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The role of larval food resources and adult movement in the population dynamics of the orange-tip butterfly (*Anthocharis cardamines*)

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Abstract Numbers of the orange-tip butterfly were recorded on a permanent transect in Monks Wood National Nature Reserve between 1982 and 1993, together with numbers of its only larval food plant in the wood, *Cardamine pratensis*. Females of the butterfly lay their eggs on the newly opened flower heads of *Cardamine* and the larvae feed on the developing seed pods. They are extremely selective in their choice of plant for egg laying, choosing mainly large flower heads growing in open sunny locations. Larval survival is greatly reduced if the flower head is more than 8 days old at the time of egg laying, because the seed pods become too tough for feeding. Earlier studies showed that only one larva can survive on a flower head, because larvae are cannibalistic, but females tend to avoid plants carrying more than one egg, in response to an oviposition-deterring pheromone laid down at the time of egg laying. The numbers of flower heads of *Cardamine* fluctuate enormously between years, and the numbers of eggs follow these closely. There is a strong correlation between number of eggs laid and the availability of suitable flower heads, and this correlation was shown to be real and causal by the experimental provision of extra flower heads, which resulted in more eggs, laid over an extended period of oviposition. The main causes of mortality of the butterfly's young stages were egg infertility, cannibalism, predation, starvation, the grazing of flower heads by deer, and possibly the failure of the newly hatched larvae to feed adequately. Adult numbers were only weakly correlated with the numbers of young stages in the wood, and there appears to be a considerable amount of movement by the butterfly through the wood and surrounding farmland.

Key words Butterfly · Intra-specific competition · Oviposition-deterring pheromone · Resource partitioning

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Introduction

The role of resource limitation in insect population dynamics has been a topic of debate for many years. Early workers, such as Milne (1957), argued that competition for resources was likely to occur only at very high densities, and that the majority of populations exist at levels well below those where resources are limiting. In contrast, Dempster and Pollard (1981) showed that populations of many species appear to be determined primarily by fluctuations in their food resources, even though they may be occurring at low densities.

Two aspects of the ecology of insects may have led to an under-estimation by early workers of the importance of resources in determining population size. First, it is now recognised that many insects have highly specialised needs, so that usable resources may be in far shorter supply than appears from casual observation. Secondly, some species of insect deter competitors and corner resources for their own use, or that of their progeny, by advertising their presence by use of chemical and visual cues.

The orange-tip butterfly, *Anthocharis cardamines* (L) (Lepidoptera, Pieridae), is an ideal species on which to study the interaction between its population and its food resources. It is widespread throughout southern Britain (Heath et al. 1984), but always occurs at rather low densities. The butterfly's young stages feed on the developing seed heads of a limited range of cruciferous plants, (Wiklund and Ahrberg 1978; Courtney and Duggan 1983), so that larval food resources can be easily quantified in the field. In the south of England, two species of plant are of particular importance, *Alliaria petiolata* (Bieb.) and *Cardamine pratensis* (L.), the former along hedgerows and tracks in arable farmland, and the latter in wet pastures and woodlands.

The butterfly has a single generation each year, emerging as an adult in late April or early May, from pupae that have overwintered. The female lays her eggs on the flower heads of its larval food plants, just as their flowers are beginning to open. On hatching, the larva first eats the egg-shell and then feeds on the flowers, before feeding on the developing siliquae (seed pods) of the plant. There are five larval instars, and the fully grown larva leaves its food plant in July to pupate on low vegetation. Pupae are extremely difficult to find, but the earlier young stages can be followed easily throughout their development, since most individuals complete their development on a single plant.

There is circumstantial evidence to suggest that competition for food can occur between larvae on a food plant. It is very unusual for more than one larva to complete its development on a single flower head, because the larvae are cannibalistic (Courtney and Duggan 1983). The first to hatch normally kills others that it encounters, and so there is clearly an advantage in hatching first, as later layings on the same flower head are unlikely to be successful.

