

METABOLIC COST OF CHANGES IN DIET AND NEUTRALIZATION OF ALLELOCHEMICS

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Larvae of *Pieris brassicae* and *Mamestra brassicae* use food on which they have been grown more efficiently than a novel food. This physiological adaptation to a certain food may be regarded as a functional reason underlying changes in food selection behaviour due to previous experiences ("preference induction").

Larvae of *Manduca sexta* show a reduced efficiency of digestion when the diet contains nicotine or atropine, alkaloids occurring in acceptable food plants. It is concluded that insects may spend a considerable amount of energy detoxifying host-plant specific allelochemicals.

The fastidious food plant preferences shown by most phytophagous insects form one of the central themes of insect-host plant studies. Only recently students of feeding behaviour have realized that food preferences may be modified by previous feeding experience. Jermy *et al.* (1968) showed that some lepidopterous larvae develop a predilection for the host plant species on which the individuals have fed for some time. Other examples of preference induction are found in Coleoptera (Phillips, 1977) and Phasmida (Cassidy, 1978).

This learning behaviour may be of general occurrence among insects. What is its function? An attractive hypothesis would be to relate the behavioural conservatism to physiological consequences of a change in diet. Conceivably an insect adapts and gradually optimizes its digestive system to the food to which it is exposed for some time. It follows that it would utilize a novel type of food less efficiently. When there is a premium on using as little food as possible, it would pay to evolve a food preference behaviour which keeps the insect on the host plant species from which it has fed for some time. The first hypothesis we have tested is: insects grown on a certain food type utilize this food more efficiently than conspecifics which have had no experience with this food.

Natural food plants contain not only nutrients, but also allelochemicals. The latter compounds presumably serve as a defence system to deter herbivores. This hypothesis launched by several authors and elegantly expressed by Fraenkel (1959) necessitates that those insect species which adopt a certain plant as a food source have to neutralize the toxic effects of its allelochemicals. This barrier is presumably of considerable importance, since the interaction in nature has been long and intense. Any insect which succeeded in overcoming this chemical barrier has

probably to pay for it continuously. Some recent reports (e.g., Erickson & Feeny, 1974; Dahlman, 1977) discuss the metabolic cost of neutralizing allelochemicals which occur in *non*-host plants, but knowing the energy spent on detoxification of host-plant specific allelochemicals is also essential to appreciate certain physiological pressures on the development of insect-host relationships. The second hypothesis we set out to test is: insects allocate a sizeable amount of energy to neutralize allelochemicals, which occur in their usual host plants.

MATERIALS AND METHODS

Two oligophagous species, *Manduca sexta* (Johan.) (Sphingidae, Lepidoptera) and *Pieris brassicae* L. (Pieridae, Lepidoptera), and one polyphagous insect, *Mamestra brassicae* L. (Noctuidae, Lepidoptera) were obtained from laboratory cultures. All experiments were performed on last larval instars: for *Manduca* and *Pieris* the 5th instar, and for *Mamestra* the 6th instar. The insects were grown on artificial diets (*Manduca*: Hoffman *et al.* 1966; *Pieris*: Ma, 1972; *Mamestra*: Nagy, 1970. The *Mamestra* diet was enriched by 0.4% w/w Vitamin Diet Fortification mixture and 0.4% v/w linseed oil per 1000 g of diet) or plants till their last larval moult. The following utilization indices as defined by Waldbauer (1968) were determined: approximate digestibility (AD: food digested/food ingested), efficiency of conversion of ingested food (ECI: growth/food ingested), efficiency of conversion of digested food (ECD: growth/food digested). Insect growth refers to dry weight difference between newly moulted last instar larvae and young pupae. The insect cultures were maintained and the experiments carried out at 25°. Atropine was obtained from Fluka AG, nicotine from Baker Chemical and sinigrin from Aldrich.

RESULTS

The efficiency of converting plant material into body tissues appears to be higher in *Pieris* larvae when the insects were physiologically adapted to the type of food by previous exposure (Table I, Exp. 1 and 2). *Mamestra* larvae also show a higher ECD in Exp. 3. (Table I) and a higher AD (Exp. 4) on food to which they were accustomed, but Exp. 3 showed an increased AD on the novel food.

The effects of allelochemicals on food utilization are shown in Exp. 5 and 6 (Table I). *Manduca* larvae show a reduction in their ECD when the diet contains atropine or nicotine and the latter compound likewise affects ECI. These alkaloids, which occur in their host plants, do not seem to influence AD. In the case of *Mamestra* no discernible effects of sinigrin is found.

DISCUSSION

The hypothesis that insects utilize food to which they are adapted more efficiently than a novel food is supported by the results given, though the data

TABLE I

Utilization by last instar larvae of novel food compared with food previously experienced and the effects of host-plant specific allelochemicals, on *Pieris brassicae*, *Mamestra brassicae* and *Manduca sexta*. Nic. = nicotine. Atr. = atropine. Sin. = sinigrin. Significant differences as compared to the controls (insects since hatching continuously exposed to the same type of food) are indicated by * ($P < 0.05$) and ** ($P < 0.01$).

