

Ecology and predation of *Sesia apiformis* (Clerck, 1759) (Lepidoptera: Sesiidae)

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Synopsis

During 2013, the authors studied the emergence of *Sesia apiformis* from a hybrid black poplar tree in Cambridge (Newland & Sawyer, 2014). In 2014 they continued their study and 18 moths emerged some three weeks earlier than in 2013. For the first time, the escape of an adult male from its pupa was watched and photographed. Predation of adult moths by birds before the moths had dried their wings or completed mating and ovipositing was exceptionally heavy. Possible explanations for the early emergence and high rate of predation are suggested.

Key words: Lepidoptera, Sesiidae, *Sesia apiformis*, eclosion, exuviae, thermal-time, predation, mimicry.

Introduction

In our previous paper (Newland & Sawyer, 2014) we reported our observations of the emergence in 2013 of adult *Sesia apiformis* (Clerck, 1759) from a hybrid black poplar tree in Cambridge. In 2014 we made similar observations, monitoring the tree every day from 4–19 June. During this period, 18 adult moths emerged, the last on 15 June. Details are given in Table 1. Exit galleries were more evenly distributed around the circumference of the tree than before but mainly avoided areas of bark used last year. Several moths emerged from the western side which had not been used in 2013. The heights of the exit holes (where known) are listed in Table 1.

It can be seen that all the moths emerged during the first two weeks of June 2014. Their number was unusually large, 18 being recorded between 4–15 June. In 2013, 10 moths had emerged about three weeks later, between 24 June and 3 July. In earlier years, one of us (TJS) has looked for *Sesia apiformis* on this tree at approximately 08.00 h. Typically one or two moths had been seen per year, usually in the second week of June (although more could have emerged unnoticed). On that evidence, we conclude that moths emerged early in 2014, and late in 2013. We comment below on possible reasons for this difference in timing and for the high rate of predation in 2014.

History of emergence of adult moths

Our early morning (about 08.00 h) inspections revealed no moths on the tree until 7 June. However, two empty pupal exuviae were found protruding from the trunk on the afternoon of 4 June. From these exuviae, we discovered that one had

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Table 1. Details of the eighteen moths that were found in 2014.

Date 2014	Temperature at 10.00 h (°C)	Identifying number	Sex	Height of exit hole (m)	Diameter of segment of pupal exuviae behind wings (mm)	Length of pupal exuviae (mm)
4 June	12	1	male	0.54	6.5	25.2
		2	female	0.25	8.0	28.4
7 June	14	3	male	0.23	6.6	26.7
		4	female	0.46	8.6	30.1
		5	male	0.58	6.9	25.2
8 June	21	6	male	0.50	6.6	26.6
10 June	18	7	male	0.00	6.0	23.3
		8	male	0.23	6.7	27.4
		9	male	0.00	6.6	27.6
11 June	15	10	female	exuviae not found	-	-
13 June	18	11	female	0.42	7.8	29.7
		12	female	exuviae not found	-	-
		13	male	0.09	6.9	25.8
14 June	17	14	male	0.22 exuviae eaten by bird	-	-
		15	female	0.14	8.0	30.7
15 June	15	16	male	exuviae found fallen on ground	6.9	24.5
		17	male	0.25	6.6	24.9
		18	female	0.17	7.8	29.4

been a male and the other a female moth. We presumed that they must have emerged after 08.00 h, after which they had time to mature, possibly mate, and leave the tree before we discovered their exuviae.

No more moths emerged for three days until 7 June when the tree was monitored from 07.15 h for about an hour, and no new emergences seen. The following day, 8 June, the tree was monitored from 07.00–09.00 h. On arrival at 07.00 h, DEN found three protruding exuviae; either these had emerged after about 08.00 h on 7 June, or before that time on 8 June. We concluded the former and, in Table 1, record these moths as having emerged on 7 June. By examining the exuviae, we found one had been a female and two had been males. Only later did we conclude that, possibly, these moths may have emerged on 8 June before 07.00 h and been immediately predated. A fourth (male) moth emerged at 07.15 h and was closely monitored until 09.00 h when it was still on the tree when the observer (DEN) left. Because 8 June was the hottest day of the emergence period, that may have hastened the time of day when eclosion occurred.