This study started in 1982 in Monks Wood National Nature Reserve (157 ha, National Grid Reference TL 52/200800), where *Cardamine pratensis* is common throughout the rides (tracks) and open glades in the wood, and is the butterfly's only larval food plant present. In 1987 and subsequent years to 1993, a small patch of *Alliaria* was found at the north-eastern corner of the wood (North Gate), but the plants were in continuous shade and no eggs were ever found on them.

Numbers of the adult butterfly have been recorded in the wood each year since 1976 as part of the National Butterfly Monitoring Scheme (Pollard et al. 1986). For this, counts of butterflies seen on a permanent transect through the wood are recorded, and the sum of weekly counts of a species gives an index of abundance. Conditions during counting are standardised as far as possible, in terms of time of day and weather conditions. These data are shown in Fig. 1, where it will be seen that the index of abundance of the butterfly has fluctuated 6.5-fold over 18 years. The objective of this study was to examine whether these changes were related to the abundance of *Cardamine* flower heads.

Methods

A Permanent 3600-m transect was set up in the rides through the wood in 1982, passing through some of the best areas for *Cardamine*. The transect was marked into 100-m lengths, and flowering *Cardamine* plants were counted and their locations recorded on the transect twice a week during the summer.

Each year a rough estimate of the total number of flower heads in the whole wood, at the time of peak flowering, was obtained by searching all rides and open glades within the wood. This count took 2 days. The transect included just over a quarter of the total length of rides in the wood, but the annual counts suggest that it contained 25–44% (mean 37%) of flowering *Cardamine*.

The original intention was to search every flower head on the transect for the young stages of the butterfly. In 1982, we started by marking every flower head with a numbered cane, and these marked plants were to be searched for *Anthocharis* eggs and larvae twice a week, until the last larva had left the plants to pupate. However, the number of flower heads became so large that they could not be searched in a day, so after the 2nd week only every fourth flower head was marked and searched. New flower heads (in bud) are easily recognised, and every fourth one encountered was added to the total searched on subsequent occasions. In 1983, the number of flower heads was still high, so every second flower head was marked and searched, from the start. However, from 1984 onwards, the numbers of *Cardamine* were more manageable and so every flower head was numbered and searched in this way. After 1987, counts stopped at the end of egg laying, ie, larvae were not counted.

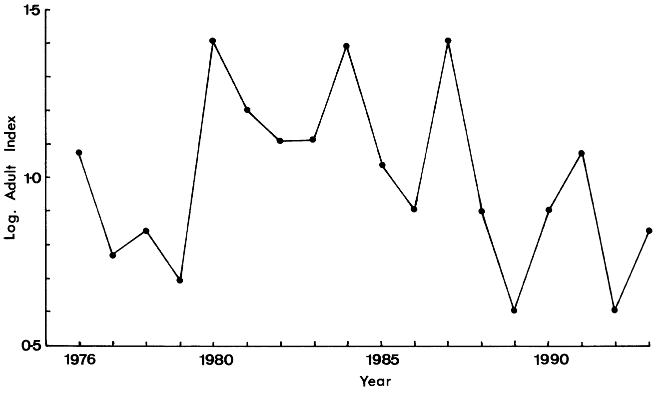

Fig. 1 Annual index of orange-tip abundance from the Butterfly Monitoring Scheme counts in Monks Wood

Each year, the numbers of individual flowers making up each flower head were counted when the plants were marked, and in 1983–1986 and 1990 the numbers of siliquae (seed pods) were counted on undamaged marked plants, at the end of the season. The individual flowers of *Cardamine* open and die sequentially from the bottom of the flower head, so large flower heads are available to ovipositing females for longer than small heads. The date when all flowers had died on each marked flower head was recorded, and these data were used to calculate the daily availability of open flower heads for the butterfly.

In 1982 and 1983, 30 fully grown larvae were brought into the laboratory and reared for parasitoids. After that, however, larval numbers became too low to do this.

