NOTES ON THE EARLY STAGES OF THE TRIANGLE *HETEROGENEA ASELLA* ([D. & S.], 1775) (LEP.: LIMACODIDAE)

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Abstract

Observations were made on the larva of *Heterogenea asella* ([D.& S.], 1775), in Devon, England, including descriptions of the first instar, feeding signs and other larval evidence as well as cocoon formation and incidence of parasitism.

Keywords: Lepidoptera, Limacodidae, *Heterogenea asella*, first instar, larval feeding, cocoon formation, parasitoids.

Introduction

Until 2004 *Heterogenea asella* had not been recorded in South Devon (Vice-county 3) since 1891, and was not known from North Devon (VC 4) until 1999 (McCormick, 2001), where, so far, it has been found only in one locality. In 2004 and 2005 respectively, 16 and over 45 larvae were found in two areas about 5 km apart in South Devon.

Modern British publications suggest that the larva feeds on the upperside of leaves of oak (*Quercus* spp.) and beech (*Fagus sylvatica*) high in the canopy. Barker, Fuller & Shreeves (2000) consider threats to the species and conclude that, other than large-scale clearance of trees on which it breeds, any threats are presently unknown due to poor knowledge of its ecology. Ellis (2000) states that it is not clear whether high forest or coppice/recent plantation is the preferred habitat.

Our observations are that the larva does not always occur high in the canopy and, at least on oak, it feeds on the underside of the leaves. We found larvae in areas of mature deciduous trees. We describe and illustrate what seem to be previously unpublished characteristic feeding signs and larval evidence which may enable more records to be made, and provide an account of the first instar and cocoon formation. We also consider the incidence of parasitism, which may have a significant effect on populations.

Distribution and certain historic accounts

Porter (1997) gives the British distribution as Wiltshire, Hampshire, Sussex, Kent, Oxfordshire, Buckinghamshire and Lincolnshire, where it is local in a few mature woods. He omits Warwickshire, Worcestershire, Cornwall and Devon, although records are indicated from these counties according to the distribution map provided for the species by Skinner (1985). Presumably the reason that Porter does not mention Devon is because of the lack of records between 1891 (Basden-

Smith, 1891) and the publication of his book in 1997. The species has also been found in two Essex woods (Waring, Townsend & Lewington, 2003). On this basis, *H. asella* has only been recorded from 12 counties in the British Isles, all in England.

One of the main areas for the species is the New Forest, South Hampshire (VC 11). It may be significant that Goater (1974) gives a number of records from VC 11, but all, apparently, of adults. Several have been published in this journal over the years and, as far as we can trace, for the period from 1880 to date all are of adults, mainly at light, except the following larval records:

at least two larvae, foodplant unstated, in the 'New Forest' in the autumn of 1880 (Jobson, 1881),

several larvae, foodplant unstated, between 1884 and 1892 at Lyndhurst (Hewett, 1890; Hewett, 1893),

a larva beaten from an unspecified source in the 'New Forest' in 1933 (Symes, 1961).

Hewett (1890) records collecting various larvae at Lyndhurst between 15 and 16 September 1890, including one larva of this species on beech 'after about one hour's search'. Later he published a note (Hewett, 1893) which illustrates the avarice of certain collectors. If the species could not be found at Lyndhurst after 1892 then his note shows the potential reason, and so we quote it in full:

'*My experience of* Limacodes asella *may be to the point. When I began collecting these in 1884 I took twenty or so larvae in October at Lyndhurst. Two years after (I could get none in '85) I searched for two hours and took one. I took it at almost the outset, so that my eye was not at fault. I bred that one and went down in 1886 and have been every year up to the present. I took five or six in 1888, I think Mr. H. A. Hill was with me, and took about the same number. Mine all died and so did his. Last year (1891) I took two and bred both. This year I went again, in rather a despairing mood and got several dozens, and Tate of Lyndhurst took two or three hundred I believe. I talked to him about them, and his experience exactly coincides with mine. Obviously then* asella *comes and goes. I hope the few members of the Exchange Club who have had larvae from me got them to pupate as well as mine have done – on the leaf or twigs. I have never taken the pupae in the wilds, nor has Tate. We have both searched carefully. Goodness knows where they go. The larvae must be searched for; no one can beat them in numbers. The picture in the Ray Society book is perfect, and from larvae of mine I believe*.'

