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Observations on co-existing late-instar caterpillars of the Orange-tip butterfly, *Anthocharis cardamines* (Linnaeus) (Lepidoptera: Pieridae)

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Abstract

Co-existence between late instar larvae of *Anthocharis cardamines* on multiple occupied *Lunaria annua* plants was monitored in a suburban Edinburgh garden and a stand-off between final instar larvae on *Sisymbrium officinale* in countryside near Leipzig was recorded photographically. Occupation of mauve-flowered *Lunaria* plants was significantly higher than white-flowered ones. The notion that the resting behaviour of final instar larva along the top of seed pods camouflages them is challenged. Although not part of that argument, a major predation event by *Vespula vulgaris* was seen on *Lunaria*.

Key words: Conflict, behaviour, camouflage, flower colour, choice, predation, *Vespula vulgaris*

Introduction

Larvae of the Orange-tip butterfly, *Anthocharis cardamines* (Linnaeus) (Lepidoptera: Pieridae), are known to be fierce cannibals, evidently (along with a reluctance to oviposit on plants already bearing eggs (Wiklund & Ahrberg, 1978; Thomas, 1984)) an adaptation enabling the effective use of relatively small and scattered food plants, which would be capable of supporting only one or very few larvae. Many general citations of cannibalistic behaviour do not specify which instars practice it, although consuming eggs is often especially mentioned and sometimes there are direct statements that the young larvae are cannibals. However, we have not seen publications that express cut-off points for the behaviour or that either record or specifically refute the occurrence of cannibalism among older caterpillars.

In this paper we provide some limited evidence that, once a certain growth point (which we are alas unable to pin down) is reached, the strategy may change to one of avoidance and re-spacing rather than lethal aggression, at least on large plants potentially capable of supporting all the larvae present.

Part 1. Coexistence and then carnage in an Edinburgh garden

Mark R. Shaw

Owing to Covid-19, relative old age, and the best weather for many years, I spent more time in the garden in the spring and early summer of 2020 than usual, and perhaps kept a sharper eye out for interesting insect activity. In this quite sunny south Edinburgh garden (at 48 St Albans Road, EH9 2LU) adult Orange-tip butterflies are frequent most years, and self-sown Honesty (*Lunaria annua*) plants are dotted around in both sunny and partly or completely shaded places. In past years young Orange-tip larvae had occasionally been found feeding on them, but they seemed always to fail (though for unknown reasons). In the last couple of years an effort had been made to increase the quantity of purple-flowered Honesty in the garden (just by scattering seed collected locally) and by 2020 there was approximate parity with the white-flowered strain.

In the first half of May 2020 at least one female Orange-tip was noticed on a few occasions ovipositing on two tall mauve-flowered Honesty plants growing in a sunny spot (with direct insolation potentially from around 8.00 am to 4.00 pm), but at the time this was not investigated further. However, on 2.vi.2020, the last of more than a month of mostly dry and warm sunny days, immediately before overnight rain and a period of more varied weather, I decided to map the Orange-tip larvae in the garden. Although it was not surprising to find that on the whole the tallest plants had been used for oviposition, as this tendency is well-documented for *A. cardamines* (e.g. Courtney, 1982), I was astonished to find that many larvae occupied these two plants (Fig. 1) and I resolved to follow their fates. The youngest was by then in its antepenultimate instar, but as many were in the penultimate instar and a few were already in the final instar.

The relevant plants

The two mauve-flowered plants, parts of which touched each other, grew in a clump (rooted in a patch of earth of around 80 cm diameter, raised about 25 cm on its south-west side from a lawn within one metre) comprising these two

Fig. 1. Crowding of two L5 and two L4 *A. cardamines* larvae on the touching main two *Lunaria* plants (**M1** and **M2**).

Fig. 2. The main *Lunaria* clump, from the north east. Photo taken on 12.vi.2020, soon after a gale had blown the largest white-flowered plants over.