In common with many other species of butterfly, orange tip adults are active only in warm, sunny conditions, and eggs are laid only on plants in full sun. Measurements of shade were taken on 20 May 1982, 5 June 1983 and 2 June 1989, from hemispherical photographs, as described by Anderson (1964), to identify sunny areas along the transect. Photographs were taken through a Minolta fish-eye lens at the mid point of each 100-m length of the transect, using the equipment described by Warren (1981). The direct radiation reaching the ground, as determined by the orientation of the ride and the tree cover was estimated from each photograph by constructing a solar-track diagram for 52°N as described by Evans and Coombe (1959). An overlay of this solar-track diagram was placed on each photograph and the possible hourly direct irradiance was estimated, using the data for Cambridge (latitude 52°13′N) given by Anderson (1964). The latitude of Monks Wood is 52°25′N, but this will make very little difference. Each hourly estimate was then summed to give the daily direct irradiance for each section of the transect.

In 1987, an experiment was undertaken to test whether the numbers of *Anthocharis* eggs could be increased by the provision of extra *Cardamine* flowers. Vegetatively produced plantlets of *Cardamine*, collected from Monks Wood, were potted up during the winter of 1986–1987. These were grown in a glasshouse until they flowered. A total of 413 flowering plants were planted in sections 5 and 6 of the transect during the flight period of the butterfly in 1987. In an earlier attempt to do this experiment, potted plants were planted out in the sunnier areas along the whole transect in 1985. Within 4 days, however, the experiment had been destroyed by deer preferentially browsing the experimental flowers. For this reason, the introduced plants were restricted to 150 m of ride in

Table 1 The performance of *Cardamine* on the transect during the butterfly's egg-laying periods 1982–1993

Year	Total *Cardamine* flower heads	Mean no. flowers per flower head (SE)	Mean daily no. flower heads > 7 flowers in open rides during egg laying
1982	3725	13.2 (5.1)	244
1983	1909	9.1 (3.9)	170
1984	153	9.3 (2.9)	31
1985	227	6.4 (3.4)	20
1986	269	8.5 (3.5)	84
1987	733[a]	12.5 (5.3)[a]	182[a]
1988	312	6.3 (3.4)	57
1989	955	7.7 (4.3)	48
1990	526	6.0 (3.1)	43
1991	521	6.4 (3.5)	66
1992	1558	10.8 (6.2)	121
1993	596	10.8 (4.6)	150

[a] Including 413 planted

1987, and they were protected from deer with an electric fence. Flowering plants were put out as they came into bud; 193 on 29 April, 22 on 6 May, 45 on 19 May, 52 on 28 May, 47 on 3 June and 54 on 10 June. Every other flower head of these introduced plants was numbered and searched during the routine counts of the butterfly's young stages on the wild plants.

Weather data were obtained from the weather station at Monks Wood Experimental Station.

Results and discussion

Changes in the abundance of *Cardamine* flower heads

C. pratensis is common throughout the rides in Monks Wood, but a varying and small percentage of the plants appear to flower in any one year. Vegetative propagation is possibly more important than seed in the spread of *Cardamine* in the wood, as leaflets from the plants drop and take root in the wetter rides. These small plants can reach very high densities (> 100 plants m^{-2}) in some heavily shaded rides, where flowers have not been recorded. During the 12 years of this study there have been considerable changes in the distribution of flowering *Cardamine* on the transect. These changes appear to be linked with the cycle of woodland management, with bursts of flowering immediately after rides have been opened by coppicing the adjacent compartment of woodland. Gradually these rides then shade over again as the vegetation grows.

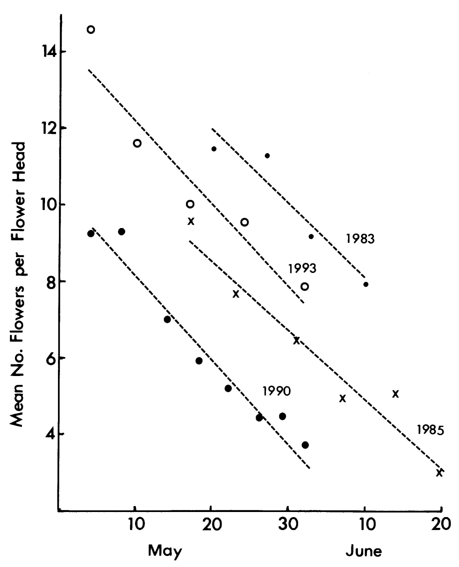

Fig. 2 Changes in the mean number of *Cardamine* flowers per flower head during early summer. The *lines* are best-fit lines from regression analyses

Table 1 shows the numbers of flower heads of *Cardamine* on the transect during the egg-laying period of the butterfly each year. This varied greatly between years, with very low numbers (153, 227, 269) between 1984 and 1986, and very high numbers (3725, 1909, 1558) in 1982, 1983 and 1992. Added to this, the sizes of these flower heads also varied greatly between years. The flower heads were largest in 1982, with an average of 13.2 flowers per head, and lowest in 1990 with 6.0 flowers per head (Table 1).