No moths or exuviae were seen on 9 June. At 08.30 h on 10 June, TJS discovered three exuviae but only one male moth on the trunk.

When discussing what was occurring, it was suggested that a Magpie *Pica pica* (Linnaeus) might be taking resting moths from the trunk. This had been observed occasionally in the past (Northfield, 2014). At that point, we realised that predation may be a problem and perhaps an explanation of why we had not seen as many moths as exuviae.

The next day, 11 June, we monitored the tree continuously from 07.00–09.30 h and thereafter intermittently until 13.00 h. At about 08.30 h, one female was discovered, not on the trunk, but on a nearby ivy leaf about one metre from the trunk. Shortly after, a male arrived and attempted (unsuccessfully) to mate with her. We moved her to the trunk at about 09.00 h and within a few minutes the same or another male flew in and successfully mated with her. They remained together until the male flew off at about 12.30 h. The female remained on the trunk until 13.00 h, when monitoring had to be discontinued. No ovipositing was observed. By studying photographs, we determined that the male was very probably the one that we had seen on 10 June.

No moths emerged on 12 June. On 13 June, one of us (TJS) arrived at 08.00 h to find that two females and one male had already emerged. Continuous monitoring could not be arranged, but frequent visits were made to the tree. The male subsequently mated with one of the females. The other female appeared to be a deformed specimen. It had disappeared from the tree by 08.40 h. The mating pair had both disappeared by 11.00 h. We do not know whether they flew away or were eaten by a predator. There is evidence that moths do sometimes leave their parent tree shortly after mating (Northfield, 2014).

On 14 June, a relatively cooler day (see Table 1), monitoring (DEN) was continuous from 06.45–09.00 h. A male emerged at 07.25 h and a female at 07.55 h. They were on opposite sides of the trunk. While photographing the female, the male was out of view and at 08.00 h it had disappeared. Its wings were not yet fully inflated and it could not fly at this time. A search was immediately made to look for it on the ground nearby but it could not be found. However a Great Tit *Parus major newtoni* (Pražák) was found in the vicinity and it settled on an old iron railing about 0.5 m from where the male had last been seen.

Subsequently it was necessary to leave the tree for a few minutes. To protect the female, which was still inflating her wings, camera equipment with two tripods were positioned as closely as possible to the stationary moth. On returning, this moth had also disappeared. A Great Tit was perched on one of the cameras, very close to where the moth had been. On being disturbed, the bird showed little fear and flew slowly round the trunk, apparently searching for further prey.

Our subsequent investigations identified a Great Tit's nest and that of a Blue Tit *Cyanistes caeruleus obscurus* (Pražák) in a tree about 100 m to the south of our hybrid poplar, both nests containing fledglings. There was also another Blue Tit's nest about 200 m away to the north. During later monitoring, we observed both Great Tits and Blue Tits patrolling the area, and pairs of birds passing the tree, sometimes hopping through at ground level. We have concluded that many of the moths that emerged this year had been taken by these birds, usually before ovipositing has been possible.

Only one more moth was seen. On 15 June, one of us (TJS) was present from 07.00 h. Two new exuviae were found, one on the ground and one protruding from the tree, and we suppose that these moths had been taken by birds. A third, female moth emerged about 09.00 h and at 10.00 h she began calling, but no male appeared, so at 11.00 h she was removed from the tree and kept in the hope that we would later find a mate for her. Unfortunately no more moths emerged from the tree. We attempted to find a male *Sesia apiformis* from a known colony in Suffolk and from a stand of Black Poplar trees at Bassingbourn, Hertfordshire,

using pheromone attractants² at the latter, but without success in both cases, and after three weeks the last moth to emerge had died.