We assume that the Ray Society book referred to is Volume 3 of *The larvae of the British Butterflies and Moths* (Buckler, 1888). Hewett lived in Winchester. For at least nine years he visited Lyndhurst and apparently collected every larva that he found, and we presume that, at least in 1892, Tate did the same. Apart from

showing how many larvae he could find, Hewett's note tells us nothing of the species' ecology, not even the foodplant(s) apart from one found on beech in 1890, but it does make clear that the larvae needed to be searched for, rather than beaten. There is, however, one point of interest which is that, at least in 1884, he found larvae in October. We refer to this later.

Lyle (1912) states that in 1911 larvae of this species 'were almost entirely absent' in the New Forest. In the same year Corbin comments (1912) that 'we seldom hear of the large 'takes'… which old Charles Turner … once took so commonly' in the New Forest. This appears to be a reference to adults and not larvae. Whether this apparent reduction in the numbers of the species was the result of over-collecting the larvae or other causes, or both, is a matter of speculation.

Earlier observations on finding the larva

Tutt (1901), possibly based on Hewett (1893), comments that the larva must be searched for and cannot be beaten in numbers. Skinner (1985) states that the larvae of Limacodidae feed on the upper surface of leaves of trees and because of suction or adhesive silk are rarely dislodged by beating. Porter (1997) remarks that the larva can be obtained by beating, but only infrequently, which, in his view, probably indicates that it lives and feeds high in the canopy well out of reach although, as we found, this is not always the case. The photographed larva (Porter, 1997, plate 2: B) is recorded as being beaten from oak, full grown, in late September. This reference to a larva beaten from oak in September is the first published record that we can trace of a larva being found since Symes' note of one in 1933. The only subsequent published record of the early stages of which we are aware is of a larva and cocoon being found on sweet chestnut, *Castanea sativa* and another larva and cocoon on small-leaved lime *Tilia cordata*, both at Stansted Forest, West Sussex on 12 September 2006 (Langmaid, 2007). None of these larval accounts mentions what seems to us to be characteristic larval feedings, at least on oak, that we describe later.

Rediscovery in South Devon

The species was first recorded in Devon on 20 June 1890 by Mr F. J. Briggs (1890) who was beating for larvae during the afternoon and a pair of this species *in copula* fell into his umbrella; the plant or tree from which he beat these is not stated. The locality is given as 'the Plym Valley' and Briggs' address is given as Egg Buckland. He includes this record in some notes from Plymouth (Briggs, 1891), adding that 'I am nearly certain that a third specimen which was secured was the same species, but not knowing the rarity of the species it was discarded, as it had been rubbed in capturing.' This appears to be one of the first records of the species in the British Isles outside of the New Forest, Hampshire. The next Devon record, and the last before 1999, is of a female from an unstated locality

somewhere in 'Plymouth' in July 1891 by Mr H. W. Basden-Smith (Basden-Smith, 1891).

Tutt (1899) summarises the then known localities of the species in the British Isles. He gives the following records from Devon: 'Plymouth (Basden-Smith), Plym Valley (F. Briggs), Kimpton (Rudd)'. The Ordnance Survey Gazetteer of Great Britain published in 1987 gives all place names from the 1: 50,000 Landranger Map Series. It lists 'Kimpton' as a place name in Hampshire and also Hertfordshire, but not Devon and so we believe that Tutt's inclusion of this name was a mistake. We have not been able to trace anything about Rudd.

In the Lepidoptera part of the *The Victoria History of the County of Devon*, Barrett (1906) states that the species had been recorded at 'Bickleigh Vale' by Mr J. Basden-Smith and in the 'Plym Valley' by Mr F. J. Briggs, but does not give any other information, not even dates. There are three places in Devon called 'Bickleigh'. Neither Briggs nor Basden-Smith in their published accounts mention 'Bickleigh Vale' and so we presume that Barrett obtained this name from one of them. There is a Bickleigh Vale within the Plym Valley, itself within the Plymouth area, which is in the far south-west of Devon, and so it is reasonable to assume that the 'Bickleigh Vale' of Barrett is within the Plym Valley and not elsewhere in Devon. This point is strengthened by the fact that in his introduction to the Lepidoptera section of *The Victoria History of the County of Devon* Barrett (1906) mentions that 'Mr W. H. Basden-Smith' had done 'good work' at Plymouth and refers to a 'Mr F. G. Briggs' of Egg Buckland. Eggbuckland (current spelling) is now part of the Plymouth suburbs, although in the late 1800s it was a small village. No mention is made in this introduction of a Mr J. Basden-Smith or a Mr F. J. Briggs, to whom Barrett refers on page 212. We assume that Barrett simply made errors in the initials.