Each year, the sizes of the flower heads decreased during the course of the summer. The first plants to flower produced the largest flower heads. Figure 2 shows data for 4 years with very different mean sizes of flower head, and it can be seen that the rates of decline were similar irrespective of the mean size.

The percentage of flowers forming siliquae was generally rather constant at 50–60% (53.4 in 1983; 56.4 in 1984; 60.8 in 1986; 60.5 in 1990), but in 1985 only 23.1% of the flowers produced a seed pod. The numbers of siliquae were not counted in the other years.

The use of flower heads by *Anthocharis*

Females lay their eggs only on plants which are growing in full sun. Plants in the shadiest rides are completely avoided, although plants in small patches of sun may be laid on, provided the female does not have to fly through a large shaded area to reach them. The data obtained from the analyses of the hemispherical photographs give only a crude measure of the extent of local insolation reaching plants, but over the 12 years, 84.6% of eggs ($n = 878$) were laid on sections of the transect receiving more than an estimated 100 mW cm^{-2} day^{-1}. Only 46.4% of the total number of flower heads recorded ($n = 5225$) were on those sections of the transect, and there were no significant differences in the mean size of flower heads on sunny and shaded sections.

The ovipositing female is also very selective in the size of plant on which she lays, choosing mainly the largest flower heads. In 1982, the mean number of flowers per flower head on which eggs were laid was 17.6, which is significantly larger than the overall mean of 13.2 ($t = 4.2$, $df = 198$, $P < 0.001$). Similar evidence of selection of the larger flower heads was found in all subsequent years, although this was not statistically significant in years when egg numbers were very low (1984, 1985, 1990). In all years the smallest flower heads (< 5 flowers) were completely ignored, even when these made up a high proportion of those available. Table 2 shows the use of flower heads of differing sizes over the whole 12 years, where it can be seen that egg laying was heavily biassed towards the larger plants ($\chi^2 = 170.9$, $P < 0.001$). As pointed out above, there was no significant difference in the mean size of flower heads on sunny and shaded sections of the rides, in any year.

Besides the size of flower head and the extent of insolation, a third factor plays an important role in determining the egg-laying behaviour of the female orange-tip. Females tend to avoid laying on those plants already carrying a conspecific egg (Wiklund and Ahrberg 1978; Thomas 1984). Shapiro (1981) found a similar tendency in females of *A. sara* and suggested that the orange colour of the eggs made them more easily detectable by the ovipositing females. The eggs of *A. cardamines* are straw-coloured when laid, and do not become bright orange for 2–3 days. The first larva to hatch is likely to succeed by cannibalizing younger individuals, so an individual requires protection from others of similar age that might hatch before it. Thus, it is unlikely that colour can provide an adequate protection against further eggs being laid on the same flower head. In fact, we now know that females deposit a pheromone at the time of egglaying which deters further laying of eggs on the same plant (Dempster 1992). Experiments showed that the pheromone is water-soluble, and so its effect is relatively short-lived in the field, particularly if it rains. Thus it is not uncommon for more than one egg to be laid on a flower head, although the distribution of eggs in the field frequently does not conform to a Poisson distribution (Wiklund and Ahrberg 1978), because plants bearing single eggs are over-represented.

Survival of the butterfly's young stages.

Table 3a shows the numbers of eggs and larvae on the transect plants from 1982 to 1987. The highest number of eggs was in 1983 when 782 eggs were laid on the transect, and the lowest was in 1985 when only 10 eggs were laid.