Exit locations

Of the 18 moths that had emerged, we identified the protruding exuviae of fifteen of these. In three cases the pupal remains could not be found and we concluded that these may have been removed by predators. Moth no. 10 was a female that we had found on an ivy leaf at ground level. Probably this had emerged at or just below ground level from a root, but we were not able to find its exit hole. Moth no. 12 was also a female and found on the trunk, but it appeared to be damaged. It had an unusually black body and a damaged wing. It disappeared shortly after we had found it. The pupal exuviae of moth no. 16 was found on the ground and this moth was never seen. We presume that it had been taken at or shortly after eclosion when the exuviae had been disturbed and fell to the ground.

We measured the height of each of these 15 exit holes and the circumferential distance (at ground level) from the exit hole of moth no. 2. These data are plotted in Graph 1 (represented by diamonds). Graph 1 shows height plotted against circumferential position normalised against the points of the compass. The zero position is the point on the trunk that lies on an east-west line at the closest point of approach to the adjacent university building. Tennis Court Road is on the west side of the tree.

For comparison, the corresponding data for the 10 moths that emerged in 2013 are plotted on the same diagram (represented by squares).

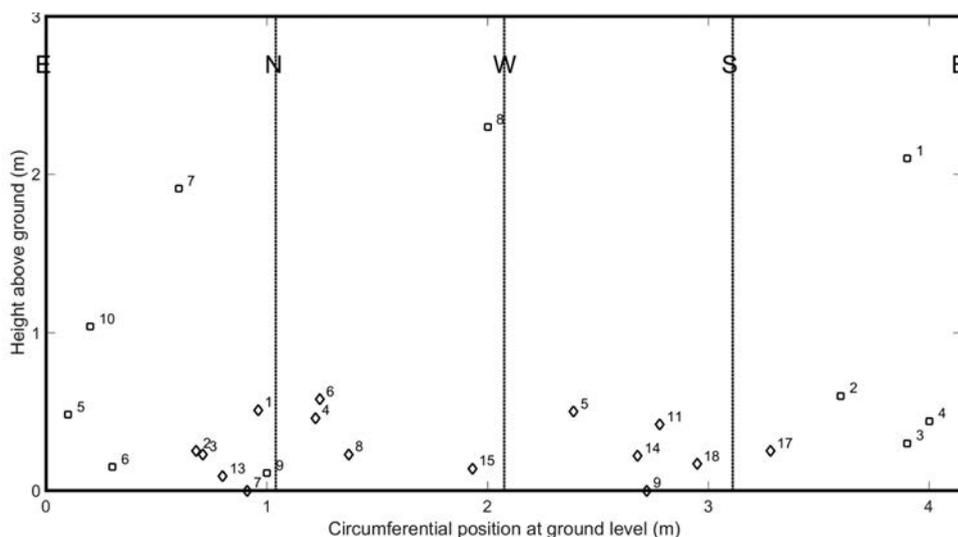
The average height of the exit holes discovered in 2014 is 0.27 m. In 2013 it was 0.94 m. The difference can be attributed largely to the occurrence, in 2013, of three exit holes at a much higher level than the other seven, the highest being 2.3 m.

Although the exit positions found in 2013 were mostly on the eastern side of the trunk, in 2014 they are more evenly distributed around the circumference. The 2014 exit holes largely avoided that part of the trunk used in 2013. Circumferential positions in 2014 only overlapped those of 2013 in two cases. The lowest exit hole found in 2013 was at a height of 0.11 m, while two were at ground level in 2014, moths emerging from tree roots, one of which was about 65 mm below the soil surface. This pupa had to climb through 65 mm of soil before eclosion could occur. Photographs of a cocoon found close to ground level (specimen no. 18), with the pupal casing retrieved from this location, are shown in Figs 1 and 2.

Dimensions of exuviae

As in 2013, the diameter (the largest diameter) and length of the pupal casings were measured for all 15 exuviae recovered in 2014. The results are plotted in Graphs 2a and 2b. These show the 2013 results in black and 2014 results in red. As before (Newland & Sawyer, 2014), males are plotted as square points and females as diamond-shaped points.

² Pheromone lures supplied by Anglian Lepidopterists' Supplies www.angleps.com



Graph 1. Locations of exuviae found on trunk; squares 2013, diamonds 2014.