Thereafter the species was not recorded in Devon until just over 100 years later, in 1999, when two males were attracted to light, one on 26 June and the other on 9 July, near Great Torrington, North Devon (VC 4). The next Devon record was in 2004 when RJH discovered early instar larvae at four localities in South Devon (VC 3). On 19, 20 and 22 August 2004 one larva was found on each date, each about 2.5-3 mm in length, and on 29 August two more larvae, about 4 mm in length, were found, all at Lower Hooksburry Wood. On 11 September two larger larvae were noted at Cadworthy Wood and two larvae of a similar size at Dewerstone Wood. On 18 September one larva was discovered at North Wood and on the same day we found six larvae at Cadworthy Wood. Cadworthy, Dewerstone and North Woods are all part of the same complex of woods on either side of the upper part of the River Plym. Lower Hooksburry Wood is about 5 km to the south-east and borders Tory Brook, a tributary of the River Plym. Mature uncoppiced *Quercus robur* is the predominant tree in all these areas, with *Fagus sylvatica* and *Betula* species being the other main trees. The following year over 45 larvae were seen at the same localities between 4 August and 10 September. Those found on the latter date were in their final instar.

All of the larvae were on the underside of *Quercus robur* leaves that were at the ends of branches which, with two exceptions, were at head height or a little above and were discovered by examining leaves which were in reach of the ground; no attempt was made to beat branches, but on a couple of occasions RJH climbed to branches that were about five metres above the ground and found a larva on each occasion. In view of the comments recorded earlier that larvae are rarely dislodged by beating, we tried sharply flicking the top of a leaf held by the petiole and with the larva underneath and observed that this failed to dislodge it.

Most of the trees with larvae were mature and all grew either on the edge of the woods or in clearings, and so the leaves were in sunlight for some, and probably most, of the day. No larvae were found on leaves that were in the shade. It is of interest to note that South (1961) states that the moth flies in the sunshine, chiefly in the afternoon whereas Skinner (2009) states that it flies occasionally in the afternoon sunshine but more frequently at night when both sexes come to light.

Larval feeding signs and other larval evidence

The larvae in Devon were discovered because they make what appear to be characteristic feeding signs until their penultimate and last instars. We cannot trace that these signs have been mentioned in the British literature, but Brooks (1991) describes the feeding of the closely related The Festoon *Apoda limacodes* (Hufnagel), whose foodplants are also oak and beech. She states that:

'The eggshell is not eaten. The larva rests on the underside of the leaf and feeds at the edge. Until it is about 5 mm long, the larva feeds only on the lower cuticle, leaving the upper cuticle intact. This produces a brown filigree pattern on the leaf. After this, it eats the whole substance of the leaf at the tip, feeding actively in sunshine. Due to the absence of prolegs, locomotion consists of a gliding motion with a slight side-to-side rocking. The ventral suckers adhere very firmly to a ribbon of silk which is laid down by the larva, and which in appearance resembles a slug trail ...'

The text is accompanied by photographs of the ovum, larva, in several instars including the first, cocoon, pupa and adults. The slug-like trail which she describes as a ribbon of silk is visible in one of the photographs of the larva on an oak leaf.