The survival of individual eggs and larvae were followed until they died, disappeared, or left the plant to pupate. Unless a corpse was found, deaths were assumed to have occurred during the last developmental stage in which they were recorded. All instars took longer than a week, so this should not cause large errors in the estimated time of death.

Six main causes of mortality were identified (Table 3b).

1. *Egg infertility*. A small percentage of eggs showed no development and failed to hatch. This was normally under 10%, although three of the ten eggs in 1985 appeared to be infertile.

Table 2 The number of flower heads of different sizes, and the use of these by ovipositing females (data for the 12 years combined)

	Number of flowers per head						
	1–5	6–10	11–15	16–20	21–25	> 26	Total
No. of flower heads	1458	2029	1220	407	85	26	5225
No. with eggs	9	256	354	199	44	16	878
% Used	0.6	12.6	29.0	48.9	51.8	61.5	16.8

Table 3 a Numbers of the young stages of the orange-tip on the transect 1982–1987. **b** Percentage mortality of the young stages of the orange-tip caused by different factors 1982–1987

a		Larval Instars				
Year	Egg	I	II	III	IV	V
1982	518	421	275	243	162	97
1983	782	642	476	438	336	224
1984	27	21	14	9	8	5
1985	10	6	3	2	2	2
1986	60	53	34	32	27	18
1987	191	108	40	27	18	12

b	Year						
Mortality factor	1982	1983	1984	1985	1986	1987	Mean
Infertility	3.1	2.4	0.0	30.0	4.1	15.2	9.1
Cannibalism	12.5	22.6	0.0	0.0	10.2	16.2	10.2
Predation	3.1	8.3	5.6	10.0	6.1	4.7	6.3
Unknown (plant age?)	21.9	20.2	44.4	40.0	24.5	33.0	30.7
Grazed	18.7	2.4	11.1	0.0	2.0	15.7	8.3
Starved	21.9	15.5	16.7	0.0	22.4	8.9	14.2
Total	81.2	71.4	77.8	80.0	69.3	93.7	

2. *Cannibalism*. As noted earlier, cannibalism is well known to occur amongst *Anthocharis* larvae. Although more than one egg was sometimes laid on an individual flower head, more than one larva never survived. Other individuals were always lost soon after the first larva hatched, and such losses are assumed to have been caused by cannibalism. During the 6 years, these deaths accounted for between 0 and 23% of the butterfly's young stages. Of the losses 60% were as eggs and the rest as first-instar larvae. One might expect cannibalism to be density-dependent but the regression, of percentage killed (angular transformed) against log density (number of eggs per suitable flower head) was not formally statistically significant ($r^2 = 0.58$, $P < 0.08$). The effectiveness of the oviposition-deterring pheromone in preventing multiple layings is dependent upon weather conditions (Dempster 1992), and so the relationship between cannibalism and density may not be very precise.

3. *Grazing*. Each year some plants carrying the butterfly's young stages were grazed by deer. This mostly occurred when the flowers were young and conspicuous,

and so it accounted for mainly eggs and very young larvae. Over the 6 years, grazing destroyed 2–19% of the butterfly's young stages. The main grazers were muntjac deer (*Muntiacus reevesi* Zimmermann) and they did far more damage to *Cardamine* during the second half of the study (Cooke 1993).

4. *Starvation*. Larvae sometimes ran out of food on small plants before they had completed their development. We sometimes found such larvae on vegetation near the remains of the plant, but frequently they just disappeared. Even in a good year, the flowering plants were so sparsely distributed that there was little chance of a caterpillar finding another plant, after having eaten out its original flower head. Only two cases were recorded in the 12 years of an old larva being found on a plant on which no eggs had been laid, and these were within 2 m of a flower head that had been completely eaten. Although it is possible that larvae may have been taken by predators whilst off the plant, such disappearances have been recorded as due to starvation. This was always after the third larval instar, and estimates of mortality ranged from 10 to 22%. Rearing experiments suggest that a minimum of about 4 well-grown siliquae (equivalent to about 7–8 flowers) is required for larval development, and in the field, none of the eggs laid on flower heads with fewer than seven flowers reached the fifth larval instar. Above that size, survival showed no statistical relationship with flower head size ($r = 0.09$, NS). As seen in Table 1, the mean size of flower heads on the transect was less than 7 in some years.