(respectively **M1**, 122 cm tall, with 5 larvae; and **M2**, 116 cm tall, with 6 larvae), two other mauve-flowered plants (below 60 cm in height and without larvae), and four white-flowered plants measuring 115 cm (with no larvae), 85 cm (**W1**, with 1 larva) and two under 60 cm (no larvae) (Fig. 2). The white-flowered plants were concentrated in the more southerly position, and a paved terrace was to the north east.

Elsewhere in the garden many relatively short plants in more shaded positions were not used, but about 50 m from **M1**, **M2** and **W1** an area of more widely spaced Honesty of both colours in full sun included one plant with three larvae. This mauve-flowered plant (**M3**) was 80 cm tall; the tallest of any of the mauve-flowered plants in the vicinity, but well short of at least three equally exposed white-flowered plants that had no larvae.

Spacing of the larvae

The following notations apply. T is the top part of the plant (seed pods on single stalks direct to the main stem), and the panicles below are, in descending order, P1, P2, P3, etc. Frohawk (1934) states that there are 4 larval moults (=5 instars) and, on that basis, antepenultimate instar caterpillars are here indicated L3, penultimate instars L4 and final instars L5; the letter 'e' indicates that the larva was quiescent in proecdysis, visibly preparing for the moult from the instar indicated to the next one. With '0' indicating no larva present, the relevant plants were occupied as follows on 2.vi.2020:

M1: T/L5; P1/0; P2/0; P3/L3e; P4/L4; P5/0; P6/0; [P7 broken, wilted/0]; P8/L3e; P9/0; P10/0; P11/0; P12/0; P13/0; P14/0; P15/L4e; [P16 lowest panicle broken, wilted/0].
M2: T/L5; P1/0; P2/0; P3/0; P4/L5; P5/0; P6/L3e; P7/0; P8/0; P9/L4; P10/0; P11/L3e; P12/L4; P13/0; P14/0; P15/0; P16/0; P17 (lowest)/0.
W1: T/0; P1/0; P2/L3e; P4/0; P5/0; P6/0; P7 (lowest)/0.
M3: T/L4 + L5; P1/0; P2/0; P3/0; P4/0; P5/0; P6/0; P7/L4e; P8/0; P9/0; P10/0; P11/0; P12 (lowest)/0

Distribution on the resources

It was striking that, of the 15 larvae found in the garden on Honesty, all but one were on mauve-flowered plants (actually, purple-flowered would be a more appropriate description, were it not for my annotation system!), despite a roughly equal abundance of plants with white flowers. The difference is statistically significant versus the null hypothesis of no preference and an equal availability of suitable mauve- or white-flowered plants (two tailed Fisher's exact test, $P<0.05$). Inspection of all the Honesty plants growing in the garden revealed no other feeding damage attributable to *A. cardamines*. A preference for mauve-flowered Honesty plants over white ones might reflect the mauve flowers of one of its best-known host plants, *Cardamine pratensis* (Cuckoo Flower, or Lady's Smock), though another very regular foodplant, *Alliaria petiolata* (Garlic Mustard, Jack by the Hedge), is heavily used in the Edinburgh area and has white flowers. The possibility exists that volatiles from the two strains of Honesty differ, and that colour *per se* has little to do with it.

It was also striking that larvae were well-spaced within the occupied plant, and (from the feeding damage seen) relatively static as well as clearly being willing to remain feeding on lower panicles in relatively more shaded positions; and this despite much tenderer young seed pods being available on some unoccupied panicles nearby on the same plant. It was also interesting to observe that feeding on the same pod was often continued for days, with neither preference for nor avoidance of the actual seeds.