From our observations the larva of *Heterogenea asella* feeds in a similar, but not identical, way. Like that of *A. limacodes*, before the penultimate and final instars the larva eats only small parts of the lower cuticle but, according to our observations and unlike that species, it does not feed at the edge of the leaf. Larvae between 2.5 to 3 mm in length feed by excavating an almost rectangular section about 1 mm × 2 mm. The larva makes no more than four or five excavations in any one area of a leaf, sometimes near to but never at the leaf edge, before moving to another part of that leaf to repeat the process. Usually there are no more than 10 groups of excavations on any one leaf, but one leaf which had

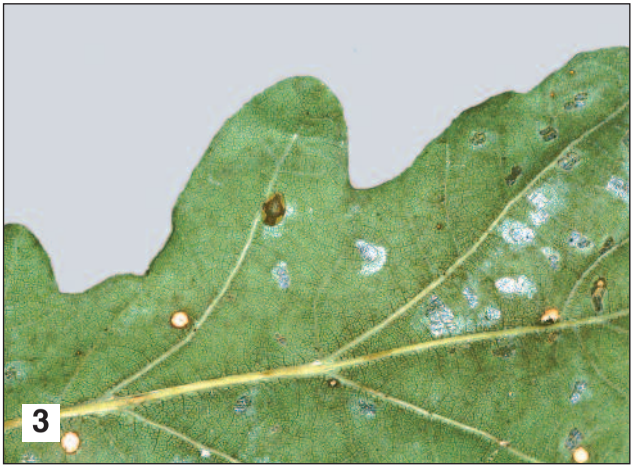

Plate 11. *Heterogenea asella* ([D. & S.], 1775).

Fig 1. Underside of leaf with early larval feeding signs, and larva. Photograph by J. M. Walters. Fig. 2. Upperside of leaf with later larval feeding signs. Photograph by J. M. Walters. Fig. 3. Underside of leaf showing whitish gloss, and larva.

been eaten by a larva about 3 mm in length had 40 groups of excavations. The remaining parts of the upper cuticle which have not been eaten are either pale green or greenish white (Plate 11, Fig. 1), and are quite noticeable when viewing leaves from the upperside, although Fig. 1 shows a leaf from the underside, with a small larva near some of the feeding signs. Indeed, it was these signs that first led RJH to investigate their cause, as in some ways they resembled early feedings of a *Coleophora* species.

As the larvae grew so did the size of the excavations, but none was more than 5 mm long. At this stage some of the excavations went through to the upper cuticle causing holes with part of the uneaten cuticle remaining (Plate 11, Fig. 2). In the penultimate and final instars the larvae ate complete sections of the leaf. The sections eaten were any part of the leaf including the edge, but, except in the final instar, the eaten sections did not cross the main veins and even in the final instar did not cross the midrib. In all instars the larva usually feeds on several leaves with the result that these have a pale green speckled appearance.

Epstein (1996) studied what he terms the limacodid group comprising seven families, including the Limacodidae, and records similar observations. He states that in early instar larvae of the Limacodidae leaf feeding is characterised by the consumption of mesophyll from one surface and that it is not until the third or fourth instars that the larvae feed on the entire leaf.

Larvae of various species, not only of Lepidoptera, feed by scraping away part of the lower cuticle of oak leaves, but there seem to be two main characters which distinguish the feedings of *H. asella*, although one of these also appears to be exhibited by *Apoda limacodes*. One is that feeding by other species usually results in the uneaten parts of the upper cuticle turning brown, but as already mentioned the early instar feeding of *H. asella* results in the uneaten parts becoming either pale green or greenish white. As already noted, Brooks (1991) records that until it is about 5 mm long the larva of *A. limacodes* feeds only on the lower cuticle, leaving the upper cuticle intact, but producing a brown filigree pattern on the leaf. The other is that the edge of the feeding usually betrays a slight whitish gloss caused by a substance produced by the larva which appears to help it adhere to the leaf. In fact quite often this whitish gloss remains as a trail showing the route taken by the larva (Plate 11, Fig. 3). This slight whitish gloss is a subtle character, but one which can be seen by turning the leaf to various angles of the light. The whitish substance did not look like silk to us as it was of uniform appearance and not made up of strands.

The larva has no prolegs. The thoracic legs are small; video footage taken by Mr J. M. Walters of one of the larvae indicates that they appear to have no role in keeping the larva on the leaf. Locomotion was seen to be by means of a wave-like movement of the undersurface of the larva. Observations of a larva on a glass slide showed that most of the ventral surface of the larva was against the glass with no apparent air gap although there were a few areas where there appeared to be an extremely thin layer of trapped air.