5. *Predation*. Predation often results in the total disappearance of a caterpillar, and so figures recorded here (Table 3b) will be underestimates. These figures are based on those cases when the prey's corpse was found. Mostly these were young larvae showing characteristic darkening around a wound, usually at their tail end. This is consistent with the damage done by spiders, and it is likely that these are the main predators.

6. *Unknown causes*. Frequently, young caterpillars, first- and second-instar, disappeared without trace. Some were probably taken by predators, but Courtney and Duggan (1983) suggest that many fail to feed adequately if the siliquae are too tough. I think that this is very likely, and that the timing of hatch in relation to the developing flower head is very important in determining early larval survival. Mortality increased significantly on flower heads which were 8–11 days old at the time of egg laying ($\chi^2 = 13.3$, $P < 0.01$), and no larvae survived on flower heads that were older than this (Table 4). There appears, then to be a period of only about 8 days after the flowers start to open, before siliquae become too tough for young caterpillars to feed.

Other, occasional causes of mortality include the egg parasitoid *Trichogramma* sp. (2 eggs), drowning (1 first instar) and being trapped in secretions of *Philaenus* sp. (1 first instar). Surprisingly, no parasitoids were recorded in the caterpillars, but data were collected in only two years. The tachinid *Phryxe vulgaris* Fallen was regularly bred from caterpillars collected from other sites, and Courtney and Duggan (1983) found this non-specific parasitoid to be important in their Durham population.

Table 4 Survival of orange-tip caterpillars on flower heads of *Cardamine* of differing ages

Age (days)	1	2–4	5–8	9–11	12–14	15–18	19–22
No. eggs laid	123	46	40	18	8	4	2
% Surviving to V instar	25.2	23.9	27.5	11.1	0.0	0.0	0.0

The number of eggs laid

Variations between years in the numbers of eggs laid closely followed changes in the total numbers of *Cardamine* flower heads present on the transect. There was a significant correlation between log number of eggs and log number of flower heads ($r = 0.72$, $P < 0.01$). The data for 1987 were excluded from this and subsequent analyses, because flower-head numbers were manipulated in that year.

Because of the highly selective behaviour of ovipositing females, a better measure of the availability of flower heads is likely to be given by the numbers of those with more than seven flowers (4 siliquae), growing in open rides (Table 1). Most eggs were laid in sections of the transect receiving more than 100 mW cm^{-2} radiation per day, so this figure was taken as defining an open ride. Using these criteria for suitability, the mean daily availability, during oviposition, of suitable flower heads was calculated (shown in the last column of Table 1), and used instead of total numbers of *Cardamine* in the correlation. This greatly improved the significance of the correlation between log number of eggs laid and log number of flower heads ($r = 0.92$, $P < 0.001$) (Fig. 3).

This analysis was taken further by using multiple regression to test the importance of the number of adults and the effects of weather on the number of eggs laid, as well as the availability of suitable flower heads. Log adult index (from the Butterfly Monitoring Scheme) was used as the measure of adult abundance, as this has been shown, for a number of butterfly species, to be well correlated with actual numbers present (Pollard and Yates 1993). As a measure of weather during oviposition, temperature, rainfall and hours of sunshine were integrated into a weather index (I), as proposed by Davis (1968), so that

$I = 10$ (daily mean temperature, °F) $+ 20$ (daily mean sun, h) -7 (total rain, inches)

The regression model accounted for 91% of the observed variability in log egg numbers ($P < 0.02$), with log number of suitable *Cardamine* accounting for 85% of the variability ($P < 0.001$), but with no other term, or their interactions, making a significant contribution.

