLT, P. J. & MOLINA, O. (1996) Host-finding by cabbage looper moths (Lepidoptera: Noctuidae): learning of host odor upon contact with host foliage. *J. Insect Behav.* **9**: 899–908.

KAROWE, D. N. (1989) Facultative monophagy as a consequence of prior feeding experience: behavioral and physiological specialization in Colias philodice larvae. *Oecologia* **78**: 106–111.

LEE, J. C. (1990) *Learning and nutritional aspects of individual polyphagy in the insect herbivores Schistocerca americana, Dactylotum variegatum and Trichoplusia ni.* Dissertation. University of California, Berkeley, California, USA.

MERZ, E. (1959) Pflanzen und Raupen. Über einige Prinzipien der Futterwahl bei Gross-Schmetterlingsraupen. *Biol. Zentrbl.* **78**: 152–188.

MIRA, A. & BERNAYS, E. A. (2002) Tradeoffs in host use in Manduca sexta: natural enemies vs plant quality. *Oikos* [in press]

MONTLLOR, C. & BERNAYS, E. A. (1993) Invertebrate predators and caterpillar foraging. Pp. 170–202. *In* STAMP, N. E. & CASEY, T. M. (eds) *Caterpillars; Ecological and evolutionary constraints on foraging.* Chapman and Hall, New York.

NOLDUS, L. P. J. J. (1991) The Observer: a software system for collection and analysis of observational data. *Beh. Res. Methods Instrum., 7 Computers*, **23**: 415–429.

PESCADOR, A. R. (1993) The effects of a multispecies sequential diet on the growth and survival of tropical polyphagous butterflies. *Entomol. Exp. Appl.* **67**: 15–24.

PORTUGAL, A. H. A. (2000) Abstract. International Meeting of Chemical Ecology.

POULTON, E. B. (1885) The essential nature of the colouring of phytophagous larvae [and their pupae] with an account of some experiments upon the relation between the colour of the larvae and that of their food plants. *Proc. R. Soc.* **237**: 269–315.

ROEDER, T. (1999) Octopamine in invertebrates. *Progr. Neurobiol.* **59**: 533–561.

SIMPSON, S. J. (1982) Patterns in feeding: a behavioural analysis using Locusta migratoria nymphs. *Physiol. Entomol.* **7**: 325–336.

SIMPSON, S. J., SIMMONDS, M. S. J., WHEATLEY, A. R. & BERNAYS, E. A. (1988) The control of meal termination in the locust. *Anim. Behav.* **36**: 1216–1227.

SINGER, M. S. (2000) *Ecological maintenance of feed-mixing in the woolly bear caterpillar Grammia geneura (Strecker)(Lepidoptera: Arctiidae.)* Ph.D. Dissertation, University of Arizona, Tucson, Arizona, USA.

SNYDER, M. J. & GLENDINNING, J. I. (1996) Causal connection between detoxification enzyme activity and consumption of a toxic plant compound. *J. Comp.Physiol. A* **179**: 255–261.

STAMP, N. E. & WILKINS, R. T. (1993) On the cryptic side of life: being unapparent to enemies and the consequences for foraging and growth of caterpillars. Pp. 283–330. *In* STAMP, N. E. & CASEY, T. M. (eds) *Caterpillars; Ecological and evolutionary constraints on foraging.* Chapman and Hall, New York.

SUTHERLAND, D. W. S. & GREEN, G. L. (1984) cultivated and wild host plants. Pp. 1–13. *In* LINGREN, P. D. & GREENE, G. L. (eds) *Suppression and management of cabbage looper populations.* USDA Tech. Bull. 1684.

THOMPSON, J. N. (1994) *The coevolutionary process.* Chicago Univ. Press, Chicago.

WESELOH, R. M. (1993) Potential effects of parasitoids on the evolution of caterpillar foraging behavior. Pp. 203–223. *In* STAMP, N. E. & CASEY, T. M. (eds) *Caterpillars; Ecological and evolutionary constraints on foraging.* Chapman and Hall, New York.

YU, S. J. (1986) Consequences of induction of foreign compound-metabolizing enzymes in insects. Pp. 153–174. *In* BRATTSTEN, L. B. & AHMAD, S. (eds) *Molecular aspects of insect–plant associations*. Plenum Press, New York.

APPENDIX 1

Analysis of lepidopteran species tested for induction of preference includes all species listed in JERMY (1987) and the following:

Colias philodice (KAROWE 1989)
Thyridopteryx ephemeraeformis (WARD *et al.* 1990)
Diacrisia virginica (DETHIER 1988)
Pseudaletia unipuncta (USHER *et al.* 1988)
Pieris rapae (RENWICK & HUANG 1995)
Mamestra brassicae (JERMY *et al.* 1987)
Vanessa cardui, *Heliothis virescens* (BERNAYS unpubl.)

DETHIER, V. G. (1988) Induction and aversion-learning in polyphagous arctiid larvae (Lepidoptera) in an ecological setting. *Can. Entomol.* **120**: 125–131.

JERMY, T., HORVÁTH, J. & SZENTESI, Á. (1987) The role of habituation in food selection of lepidopterous larvae: the example of Mamestra brassicae. Pp. 231–236. *In* LABEYRIE, V., FABRE, G. & LACHAISE, D. (eds) *Insects-Plants*. Junk, Dordrecht.

KAROWE, D. N. (1989) Facultative monophagy as a consequence of prior feeding experience: behavioral and physiological specialization in Colias philodice larvae. *Oecologia* **78**: 106–111.

RENWICK, J. A. A. & HUANG, X. P. (1995) Rejection of host plant by larvae of cabbage butterfly: diet-dependent sensitivity to an antifeedant. *J. Chem. Ecol.* **21**: 465–475.

USHER, B. F., BERNAYS, E. A. & BARBEHENN, R. V. (1988) Antifeedant tests with larvae of the caterpillar of Pseudaletia unipuncta: variability of behavioral response. *Entomol. Exp. Appl.* **48**: 203–212.

WARD, K. E. RAMASWAMY, S. B. & NEBEKER, T. E. (1990) Feeding preferences and their modification in early and late instar larvae of the bagworm, Thyridopteryx ephemeraeformis (Lepidoptera: Psychidae). *J. Insect Behav.* **3**: 785–796.

Received 31th March, 2001, accepted 20th December, 2001, published 14th February 2002