Epstein (1996) states that with larvae of the Limacodidae, a family with a worldwide distribution, and those of the Dalceridae, of the New World, he found a liquid on the ventral surface of the larvae which he considers to be, at least in part, semi-fluid silk. He records that this apparently sticky silk is dabbed on the substrate with a brush-like spinneret, sometimes in a figure of eight. Using scanning electron microscopy he found no secretory pores on the ventrum that could produce fluid. We studied the video footage taken by Mr J. M. Walters of *H. asella* larva on a glass slide, but we could not see any secretion from the mouth parts as it moved across the slide.

Epstein, Geertsema, Naumann & Tarmann (1998) state that the specialised ventrum of the larva enables it to adhere to foliage, 'often aided by semi-fluid silk or fluid secreted with the silk from the spinneret, which enhances surface tension.' Hasenfuss (1999), however, takes a slightly different view. He studied adhesive devices in larvae of 71 species of Lepidoptera. He describes the presence of a mobile lipid coating, at least 2 μm thick, on all cuticular surfaces. He states that the adhesive effect of a thin fluid film between two solid surfaces is due to 'capillary' or meniscus forces. The force of adhesion depends on the reciprocal of the distance between the surfaces. He explains that liquid lipids with comparatively low surface tension will work properly as adhesive fluids because plant leaves are covered by a 'wax layer' i.e. lipids with low surface tension. He describes how the fluid will rupture anywhere during detachment leaving tiny involatile droplets adhering to the substance which will remain liquid for months. He states that in *A. limacodes* the thoracic legs are reduced to small appendages, the prolegs are completely absent and the ventral surface of the abdomen is flattened to a very effective sole exhibiting close analogies to the sole of snails. He comments that in contrast to snails, the adhesive fluid is of a lipid nature.

We are confident that the whitish substance left behind on the oak leaf by *H. asella* larva is a thin layer of adhesive lipid secreted by the ventral surface of the larva. The larval shape gives a relatively large ventral surface area/mass ratio which aids the highly effective adhesion.

First instar

The impression given in the British literature is that the larva has the same general appearance in all instars, namely a green or yellowish green body with a broad reddish-brown or purplish-brown dorsal band broadening anteriorly and more so before the middle, giving the appearance of a rough cross or saddle, although sometimes most of the posterior area is reddish-brown or purplish-brown, and with not very obvious spines. From our observations, larvae that are between 2 and 3 mm long and in at least their second instar are often entirely pale green, sometimes with the area that will become the shape of the rough cross or saddle faintly outlined in pale brown, but as they grow this area becomes darker. The first instar, however, appears quite different.

The only accounts of the first instar of *H. asella* that we can trace in the British literature are those given by Standish (1876), Buckler (1888) and Tutt (1899). Standish obtained ova from a captive pairing of the species. He describes the resulting larvae on the first day of their emergence as 'whitish and very minute'; he was not able to provide them with food until their second day and records that he could not get any to feed. Buckler had ova supplied to him, which he kept in a chip box. He observed them changing colour immediately prior to the larvae emerging and says: '*At this critical moment, being otherwise engaged for some hours, I was unable to know that they were hatched and requiring food, though I was keeping them in a glass-topped box in order to observe the changes of colour. When I returned to them all were dead except one, a mere speck, which was slowly moving on the chip; one dead lay at the bottom of the box, and others I found dead, wedged into the junction of the box and its lid. As well as my strongest lens would show them to me, these very small specks of creatures were of an ovate roundish figure, dark brown above and pale greenish beneath, – in short, miniature representations, apparently, in all respects of the mature larva. The solitary living larva I placed on a leaf of beech, and put two other leaves over it, but on looking for it two days later was unable to see it, and concluded it had somehow escaped ...*'. Thus the impression given by Buckler is that, except for size, the first instar is the same as the others, but this is not so. Indeed this was partly recognised by Tutt (1899). He records that '*The* newly-hatched *larva, according to Buckler, is a mere speck, of a rounded ovate figure, dark brown above and pale greenish beneath, in short, a miniature representation, apparently, in all respects, of the mature larva'*, but, in a separate paragraph and under a separate heading, he then goes on to consider the larval spines. We consider that it is worth quoting the whole of what he then says, as follows.

