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Increase in larval foodplant diversity during a population explosion of the moth, *Panaxia dominula* (L.) (Lepidoptera : Arctiidae)

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Summary

For over 50 years the annual population size of a colony of *Panaxia dominula* (L.) fluctuated from a low of about 200 to a high of about 18,000, but in 1991 and again in 1992 there was a population explosion to about 100,000. A similarly high population occurred at another colony 5 km away. The larvae normally feed on *Symphytum officinale* and a few other species of plants, but during the population explosion they utilised 43 species belonging to 28 families. At one of the colonies many larvae fed on the spore-bearing cones of *Equisetum*, a genus rarely utilised by Lepidoptera, and totally unrelated to the normal food-plants. It is suggested that although the observations reported are not unexpected, there has rarely been an opportunity to document the phenomenon because of a scarcity of long-term population estimates of herbivorous insects.

Résumé

Pendant plus de 50 ans, la population annuelle d'une colonie de *Panaxia dominula* (L.) a varié en quantité : entre env. 200 et env. 18.000 individus. Mais en 1991, et de nouveau en 1992, il s'est produit une véritable explosion de cette population : environ 100.000 individus. Dans une autre colonie, à 5 km de là, on a observé une très forte population similaire. Normalement, ces chenilles se nourrissent de *Symphytum officinale* et de quelque autres plantes. Pendant l'explosion de la population, elles se sont en revanche nourries de 43 espèces de plantes, appartenant à 28 familles. Dans l'une de ces colonies, les chenilles se sont nourries de cônes (porteurs de piquants) d'*Equisetum*, genre rarement utilisé par les chenilles, et absolument sans rapport avec les plantes nourricières normales. Bien que ces observations ne soient pas inattendues, on a rarement eu l'occasion de confirmer un tel phénomène, étant donné le petit nombre d'estimations de populations à long terme chez les insectes phytophages.

Introduction

It might be expected that there would be an increase in the variety of species of food-plants utilised when the population size of a herbivorous insect undergoes a dramatic increase. There is, however, rather little evidence (Ward, 1988 and pers. comm.), mainly because there are very few long-term investigations in which, (1) population size has been monitored generation after generation and (2) there is a sudden population explosion. Hence, when in 1991 and 1992 the colony of scarlet tiger moths, *Panaxia dominula*, at Cothill, Oxfordshire, England, suddenly became at least five times as large as in any year since 1941 when the population size was first estimated, there was an opportunity to see if there was a concomitant increase in larval food-plant diversity. *P. dominula* has one generation a year and the moths appear in July ; the females scatter their eggs and so food-plants are selected by the larvae.

Sources of information

The population size of adult *P. dominula* at Cothill was estimated by capture-mark-recapture in order to monitor fluctuations in frequency of what was claimed to be a phenotypically recognisable allele (Fisher & Ford, 1947 ; Ford, 1975 ; Jones, 1989 ; Owen & Clarke, 1993). In 1941-1990, the estimated size of the population varied from a low of 216 to a high of 18,000. In 1991 and 1992 the size of the population was not easy to estimate by the usual methods, but was in the region of 100,000, by far the highest since records began ; by 1993 it had returned to the 1941-1990 level. As part of the genetic research, an artificial colony was established in 1951 at North Hinksey, 5 km from Cothill. This colony was monitored for allele frequency in 1952 and 1959-1961, and although the population size was not estimated, the moth was evidently not especially common (Sheppard & Cook, 1962). The colony was not examined again until 1988 when only two moths were found, but in 1991 and especially in 1992, there were huge numbers (Owen & Clarke, 1993) : what had happened at Cothill had also happened at North Hinksey ; moreover by 1993 the population was again low, as at Cothill.

In the late 1950s, the Cothill population was at its highest since 1941, reaching an estimated 14,000-18,000 in 1957, an all-time high until the population explosion in 1991-1992. At this time, Cook (1961) investigated larval food-plant specialisation and found that larvae are chiefly dependent on *Symphytum officinale*, but also utilise *Filipendula*

ulmaria and *Eupatorium cannabinum*. No other food-plants were recorded and L. M. Cook (pers. comm.) cannot recall additional species, although (as he admits) it is a long time ago. However, there is no doubt *P. dominula* is a fairly polyphagous species : it has been recorded from about 30 species of plants in Britain alone (Cook, 1961 ; White, 1985) and from about 20 species elsewhere in Europe (Cook, 1961). But at Cothill and at many other colonies in southern Britain, the larvae are chiefly *Symphytum*-feeders, a phenomenon which Cook (1961) interprets as an example of food-plant specialisation at the edge of the geographical range of the species.

Foodplants during the population explosion

At Cothill and North Hinksey small, pre-hibernation larvae feed from August to November on *Symphytum* and *Eupatorium*. Hibernation occurs in leaf litter especially among dead and decaying leaves of *Symphytum*, and the larvae start feeding again in March. At this time of the year there are few suitable plants other than the new shoots of *Symphytum*. In 1958, when larval densities were quite high, the new growth of *Symphytum* was eaten down to ground level, and some larvae may have starved (Cook, 1961 ; 1962). In 1991 and 1992, at both Cothill and North Hinksey, vast numbers of larvae quickly consumed all available *Symphytum* and then switched to other species of plants. By May, when larvae were in their last instar, they were feeding on many species of plants, often defoliating small *Quercus* and *Corylus* trees, and moving from species to species as new leaves became available. In warm weather, *P. dominula*. larvae are extremely active and at times hundreds could be seen leaving defoliated trees and climbing up others to reach the foliage.