A digital vernier was used for measurement. Obtaining exact measurements from discarded exuviae is difficult because some pupae have curled more than others, so estimates have to be made for some specimens. Accuracy is typically ± 0.2 mm on diameter and ± 0.5 mm on length, which is about $\pm 2\%$ in both cases.

Our conclusions from these graphs are that, on average, pupae were plumper in 2014 than in 2013 and slightly larger overall. Their average diameter-to-length ratio (Fig. 2b) was 0.264 in 2014 compared with 0.245 in 2013 (a statistically significant difference, p -value 0.005). Since the 2013 moths emerged about three weeks later than those in 2014, this result might be thought surprising. However, the exceptionally warm spring in 2014 may have been a factor in growth of the moths and their host tree.

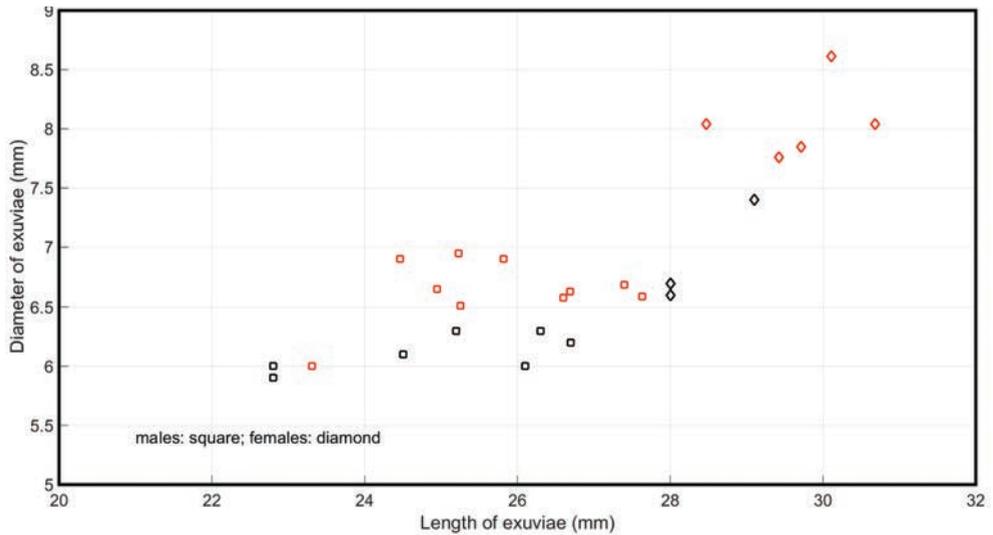
Influence of temperature

Historic temperature records for Cambridge (Meteorological Office, 2014) give daily maximum t_{max} and minimum t_{min} temperatures, averaged on a monthly timescale. The results of plotting $(t_{max} + t_{min})/2$ for the last four years are shown in Graph 3. The time base is measured in months, starting at 1 for January 2011 and finishing at 48 for December 2014.