'*The newly-hatched larva appears to be very similar to that of* C. avellana *(*testudo*)* [now Apoda limacodes]. *The spines appear to be in precisely the same position as in that species,* i.e., *a double dorsal row with the alternate members absent, and a lateral series, with a more complicated arrangement on the thoracic segments. Possessing a series of specimens showing the different stages in the process of extrusion, it is equally clear, in fact quite certain, that the spines before hatching are invaginated into the interior of the larva, precisely as in* C. avellana*, and are extruded and assume their exterior position shortly after the larva leaves the eggshell, in the manner thus described in the case of the latter species. There is, however, a very important difference in the structure of the dorsal spines,* viz., *each one has two branches instead of being simple. As it evaginates at first a simple straight portion protrudes, but is seen to enclose not one but two terminal portions, the portions that from the first appear to be stiff and hardened; then the soft evaginating portion divides into an anterior and posterior horn, separating from each other at an angle of 80°-90°, and the hard terminal portions, at first parallel to each other, cross one another at an angle, and finally form the*

extremities of these two branches. There is in C. avellana *a short process about half way up the soft (invaginated) portion of the spine, that seems to have no use or meaning, but is probably the representative of the second spine in* H. cruciata *(*asella*). The principal one of these, that is the longer and rather thicker one, inclines slightly backwards, and is altogether of a length about equal to 3/5 of the diameter of the larva, or about 0.13 mm. The shorter and rather more slender one, which might be regarded as a branch of the other, but which is more nearly equal than that description would imply, points decidedly forwards. The larger branch terminates in a three-spined point, and has several very minute points on its stem: the smaller one terminates usually in two points. The lateral spines appear to be simple (as regards branching), and expand terminally into a three-spiked coronet (Chapman).*'

Despite the detail recorded, no mention is made of the colour of the first instar larva. We have not been able to trace whether what Tutt says about the spines was taken from a publication by Dr T. A. Chapman or information which he gave Tutt.

On 11 August 2005, RJH found six larvae at Lower Hooksburry Wood. Four that were between 2.5 and 4 mm long had the typical appearance of the larvae illustrated by Buckler (1888) and Porter (1997), although the one that was 2.5 mm long was entirely pale green. Two others, both on the same oak leaf, were 1 mm long and were presumably first instar. They differed significantly from the other four. Confirmation that they were *H. asella* was provided a day or so later, when, after ecdysis, they took on the appearance of the other larvae. The following description was made by examining both those larvae under a microscope. Unfortunately, during the time of observation their heads were always retracted and so could not be described:

Body translucent whitish, with no indication of the rough cross or saddle that usually appears in the second instar, with creamy white contents, 10 pairs of erect spines on dorsum each branched from near base into two with a minute brownish bifurcate tip to each branch, remainder of body covered with unbranched setae each having a similar minute brownish bifurcate tip. The setae along the lower edge of the body are more or less at right angles to it. The appearance of the larva is like a minute sea-urchin. Following ecdysis, the 10 pairs of branched spines are lost and are replaced with unbranched firm black, or brownish black, spines which are not erect but are at an acute angle to the body with the two spines in each pair crossing each other. The unbranched setae of the first instar are not replaced, but the body is covered with what Buckler describes as pubescence and which in fact are minute spines. It then assumes the colour and markings described above on page 104.

Brooks (1991) has photographs of the first, penultimate and final instars of *A. limacodes*. She states that when newly hatched the head is black and the body white and spiny, and this account is clearly shown in the photograph, but after successive moults the body becomes greener and the spines shorter. Epstein (1996) notes that in the Limacodidae the first instar larvae usually differ from the

later instars in the types of setae or in the degree of spinosity. He says that this is exemplified by species having late instars that are smooth-backed and non-urticating, and that these species have first instars with bisetose tubercles or warts which are lost in subsequent instars.

Other observations

On 23 and 24 August 2005, RJH observed two approximately half-grown larvae eat their shed skins following ecdysis. Both fed with their heads retracted beneath the thorax, clasping the old skin by using flaps on each side of the prothorax. The entire skin was consumed, including the dorsal spines. Epstein (1996) describes the same method of feeding, using flaps on each side of the prothorax, on leaves for middle to late instars of the Limacodidae.