Exp. no.	Larval food	Test food	Insect species	N	Growth (mg)	AD \pm S.E.	ECI \pm S.E.	ECD \pm S.E.
1	cabbage	cabbage	<i>Pieris</i>	14	70	42.8 \pm 1.7	23.6 \pm 0.7	56.6 \pm 3.4
	nasturtium	cabbage		13	68	41.2 \pm 2.1	16.6 \pm 0.5**	42.0 \pm 2.8**
3	cabbage	cabbage	<i>Pieris</i>	12	70	36.7 \pm 1.5	23.0 \pm 0.7	64.7 \pm 4.3
	diet	cabbage		15	73	26.1 \pm 0.7**	18.0 \pm 0.3**	70.2 \pm 2.3
	cabbage	cabbage		13	80	38.4 \pm 0.8	17.9 \pm 0.4**	47.0 \pm 1.5**
4	(var. conica)							
	diet	diet	<i>Mamestra</i>	16	93	45.8 \pm 1.0	21.2 \pm 2.1	47.1 \pm 2.3
5	cabbage	cabbage	<i>Mamestra</i>	15	91	48.2 \pm 0.3*	18.8 \pm 0.2	39.1 \pm 0.5**
	diet	cabbage		20	91	40.0 \pm 0.8	20.5 \pm 0.3	51.7 \pm 1.2
6	diet	diet	<i>Manduca</i>	19	70	36.8 \pm 0.6**	19.5 \pm 0.6	53.1 \pm 1.5
	diet	diet		16	951	61.7 \pm 0.7	29.9 \pm 0.3	48.5 \pm 0.4
	diet	diet + 0.1% Nic.		17	906	58.6 \pm 0.6	27.5 \pm 0.9*	47.1 \pm 0.9
	diet	diet + 0.5% Nic.		15	962	62.9 \pm 0.6	25.3 \pm 0.2**	40.3 \pm 0.5**
6	diet	diet + 0.1% Atr.	<i>Mamestra</i>	17	875	64.0 \pm 0.7	29.1 \pm 0.6	45.5 \pm 0.9**
	diet	diet + 0.1% Sin.		18	124	46.4 \pm 0.4	21.5 \pm 0.3	46.4 \pm 0.8
	diet			15	116	47.0 \pm 1.6	22.0 \pm 0.9	46.9 \pm 1.0

available are too limited to allow a definite conclusion.

An increase of the ECI when the insect feeds continuously on the same food could have an ecological advantage: a smaller amount of plant tissue is required for growth than on a mixed diet. The insect eats as little as necessary from its host, a feature of an optimal predator-food relationship. As insects on different hosts may show differences in their intestinal enzyme concentrations (Ishaaya & Swirski, 1976), enzyme induction in the gut probably enhances digestion.

Nicotine and atropine markedly reduce the efficiency of digestion, or, in other words, their neutralization requires a considerable amount of extra food. A maximum reduction of 15% is seen at concentrations used in our experiments, which do occur in plants. Even differences of a few percent (which would escape our attention in the experimental procedure used) or less are of significance in an ecological context. Therefore, the big differences observed in *Manduca* are not nullified by the fact that digestion in *Mamestra* is imperceptibly affected by sinigrin.

Since several physiological mechanisms have been developed which render *Manduca* resistant to solanaceous alkaloids, it is impossible to indicate where the extra energy consumed is used. Induction of detoxifying enzymes (Brattsten & Wilkinson, 1973) possibly accounts for part of the increased food requirements.

It is thus concluded that food selection characteristics which are based on previous experience of the individual insect are correlated with its physiological capacity to utilize the food. It remains to be tested whether these two processes in some way interact within the individual via a feedback from the insect's physiological state on its feeding behaviour. Alternatively, selection may have favoured the combination of plasticity of food selection behaviour and efficiency of the digestive process and the link between them is entirely genetic.

RÉSUMÉ

LE PRIX MÉTABOLIQUE DU CHANGEMENT DE DIÈTE ET DE LA NEUTRALISATION DE PRODUITS ALLÉLOCHIMIQUES

Les chenilles de *Pieris brassicae* et de *Mamestra brassicae* digèrent la nourriture où elles ont poussé d'une manière plus efficace qu'un nouveau genre de nourriture.

Cette adaptation physiologique à la nourriture est probablement la raison fonctionnelle qui est à la base de changements dans le comportement du choix alimentaire qui sont en rapport avec des expériences antérieures ("induction d'une préférence").

L'efficacité de la digestion dans les chenilles de *Manduca sexta* subit une diminution, quand on ajoute à leur aliment artificiel de la nicotine ou de l'atropine, des alcaloïdes qu'on trouve dans des plantes nutritives acceptables. Voilà pourquoi nous en venons à la conclusion que les insectes consacrent parfois une quantité considérable d'énergie à la détoxification de matières allélochimiques qui se trouvent dans leur plante-hôte.

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