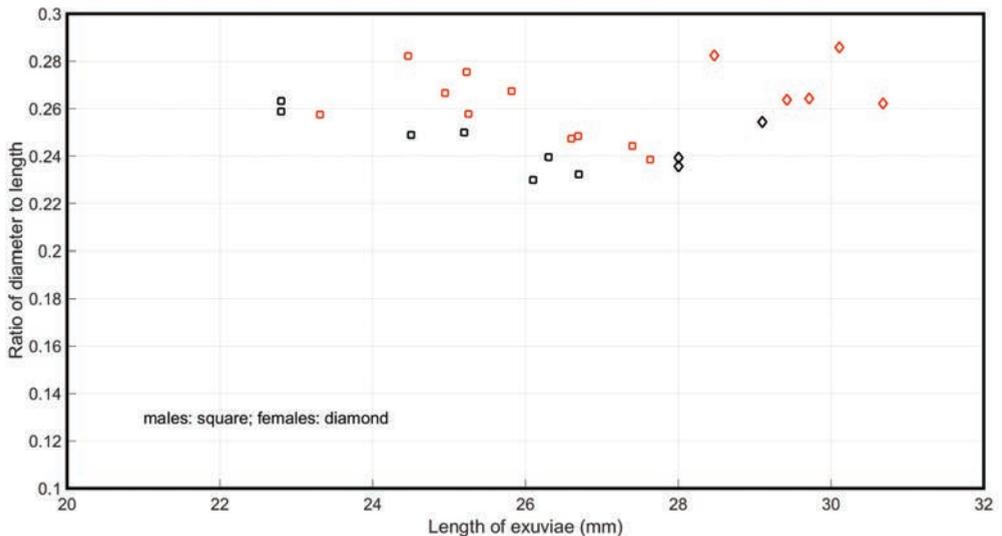
A green line marker is placed at mid-June 2011, when it is assumed that the 2013 cohort of moths would have begun their metamorphosis, and a red line marker at mid-June 2012 for the 2014 cohort. Double green lines at June/July 2013 and double red lines at early June 2014 indicate the known period of emergence of the 2013 and 2014 moths.

It can be seen that the 2013 cohort experienced colder winter temperatures in 2012–2013 than the 2014 cohort experienced in winter 2013–2014. This may have been a factor holding back the development of the 2013 cohort.

It is interesting that research on the effect of temperature on the rate of insect and plant development has suggested that a driving factor is the product of

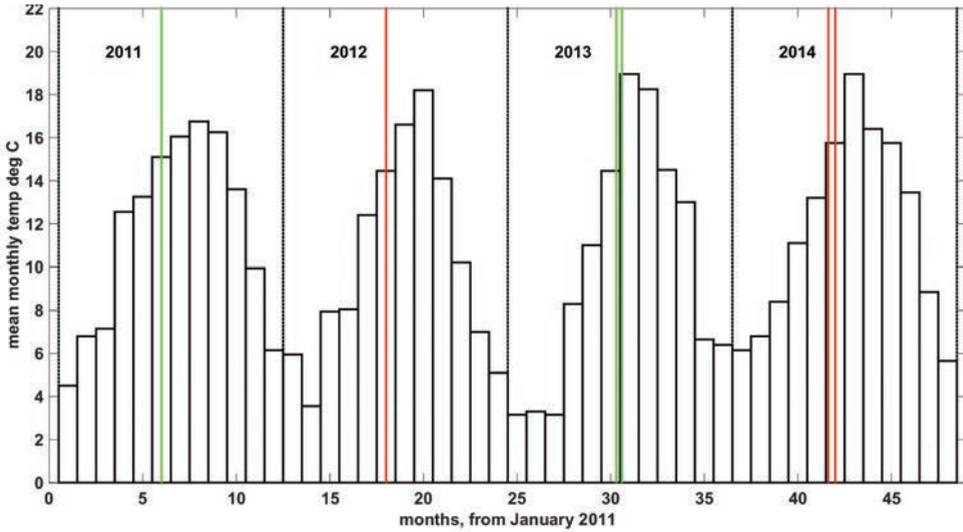


Graph 2a. Diameter versus length of pupal exuviae (maximum diameter measured behind wing case). 2013 results black, 2014 red.