There is the possibility that the female adults may use the same trees each year for egg-laying. RJH noted in successive years that larvae could always be found on certain trees, but other trees within no more than a 50 metre radius and with a similar aspect in the open apparently had no larvae. If this is not just coincidence then the question arises as to whether this is because the female usually does not leave the tree on which it developed from the egg or, if it does, whether some trees have attributes which others lack.

Tutt (1897) states that he knows nothing of the habits of the adult except that when breeding the species he found that they copulate at mid-day and fly about the breeding cage in the afternoon. It may be significant that in the same note he describes the female of *A. limacodes* as lethargic and falling down to the ground when disturbed by beating whilst the male 'flies wildly'.

Oates (2008) describes the use of certain trees by male Purple Emperor butterflies *Apatura iris* (L.) in mate-location strategies and concludes that the most favoured sites are those out of main air turbulence and that gaps in the canopy foliage density appear to be an important factor. Interestingly, he also reports that when a male searching for a female flushes out a mated female, she will drop like a stone to the ground. Newland (2009) states that the combination of shelter and canopy gap also seems to be important in the choice of sites by male Purple Hairstreak butterflies *Neozephyrus quercus* (L.). Although these observations are on the choice of sites for two butterfly species, they may be indicative that areas with gaps in the canopy have an important role for other Lepidoptera. Further, if females of *H. asella* readily drop to the ground in the same way that *A. limacodes* do according to Tutt or as mated females of *Apatura iris* do according to Oates, then the question is whether they then attempt to ascend by crawling up the trunk of a tree, or by flying. If they normally crawl then the chances are high that they will return to the tree from which they fell.

Where the cocoon is formed on the leaf, as recorded by Langmaid (2007), then a very limited dispersal may be possible due to wind action during the winter months.

Cocoon

Skinner (1985) states that the cocoon is described by Tutt (1899) as a quarter of an inch long, dark brown marbled with grey and it is either on a leaf or in the fork of a twig. Langmaid's observations refer to the cocoons being found on leaves and not on twigs (J. R. Langmaid, pers. comm.). Tutt's account appears to be based on Buckler (1873). Although a moth emerged from the cocoon described by Buckler, he does not state that the cocoon has a hinged lid at one end which opens on eclosion of the moth, and Tutt does not mention this either, but Skinner (1985) does in his account of the Limacodidae.

On eclosion the pale yellowish brown exuviae are partially extruded from the cocoon, but this is not mentioned in any of the above publications, nor can we trace any reference to this in the British literature. Porter (1997) states that the cocoons of *A. limacodes* and *H. asella* are boat-shaped, but according to our observations the cocoon of *H. asella* is oval-elliptical. SDB was able to observe the cocoon formation over a twelve hour period on 28 September 2005, making detailed notes at least every 30 minutes and often more frequently than that. The following is a summary.

Almost at the outset the larva lost the definition of markings and during most of the time whilst it was visible the larva was 'hunched up' with the head tucked down. The dorsal vessel pulsated very frequently. For approximately the first five and a half hours the larva produced silk intermittently, often in short bursts of activity, but without forming a cocoon. During this time the larva rotated its position several times and occasionally raised itself up to produce silk. After about five and a half hours the larva began a period of intense activity starting by backing under some of the silk already produced and then spinning more silk so as to eventually enclosed itself completely, but larval activity was still discernable through the cocoon as it was being formed. On occasions it was clear that the larva was lying on its dorsum, producing silk. At one point the larva moved through a vertical, lateral and horizontal position in one minute. Rotational movement within the cocoon continued periodically. This activity seemed to be completed when the larva eventually ended up on its dorsum, with a hole visible at the head position, although this eventually became covered over leaving an indentation indicating the final position of the head. About eight hours after observations commenced the cocoon was fully formed. In the final three hours of observation the cocoon gradually became chalky white/grey and pitted overall.

Foodplants and phenology

Before 2006, the main known foodplants in England were oak and beech, but now sweet chestnut and small-leaved lime must be added (Langmaid, 2007). There is the possibility that on at least one occasion larvae have been found on birch *Betula* sp., because Fletcher (1880-81) comments that a few larvae were 'taken' off oak and birch in September. Fletcher was an accurate observer and so his

reference to birch must be correct unless he had written 'beech' and an editorial or typographical error changed this to 'birch'.

