Leaf-scratching – a specialized behaviour of danaine butterflies (Lepidoptera) for gathering secondary plant substances

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Danaine butterflies have long been recognized to be attracted to and "feed" at withered plants of certain genera (mainly of the Boraginaceae, Asteraceae, and Fabaceae) (for refs. see e.g. Pliske 1975, Boppré 1978, 1981), which are characterized by the presence of pyrrolizidine alkaloids (PAs). The butterflies apply from their proboscides a fluid capable of dissolving PAs and then reimbibe it. The uptake of PAs does not provide energy – the males require these secondary plant substances as precursors for the biosynthesis of a pheromone component (for review see Boppré 1978). In addition, both sexes store them (Edgar et al. 1976, 1979, Boppré unpubl.), apparently for defense (see Rothschild et al. 1979, Eisner 1980, Conner et al. 1981, Boppré in prep.). Thus, the Danainae are typical pharmacophagous insects (cf. Boppré 1983).

Apart from danaines, other Lepidoptera (e.g. many Ithomiinae, Arctiidae, Ctenuchiidae; e.g. Pliske 1975, Boppré 1981) and also Coleoptera (*Gabonia* (Chrysomelidae); Boppré and Scherer 1981) and Orthoptera (*Zonocerus* (Pyrgomorphidae); Boppré et al. 1983) have been found to gather PAs from dry plants, and some species of each of these orders are known to sequester PAs obtained with their larval food. These independent relationships between insects and PA-containing plants appear to represent a model system for comparative studies on co-evolution and adaptation (cf. Boppré and Schneider 1982).

For danaines, not only withered plants but also nectar and damaged plants are sources of PAs, and they may even imbibe from carcasses of PA-storing insects (Owen 1971, Bernays et al. 1977, Boppré 1981 and unpubl.). Danaine butterflies have also been reported scratching and sucking at living plants: Johnston and Johnston (1980 and pers. comm.) in Hong Kong observed species of *Danaus* and *Euploea* scratching leaves of *Crotalaria retusa* (Fabaceae) and imbibing the sap which oozed out. Similar behaviour has been noted in Australia by Sankowsky (in: Edgar and Culvenor 1975) at leaves of *Parsonsia straminea* (Apocynaceae), and on the Loyalty Islands, Edgar (pers. comm.) saw *Danaus affinis* scratching a leaf of *Tournefortia argentia* (Boraginaceae).

Field observations from East Africa, reported here, provide some details on danaine butterflies' ability to damage fresh plant tissue in order to gain access to and obtain PAs. At the end of the rainy season in May 1982, in a valley near the Shimba Hills (Kwale District, Coast Province) in Kenya, large assemblages of *Tirumala petiverana* (Doubleday), together with several *Danaus chrysippus* (L.) and *Amauris ochlea* (Boisduval) were found on living plants of *Heliotropium pectinatum* Vaupel¹ (Boraginaceae) (Fig. 1). The butterflies, most if not all of which were males, congregated and imbibed sap from damaged parts of fresh leaves. This damage varied from a few surface scratches to whole sections of leaf torn away (Figs. 2–7). It was clearly seen (and documented on super-8 movie film) that this damage was caused by the butterflies themselves: from time to time they made scratching movements with a midleg (the fore-legs of Danainae are reduced as in all Nymphaloidea), which injured the leaf surface. Simultaneously, the butterflies sucked up oozing sap but sometimes they applied and reimbibed droplets with their proboscises – as they do at dry plants.

Almost all leaves of the *Heliotropium* population had holes of varying diameter (1–4 mm) made by flea beetles (Longitarsus gossypii Bryant, Chrysomelidae, Alticinae) (Figs. 5-7). Close inspection of leaves which were only slightly damaged by butterflies revealed that the danaines had scratched radially from these holes, and it appears that the edges of the holes release the chemical cues responsible for attraction of danaines, i.e. PAs or breakdown products of PAs, respectively. However, the butterflies usually did not scratch and suck individually but rather occurred in groups. Also, they attacked certain plants only. Very likely, scratching of a 'pioneer' butterfly at any beetle hole leads to an increase of PA-release, thus increasing the attractiveness of that particular leaf. Furthermore, it was apparent - as at dry plants - that conspecifics are an additional, visual attractant. In such ways, aggregations build up and the butterflies eventually scratch irregularly and affect neighbouring leaves. Such loci were found to be visited for several successive days, and within three weeks of observation, several plants were newly attacked. Numerous twigs with scratched and entirely wilted leaves were seen which were not attractive for butterflies; apparently these had previously served as PA-sources.

Rhodogastria moths (Arctiidae) take advantage of danaine-damaged plants. Nocturnal observations revealed that the moths apparently preferred and assembled at those *Heliotropium* plants which had been recently scratched by danaines (Fig. 3). *Rhodogastria* were not seen to exhibit scratching behaviour themselves.

¹ Since the taxonomy and nomenclature of the genus *Heliotropium* is in a dubious state, the identification is provisional. Reference specimens are deposited at the Royal Botanical Gardens, Kew



Fig. 1. *Tirumala petiverana* assembling, scratching and sucking at *Heliotropium pectinatum*

Fig. 2. Male *T. petiverana* ingesting PAs from a scratched leaf of *H. pectinatum*

Fig. 3. *Rhodogastria spec.* ingesting PAs from a *H. pectinatum* leaf previously damaged by danaine butterflies

Fig. 4. *H. pectinatum* damaged by danaine butterflies

Figs. 5–7. Herborized leaves of *H. pectinatum* viewed from upper side to show holes made by *Longitarsus gossypii* and damage caused by scratching of *T. petiverana.* Scale bars: 1 cm

Leaves scratched with fingernails or damaged by squeezing, instantly attracted Danainae and *Rhodogastria*, respectively, but intact leaves offered simultaneously were always neglected. This demonstrates that *Heliotropium* leaves must be either freshly damaged or withered in order to attract Lepidoptera and elicit PA-foraging behaviour. Although in my field observations the *Longitarsus* beetles served an important role for the butterflies, any other PA-plant feeder which injures the plants will generate potential loci for danaine scratching.

As already mentioned, Danainae are usually seen gathering PAs from withered plants, and at the Shimba Hills observation area not all butterflies scratched fresh leaves – many went for dry plants. Since a variety of factors influences the attractive potency of withered plant material (cf. Boppré 1981), there is no way of conducting quantitative preference tests in order to judge if fresh leaves are better or worse PA-sources for the butterflies than dry plants. However, my observations indicate the existence of a previously unrecognized motor pattern for scratching plant tissue by Danainae, which is yet another adaptation for obtaining PAs and which again underlines the importance of PAs for these insects. Furthermore, the observations provide strong circumstancial evidence that it is only the mechanical accessibility of PAs, and not a chemical process in the course of wilting, which makes withered plants attractive as PA-sources for insects with sucking mouthparts, while fresh (intact) plants are not.

In contrast to Danainae gathering PAs from withered plants, when they usually sit in quiescent groups, at the scratching sites butterflies whirl around in clouds, buffet each other, alight and chase others away, giving the impression of strong competition for the best position at the plant. Danaines at all PA-sources are readily disturbed, flying up in response to passing objects – but then return immediately. In none of my very many observations of butterflies gathering PAs in the field or in the greenhouse have I seen even an indication of 'intoxication', and I must contradict Rothschild and Marsh (1978), who reported "violent sexual arousal" of male *Danaus plexippus* in a greenhouse while feeding on nectar of *Senecio* (which contains PAs; Deinzer et al. 1977), and suggested that PAs have a direct aphrodisiacal effect on insects.

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