The results of this analysis are rather surprising, because the butterfly appears to be so dependent on sun-

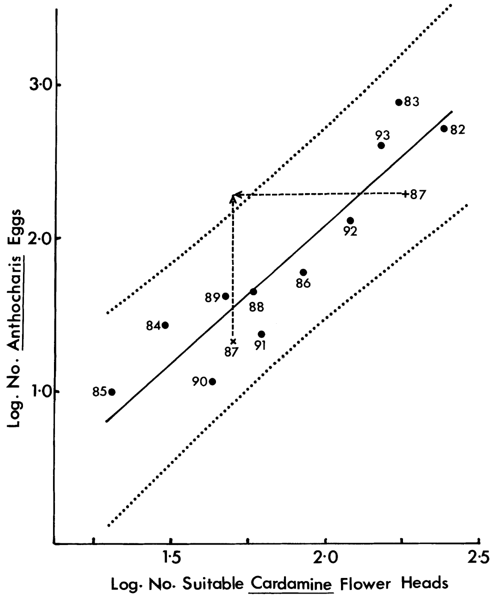

Fig. 3 The relationship between the number of eggs laid each year and the number of suitable *Cardamine* flower heads available to orange-tip females. The 95% confidence limits of the predicted numbers of eggs laid, from the regression model ($y = -1.5278 + 1.8094x$), are shown. Two points are recorded for 1987; + = total flower heads, including those planted, and x = wild flower heads only. The *arrows* joining these points show how the provision of extra plants has increased the number of eggs above the 95% fiducial limits on the predicted number for wild plants alone

shine for egg laying. It was therefore repeated, replacing the weather index with hours of sunshine, but the result was identical, presumably because females can lay all their eggs during short periods of sunshine. Clearly, the number of eggs laid is primarily dependent on the availability of suitable flower heads, and neither sunshine nor the numbers of adult butterflies is limiting over the whole season.

A test for a causal relationship underlying the strong correlation between egg and flower-head numbers was made in 1987, when 413 flowering *Cardamine* were planted out on the transect. This resulted in an increase in the number of eggs laid, from 21 to 191, an increase in keeping with the regression line shown in Fig. 3. Although the scatter of points about the regression line is large, the logarithm of the total number of eggs laid (2.2810) is significantly higher ($t = 2.58$, $P < 0.05$; Fig. 3) than the upper 95% fiducial limit of the number predicted by the regression model for the log number of wild flower heads (1.7075). Thus the provision of extra plants resulted in extra eggs being laid, demonstrating a direct effect of flower numbers on the number of eggs.

The last egg to be laid on a wild flower head in 1987 was laid on 29 May, but further planting prolonged egglaying for another 3 weeks, the last being recorded on 19 June. In all years, adult butterflies were present in the wood after the last egg was recorded, and it seems likely that these normally move out of the wood, to breed on other crucifers in the surrounding farmland, once the numbers of suitable *Cardamine* flower heads decline. The experimental plantings appear to have held these late individuals in the wood in 1987.

This study has demonstrated that egg numbers are closely tied to the availability of suitable larval food plants, and the tightness of this relationship suggests some density-dependent response by the ovipositing butterfly, but at low density. The most obvious mechanism for this is intra-specific competition which results in resource partitioning, brought about by the female's use of an oviposition-deterring pheromone, combined with larval cannibalism.

A simple count of the number of *Cardamine* flower heads in the wood gives no impression of their true availability to the butterfly. At first sight, their numbers appear to be vast compared to the very low densities of the butterfly, but this does not take account of the needs of the egg-laying female. The females are so selective in their requirements that very few flower heads are suitable at any one time. To be acceptable, a flower head must be large and growing in a sunny location. Added to this, the flower head must be free from recently laid conspecific eggs, and must be under 8 days old, if the young caterpillar is to have a reasonable chance of survival. The availability of flower heads to the ovipositing female may be reduced by an order of magnitude by these requirements (Table 1).

Adult numbers

Although the Index of adult abundance broadly followed the estimated numbers of fifth stage larvae in the previous year, the larvae producing that generation of adults, the correlation between log adult index and log number of fifth stage larvae was not statistically significant ($r = 0.63$, $df = 4$). Using the larger data set of log number of eggs in the previous year, instead of fifth stage larvae, also failed to demonstrate a significant correlation ($r = 0.40$, $df = 10$).