A list of the 43 species utilised (30 at Cothill, 25 at North Hinksey) is given in Table I. Twenty-eight families are included, with representatives of just about all the plant groups present at the two sites, with the exception of grasses, conifers and ferns. The most remarkable discovery was of larvae feeding on the spore-bearing cones (strobuli) of *Equisetum telmateia*, a tall plant that later in the year dominates the understorey vegetation at North Hinksey (but not Cothill). The cones emerge from the ground litter in spring ; in 1992 about half the available cones head been utilised, and many were destroyed. Fig. 1 shows a larva feeding on a cone. Feeding usually commences on the soft pith at the base of the cone just above the leaf sheath. As the larva proceeds upwards, it feeds on sporangiophores and sporangia,

Fig. 1. Last instar larva of *Panaxia dominula* feeding on a spore-bearing cone of *Equisetum telmateia*, North Hinksey, Oxfordshire, England, 1992.

as well as the pith, but not the leaf sheath. The cone eventually collapses sideways, especially if there are two or three larvae feeding on it.

Discussion

The diversity of plants utilised by *P. dominula* larvae in 1991-1992 indicates that food-plant specificity, which has previously been a feature of the Cothill population, is easily lost during a population explosion. There are more species of plants listed in Table I than had hitherto been recorded as larval food-plants for *P. dominula* from the whole of Britain. These observations suggest that restrictions in the range of food-plants imposed by secondary compounds and other "defences" are easily overcome during times of population increase, particularly when the normal food-plant, in this case *Symphytum*, is kept cropped down throughout the period when larvae are feeding. The exploitation of *Equisetum* was unexpected : only one species of Lepidoptera (the

Table I
Larval food-plants of *Panaxia dominula*, 1991-93, at Cothill and North Hinksey, Oxfordshire, England. ** = frequent, * = occasional

	Cothill	North Hinksey
Equisetaceae		
Equisetum telmateia		**
Salicaceae		
Salix alba		**
Salix caprea	**	**
Populus alba	*	
Betulaceae		
Betula pendula	**	
Corylaceae		
Corylus avellana	**	**
Fagaceae		
Quercus robur	**	
Aceraceae		
Acer pseudoplatanus	*	
Oleaceae		
Fraxinus excelsior	**	**
Ligustrum vulgare	*	
Cannabaceae		
Humulus lupulus	**	
Urticaceae		
Urtica dioica	*	**
Polygonaceae		
Polygonum sp.		*
Cruciferae		
Cardamine pratensis	*	
Rosaceae		
Filipendula ulmaria	**	**
Rosa canina		**
Rubus fruticosus	**	**
Rubus idaeus	*	
Malus sylvestris		*
Crataegus monogyna		**
Prunus spinosa	**	**
Prunus avium		*
Leguminosae		
Ulex europaeus	*	
Euphorbiaceae		
Mercurialis perennis		*
Grossulariaceae		
Ribes rubrum		*
Celastraceae		
Euonymus europaeus	*	
Rhamnaceae		
Rhamnus catharticus	*	
Onagraceae		
Epilobium hirsutum	*	
Umbelliferae		
Heracleum sphondylium	*	
Angelica sylvestris		*
Caprifoliaceae		
Viburnum lantana	*	
Boraginaceae		
Symphytum officinale	**	**
Labiatae		
Lamium album		*
Stachys sylvestris	*	*
Valerianaceae		
Valeriana officinalis		*
Dipsaceae		
Succisa pratensis	*	
Rubiaceae		
Galium aparine		*
Compositae		
Eupatorium cannabinum	**	**
Arctium minus	*	
Cirsium arvense	*	*
Cirsium palustre	*	*
Cucurbitaceae		
Bryonia dioica	*	
Dioscoreaceae		
Tamus communis	*	

noctuid *Hydraecia micacea* Esper) has previously been reported as feeding on it in Britain (Barrett, 1899), although a small number of insects from other orders have been recorded from it (Owen, 1993).

The unusual feature of these observations is that population size of *P. dominula* had been monitored for more than 50 years before the 1991-1992 population explosion occurred. Hence there is a good correlation between the abundance of the herbivore and the diversity of the plant taxa exploited ; I doubt whether similar figures exist for any other species of plant-feeding insect. The observations are not so much unexpected ; it is simply that in most similar situations direct evidence is lacking, Thus Voute and van der Lind (1963) report that larvae of the moth *Euproctis chrysorrhoea* (L.) (Lymantriidae) feeding on *Hippophaë rhamnoides*, move to other species of woody plants as their numbers increase, but this is a moth which in many areas exists in a permanent state of plague, and since (unlike *P. dominula*) it does not form relatively discrete colonies, the ups and downs in numbers are difficult to quantify. Similarly, Iwao (1959) states, "It is well known that under epidemic conditions the caterpillar of *Leucania unipuncta*, known as a grass-feeder, often feeds on a wide variety of plants owing to the shortage of its suitable food". I suspect the phenomenon is indeed "well-known". Ecologists I have asked respond that this is just what is to be expected, but when pressed for evidence, none is offered.

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