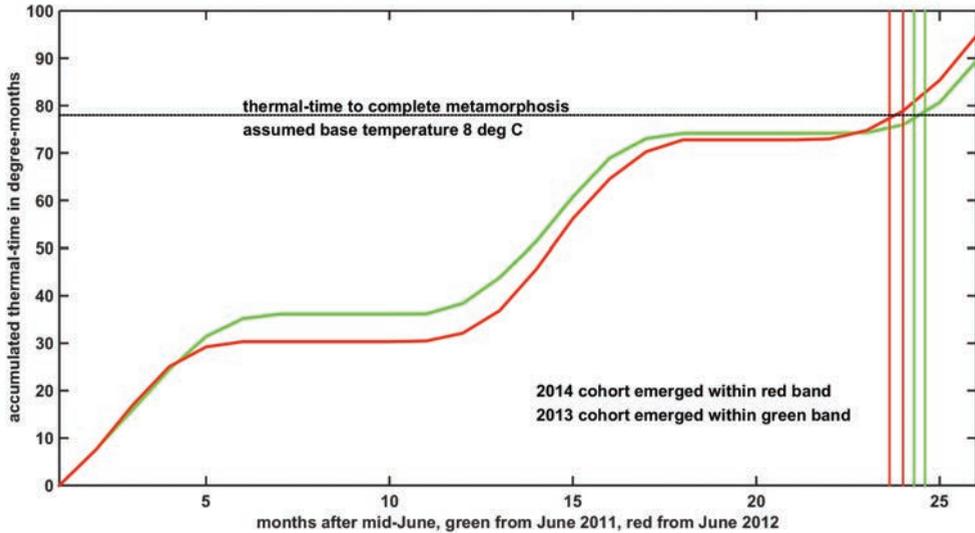


Graph 2b. Ratio of diameter to length of pupal exuviae. 2013 results black, 2014 red.

temperature \times time, subject to temperature being measured above a base temperature (see, for example, Trudgill *et al.*, 2005). This product of temperature \times time can be calculated from the data above. The choice of base temperature depends on the species involved, but taking, for example, 8°C gives Graph 4. The green graph shows how thermal-time accumulates starting from zero at mid-June 2011. The red graph shows the build-up from mid-June 2012.



Graph 3. Monthly mean temperatures in Cambridge between January 2011 and December 2014.



Graph 4. Build-up of thermal-time, calculated for a base temperature of 8°C for 2-year periods starting in mid-June 2011 (green) and mid-June 2012 (red).

These results suggest that, by their first winter, larvae that started their development in mid-June 2011 would have matured more than those that started in mid-June 2012. However, this difference would have been largely nullified by faster development during the summer of 2013 compared with the summer of 2012. During their second winter, larvae of both cohorts would have been at substantially the same stage of development, but faster development during the

spring of 2014 would have completed development of the 2014 cohort several weeks ahead of the 2013 cohort in the previous year. Although choosing a different base temperature (in the range 2–12°C) changes the calculated magnitude of thermal time, the conclusion remains unchanged that the 2014 cohort accumulated more degree months in the spring of 2014 than the 2013 cohort did in the spring of 2013.

It has been suggested (Dennis, 2015) that the location under the bark of maturing larvae may have affected their rate of development. Larvae in galleries where the bark is subjected to sunshine might be expected to mature faster than those on the shadowy side. Because of scrub around the tree, only its eastern side was unshaded. The north and south sides were partly shaded and the western side in almost permanent shade. In 2013, most of the moths emerged from the eastern side, but in 2014 the eastern side was largely ignored. We do not have enough data to reach any definite conclusions about this, but it is interesting that the two moths that emerged on the west side of the tree (one in 2013 and one in 2014) were two of the last moths to emerge.

The above analysis assumes a two-year life cycle. There have been suggestions that larvae may pupate in November of their second year. If that is the case, spring weather will be affecting development of the imago rather than the larva and the adult's size will have already been determined. Špatenka *et al.* (1999) say that the larva constructs its cocoon in the autumn but does not pupate until the following spring. They also suggest that the life cycle of *S. apiformis* may sometimes last for an additional year in the larval stage. For the American *S. tibialis* Harris, 1839, which is a very similar species, there is reliable information that that species pupates in the spring only shortly before the adults emerge (Anweiler, 2007). The upshot is that there is uncertainty about whether or not spring weather affects the size of *S. apiformis* as well as its date of emergence.

Although this analysis is highly theoretical, it lends support for the theory that rate of development depends on the combination of temperature and time. For insects, there is not as much published work as there is for plants, about which much has been written to support the theory that the product of temperature above a base level multiplied by time is a good indicator of the progress of plant development (see, for example, Last & Roberts, 2013). But temperature regulation by insects is more complicated and their body temperature may be several degrees different from the ambient temperature (see, for example, Kührt, Samietz & Dorn, 2005, and Bryant, Bale & Thomas, 1998). This, combined with the expectation that rate of development is not linearly proportional to temperature, considerably complicates thermal-time calculations for insects.