Growth and subsequent movements

The plants were monitored each morning and evening, and progress and positions noted. It was apparent that (under the conditions by then prevailing) growth was not rapid. The pause in feeding for ecdyses (both from L3 to L4 and from L4 to L5 (Fig. 3)) lasted for at least two days (in one L3 to L4 transition for

Figs 3–6. Larvae of *A. cardamines* on purple-flowered *Lunaria*; **3,** L4–L5 proecdysis; **4,** L4 and L5 close together on the top of **M3**; **5,** L4 at rest on its half-eaten pod; **6,** Late and early L5 larvae, certainly not well-camouflaged.

four days); the L4 larval feeding period was at least seven days (assessment curtailed: see below), and that for the final (L5) instar was eight to ten days (no estimate was possible for L3 larvae). Probably progression through early instars, when the weather was markedly warmer, would have been faster, and that spell of exceptional weather might underlie the success of feeding on Honesty in the garden in 2020 in contrast to previous years (though often the availability of mauve-flowered plants had hitherto been small).

The movements between panicles of larvae up to 9.vi.2020 (when catastrophe struck, frustrating my observations: see below) on **M1**, **M2** and **W1** were remarkably few. The tops of the plants were generally occupied by large larvae, suggesting some advantage in that position, and also that some form of jockeying for position might have already occurred (an alternative view is that the top of the plant is so favourable that random occupancy of it had simply led to faster growth). From **M1**, P15/L4e, which had become L5 on 3.vi.2020, moved to vacant P15 on the touching **M2** on 8.vi.2020. On **M2**, P4/L5 moved up, through vacant space, two panicles to P2 on 5.vi.2020. On **W1**, P2/L3e, which moulted to L4 on 3.vi.2020, moved down to P4 on 7.vi.20. Two larvae disappeared in this period: from **M2**, T/L5 almost certainly left to pupate on 8.vi.2020, and from **M1** P8/L3e went missing shortly after attaining L4 on 5.vi.2020 (a careful unsuccessful search at the time, and subsequent monitoring without finding feeding damage on this or a new panicle, suggested predation: there was no sign of a struggle).

On the isolated and smaller **M3**, more movement was recorded and also the observation period was not curtailed. The two larvae T/L4 and T/L5 (Fig. 4) on 2.vi.2020 had both moved by 3.vi.2020 to become P1/L4 and P2/L5, now out of direct contact. On 4. vi. 2020, the smaller (L4) moved downwards, past P2 now occupied by the larger (L5) larva, to become P3/L4 where it remained until moulting to L5 on 9.vi.2020 and moving up to the just-vacated T on 12.vi.2020, moving down from the by then badly mangled T to P1 on 17.vi.2020 until leaving on 18.vi.2020 for pupation. Meanwhile the larva that had become P2/L5 on 3.vi.2020 moved to T for 7–8.vi.2020, then down to P1 for 9–10.vi.2020 before again ascending to T on 11.vi.2020 then on the same day leaving to pupate. The third larva, starting as P7/L4e on 2.vi.2020, moulted on 3.vi.2020 and immediately moved up to P4 where it stayed until vanishing on 5.vi.2020; although by then L5 it was presumably predated as it had not fed in that instar for long, although the two other larvae on the plant at that time were in more conspicuous positions on P2 and P3 and were left. Again, there was no sign of a struggle.

I was sorry to miss seeing any of the few probable interactions between larvae leading to re-spacing, but the second part of this paper, by Helene Otto (below), suggests how it might have been.

Are these larvae really camouflaged?