There is also a curious record from poplar, *Populus* sp. At least two 'quite large' larvae were found feeding on the leaves sometime between 1929 and 1931 at Seaford, Sussex (VC 14), which is on the coast (Lanktree, 1960). The exact date and year is not known. Lanktree states that '*Although the year is no longer certain (part of each of the summers mentioned was spent in this locality, but no contemporaneously written account exists now), the month was almost certainly July; it so happens it could not have been later in any case, and it is very unlikely to have been any earlier*.' He notes that although they were fed for some weeks on poplar they failed to survive. It is not clear whether he means that they died before pupation or that they pupated but moths did not emerge. He also records that when he found the larvae he was 'rather young, but well enough acquainted with South's works'. Although the species is not known to be migratory, he wonders if the larvae could have been the progeny of a female of continental European origin. Even if it was not until the end of July that larvae were found, in our experience it is surprising that at such a date they were 'quite large'.

According to genealogical records, Lanktree was born on 16 June 1919 in Malaysia and arrived in Britain, aged 11 months, on 31 May 1920 on the board the *SS Mentor*. He died on 18 June 1975 at Kitchener, Ontario, Canada. Thus, in July 1929 he was 10 years old and in July 1931 was 12, and so would indeed have been 'rather young' as mentioned in his account. Bearing in mind that at the time they were found Lanktree was no more than 12 years old, probably had not previously found undoubted larvae of the species, apparently relied on what would have been a monochrome plate of the larva in an edition of South's *The Moths of the British Isles* and by the time that he published the record, some 30 years later, no contemporaneous written account existed, it would be understandable if some mistake had arisen.

Hewett (1893) found about 20 larvae in October, but we found larvae from 4 August to about the third week in September. A sample from two small areas over two years, 2004 and 2005, may not be representative for other parts of England, but if it is then it appears that the larval stage may cease a few weeks earlier than about 100 years ago.

Parasitoids

On 19 and 20 August 2004 RJH found one 2.5 mm long larva on each day from each of which a parasitoid larva emerged two days after collecting; both spun cocoons. An adult parasitoid emerged on 31 August 2004 from the larva collected on the first date. The second parasitoid died during emergence and was noticed a few days after 31 August 2004. The specimen that emerged is a female *Dolicogenidea* (or *Apanteles*) *lacteicolor* (Viereck) (Hymenoptera: Braconidae, Microgastrinae) (det. M. R. Shaw), and it is likely that the other is conspecific. It

is an interesting species because it was imported into North America to control *Euproctis chrysorrhoea* (L.). According to M. R. Shaw (pers. comm.) the host range is that of very early instars of hairy or at least pubescent larvae on trees/bushes, and it is known from Lasiocampidae (*Malacosoma*), Lymantriidae, Arctiidae (*Spilosoma, Hyphantria*), Nolidae, Noctuidae (*Acronicta*) and now Limacodidae.

Three of the larvae collected on 11 September 2004 produced parasitoid larvae that all made cocoons between 22 and 25 September 2004; adults did not emerge until the following year. These were all *Phobocampe alticollis* (Thomson) (Hymenoptera: Ichneumonidae, Campopleginae) (det. K. Horstmann), which has also been reared from *Apodes limacodes* from Berkshire, Essex and The Netherlands (M. R. Shaw, pers. comm.). Adults have emerged in March and April under outdoor temperature conditions (M. R. Shaw, pers. comm.), which might suggest that it needs to use other hosts early in spring.

Whilst we were searching for larvae we noticed adult parasitoids crawling over the leaves. As the larvae sit exposed on the leaves they must be an easy target for parasitoids. If this percentage of parasitism is typical, then this may be a significant factor in the scarcity of this species in the British Isles.

For this reason when RJH found larvae again in 2005 at two localities he collected several in order to observe the extent of the parasitism with the intention to return either the resulting cocoons or moths to their places of origin. In fact this was not possible because all the larvae collected produced parasitoids. Seven male and nine female *Apanteles lacteicolor* were reared from larvae collected at Lower Hooksburry Wood and one male of the same species was reared from a larva from Dewarstone Wood.

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