A large part of the Butterfly Monitoring Scheme transect passes along the same rides as those used to count *Cardamine* and *Anthocharis* eggs. Numbers of adults counted were always low and were dominated by males, because females are less conspicuous and less active. Whilst it must be stressed that these counts provide only an index of abundance, studies on other species of butterfly have shown that the index is well correlated with population sizes estimated by mark and recapture (Pollard and Yates 1993), and there is no reason for thinking that the data from the Monitoring Scheme give an inaccurate measure of adult abundance for the orange-tip.

It seems far more likely that adult numbers really are only weakly related to the butterfly's breeding success in the wood, and that there is considerable movement taking place into and out of the wood. This view is supported by the finding that adults stayed to lay on introduced plants in the 1987 experiment, 3 weeks after all wild plants were no longer suitable for egg laying. The number of adults in the wood in any one year probably depends on the relative availability of food plants inside and outside the wood. Having said this, there is no significant correlation between log adult index and log number of suitable flowerheads in the same year, but we know nothing about the abundance of food plants outside the wood.

There is some disagreement in the literature on the mobility of orange-tip adults. As a member of the Pieridae, one might expect it to be a reasonably mobile species, as the family contains many migratory butterflies. Baker (1969) lists the species amongst those expected to show very frequent voluntary displacement because the distributions of its foodplants change rapidly, and Wiklund and Ahrberg (1978) describe it as having a vagrant life style in Scandinavia. In contrast, Courtney and Duggan (1983) concluded from a mark and recapture study of the butterfly in Durham, that there was little movement between breeding sites. This has led Shreeve (1995) to suggest that the species is far less mobile in the north of Britain than in the south. Personally, I doubt that this is true. Movement is extremely difficult to quantify, and the most commonly used technique of following the spread of marked individuals invariably underestimates mobility, simply because larger and larger areas have to be searched as one moves away from the point of release, to ensure an equal chance of recapture.

With these uncertainties in mind, a study has been made using the chemical composition of individual butterflies caught in the wood, to see whether this could be used to assess the amount of movement into the Monks Wood population. This research will be published as a separate paper and is only briefly summarized here. The cruciferous food plants of the butterfly contain highly specific mustard oils, which are taken up by the caterpillars feeding on them. Chemical analysis of adult butterflies can show the food plant that they were reared on, and this can be used to give a measure of rates of immigration, as *Cardamine* is the only food plant in the wood and the plant is rare in the surrounding farmland. At present, the results from very few analyses are available, but these show that many of the adults found in the wood have not been reared on *Cardamine*, and so must have immigrated. Of 13 individuals caught in the wood and analysed, only 3 individuals were reared on *Cardamine*. Clearly, this butterfly is very mobile.

Population dynamics

Explanation of the changes in the numbers of the orange-tip in Monks Wood has proved rather more difficult than was envisaged at the start of this study. In 1982, it seemed straightforward to explain changes in adult numbers by understanding the factors determining the breeding success of the butterfly in the wood. At the end of the study it is clear that the population from which the adults in Monks Wood are drawn covers a larger area than the wood itself. Breeding in the wood is clearly determined by the availability of suitable larval food plants, and it seems probable that adults move through the area staying to breed in the wood when suitable plants are present in sufficient abundance. Otherwise, the ovipositing females move out of the wood in search of breeding sites. Thus larval food resources appear to rule the population dynamics of this butterfly in Monks Wood.

It is likely that these same processes are involved in the total population, of which that in Monks Wood forms a part. If so, one must envisage total numbers being determined largely by the availability of larval food plants within its total area. Many of its food plants are annuals, and the distribution of their flowers may change greatly from one year to another, probably even more dramatically than with the perennial *Cardamine*. The butterfly must keep pace with these changes by movement.

Finally, this study demonstrates the importance of being able to define the population structure of any species being studied. In the past, researchers have tended to study the abundance of a species in a particular locality with little regard to impacts of movement on its numbers. It may be argued that the orange-tip is an unusually mobile species, but the few recent studies in which movements have been quantified suggest that many insects are as mobile. For example, Dempster et al. (1995) showed a similar population structure and a similar interaction between resources and movement in some tephritid flies. Definition of the spatial extent of insect populations is fundamental to understanding their population dynamics and this depends on the ability to quantify movement. Unfortunately, at present, few satisfactory techniques exist to enable one to do this.

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