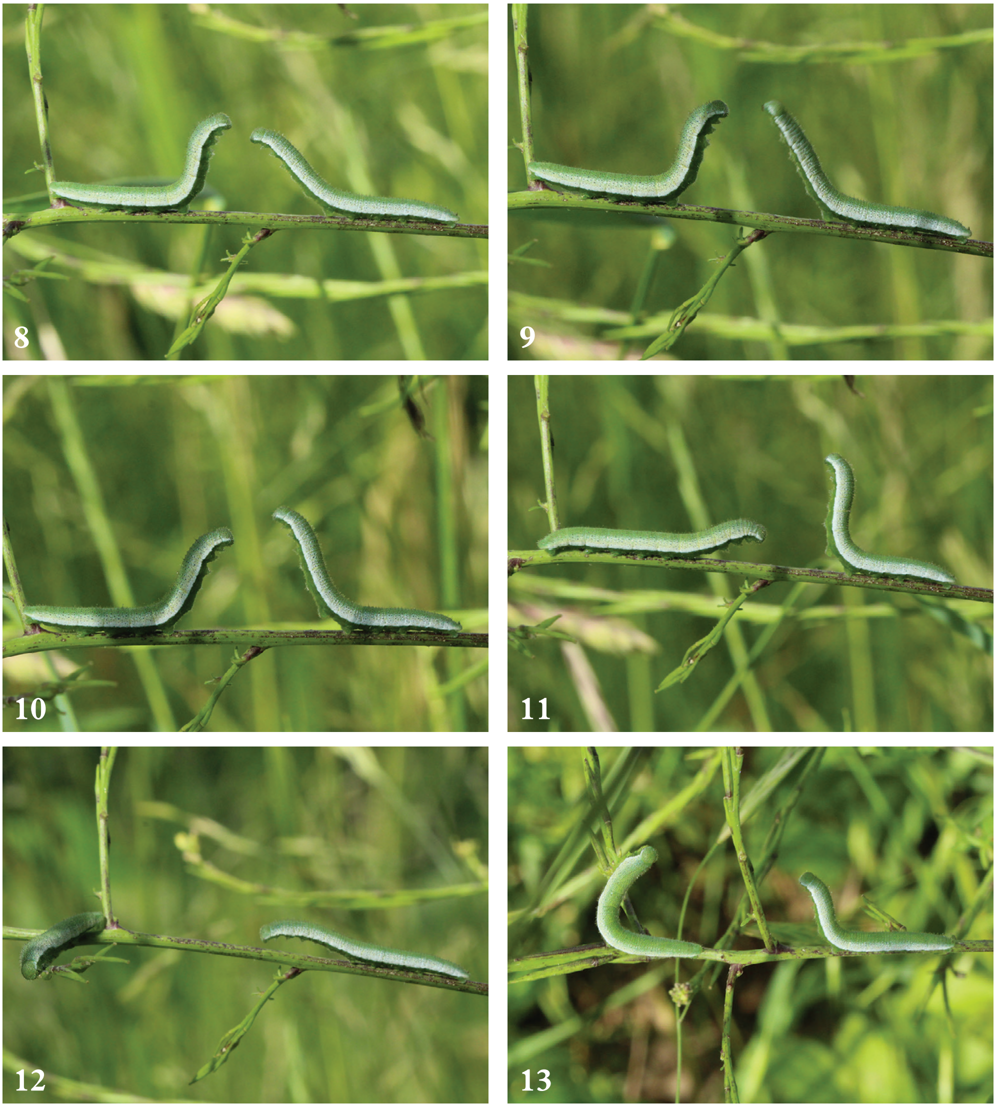
Many books suggest that the habit of the larva in resting along the top of its feeding site, a pod of the foodplant (Fig. 5), renders them well-camouflaged [against visual predators]. This may be true up to and including L3, but I really doubt that it applies in the final instar (and certainly not on these purplish Honesty plants (Fig. 6) which had evidently been preferred for oviposition), when to me the larvae were so conspicuous that I could easily see them from 15 m away if they were on the highest part of the plant (which they so often were). On the two occasions in the above account on which larvae went missing, with predation being the most likely explanation, nearby larvae went unmolested although it is scarcely credible that a predator would have failed to spot them. Moreover, my garden is not short of insectivorous birds. On a large patch of Garlic Mustard seen a few km away on 13.vi.2020 I noticed about a dozen larvae, in comparable stages of growth to those in my garden (this was the check on development rate I was seeking), all the large ones looking highly conspicuous (although of course I am not a bird!), with their pale blue-green colouration contrasting strongly with the much duller green of the pods and stems on which they were resting. I imagined that, far from their seeking camouflage, the acquisition of toxic 'mustard oils' would render them unpalatable to vertebrate predators and, at least in these late instars, allow them to benefit from a spot of sunbathing to speed up metabolism. The rather long feeding period of the instars investigated here, as well as having seen failures on Honesty in the garden in colder springs, suggested to me that digestion processes may be limiting, especially as the pods aged – with longer development times exposing the larvae to more risk.

The carnage

I had hoped to follow the progress of all the caterpillars through to the time that they left the plants for pupation, but on the adjacent plants **M1**, **M2** and **W1** on 9.vi.2020, between early morning and 10.00, tragedy struck. A worker of *Vespula vulgaris* (Linnaeus) (Common Wasp) found the caterpillars and at 9.00 I found the **M1** T/L5 mutilated and dying; within moments the wasp was back, carrying it away. Others had already been taken, and I saw the vespid, or more

Fig. 7. Worker of *Vespula vulgaris* processing part of a larva of *A. cardamines*.

likely two of them, finish the rest off. The larvae were mutilated and either, if relatively small, carried off whole or, if L5, cut up and processed before removal in parts (Fig. 7). In almost every case there was the sign of a struggle; a green smear on the respective pod where, presumably, defensive oral secretion aimed at the predator had ended up. By 10.00 only one larva, **M2** (P9/L4e), remained. I then sat by it for 6 hours, camera at the ready, but although the wasps (sometimes two at once) visited the plants almost every 10 minutes over the next few hours, systematically searching, it was not discovered and by 16.00 it was too cool for either myself or the wasps to persist. At 9.00 the following morning this



Figs 8–13. Chronological sequence showing the encounter between two L5 *A. cardamines* on *Sisymbrium* (see text).

caterpillar, still in proecdysis to L5, was found to have been mutilated and the wasp presumed to have been responsible returned to collect it shortly afterwards (in the time it took me to go back for the camera, which frustratingly I had forgotten to bring!). I have no answer for how this larva (Fig. 3), in full view, had eluded the vespid the day before; it was the only one at the time that was in proecdysis, but the vespids seemed to be hunting visually, not by scent.

Maybe next time

If we are still in this situation next year, I can imagine various interesting manipulations to try. Is the mauve-flowered Honesty of higher nutritional quality than the white-flowered variety? In which instar does cannibalism cease to occur? Would cannibalism be extended to further instars if there were to be real starvation risk on small or seriously overcrowded plants? Do insectivorous birds accept the larvae? And for that matter, what do the caterpillars taste of to us humans?

But I hope to be vaccinated and roaming elsewhere next year!

Part 2. Stand-off on *Sisymbrium*

Helene Otto

Beside woodland near Leipzig, Germany, I was fortunate to witness two final instar larvae in the process of resolving a territorial dispute apparently without violence when they came up against each other on a large plant of *Sisymbrium officinale* (Hedge Mustard). Over a period of 4 minutes just before 17.00 local time, a sequence of photos (Figs 8–13) was taken of the interaction. In the first (Fig. 8), probably soon after the caterpillars had met, the one on the left rears highest. From here, our interpretation of events is that the second caterpillar appears undaunted (Fig. 9) and proves able to rear up even higher (Fig. 10), causing the caterpillar on the left to back down (Fig. 11) and turn away (Fig. 12), though not retreating far. The victor, perhaps unsatisfied by this limited response, followed the retreating caterpillar for a distance (as seen from the changed architecture in the photos), still showing threatening behaviour but without provoking retaliation (Fig. 13) and, once the defeated party had moved further away, the issue seemed to be resolved.

References

Courtney, S. P. 1982. Coevolution of pierid butterflies and their cruciferous foodplants. IV. Crucifer apparency and *Anthocharis cardamines* (L.) oviposition. *Oecologia* **52**: 258–265.

Thomas, C. D. 1984. Oviposition and egg load assessment by *Anthocharis cardamines* (L.) (Lepidoptera: Pieridae). *Entomologist's Gazette* **35**: 145–148.

Frohawk, F. W. 1934. *The complete book of British butterflies.* Ward, Lock & Co, London.

Wiklund, C. & Ahrberg, C. 1978. Hostplants, nectar source plants and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). *Oikos* **31**: 169–183.