Observation of eclosion

Our observations in 2014 largely confirmed those reported for 2013 (Newland & Sawyer, 2014). In 2014 we were able to retrieve a complete cocoon of specimen no. 18. This had been close to the outer surface of bark that had broken away (Fig. 1). By sectioning this cocoon and then placing the retrieved pupal casing in position within the half cocoon, it can be seen that the pupa does not fit tightly within its cocoon (Fig. 2). The inner surface of the cocoon remnant is lined with a thin clay-like substance. The fibrous lining of the exit gallery, visible from

outside after the pupal casing has been withdrawn, does not extend into the cocoon remnant. There appears to be ample room for relative movement of the rear of the pupa within its cocoon.

We were able to watch and video a moth emerging from its pupa (specimen no. 6 on June 8, a male). The extruded pupa was first seen immediately after it had broken through the bark and translated so that about a third of its overall length was exposed. After a rest period of approximately three minutes, this moth took under a minute to free itself from its casing. As soon as it had pulled free, it expressed a relatively large volume of liquid meconium in a matter of only some 10 seconds before crawling higher on the trunk to allow its wings to expand and dry. Three stills taken from the video of this process are shown in Figs 3–5.

By taking careful measurements from the video stills, it has been found that the rear three segments of the moth's abdomen visibly shorten by about 20% of their length as fluid is expressed. By counting the droplets of liquid expelled and estimating the volume of each, the total volume expelled can be compared with the size of the moth's abdomen. Making this measurement, it appears that a volume equivalent to about 70% of the residual volume of the rear three segments had been expelled during the first 10 seconds of the moth's adult life.

An approximate estimate of the velocity with which fluid is expelled by the newly emerged moth can be made by measuring, to scale, how much the jet of liquid shown in Figure 4 departs from a straight trajectory. This deviation is illustrated in Figure 6, where the stream of fluid is compared with two straight paths from the moth's abdomen. It is concluded that the moth ejects liquid at a velocity of about 1 metre/second and that the abdominal pressure needed to reach this velocity is represented by a static head of about 6 cm (i.e. the internal abdominal pressure required would support a static head of liquid of 6 cm). Details of this calculation are given in the Appendix.

Although we saw specimen no. 6 before it had escaped from its pupal casing, we did not observe this pupa breaking through the bark surface. As far as we know, there have been no records of that process having been observed in the wild. We have, however, been told of observations of *Sesia bembeciformis* (Hübner, 1806) in Devon (Walters, 2004) where part of the eclosion movement was filmed. Recording started with the pupa extending about one quarter of its length out of the bark. There are several seconds of video in which the pupa appears to lever itself further out, but then retracts, before trying again. Eventually, when about a third of its length is exposed, movement of the pupa stops for a rest period, preceding the pupal casing bursting open and an adult moth escaping. Except that it starts slightly earlier, this video is very similar to the one we recorded for *S. apiformis*.

We are still unable to be certain about the mechanism by which a pupa escapes from its host tree. A possible mechanism was discussed in our previous paper (Newland & Sawyer, 2014). This involves the pupa bending from side to side, but not stretching longitudinally. Since the operative portion of the pupa remains within its cocoon in its exit gallery, it cannot be seen. However, that part of the pupal casing that is visible in the *S. bembeciformis* video (Walters, 2004) does not show any obvious longitudinal stretching or relaxation of the pupal casing. The free end of the pupa appears to move bodily in and out, without obvious stretching. An explanation for its in and out movement could be that the



Fig. 1. Cocoon close to ground level after removal of loose bark and its partial extraction by grasping with tweezers.



Fig. 2. Cocoon from Fig.1, after sectioning, with the pupal casing that had been within it.



Fig. 3. Adult starting to escape from pupal casing.



Fig. 4. Fully emerged adult extruding a stream of liquid meconium.



Fig. 5. Emerged adult completing extrusion of liquid.



Fig. 6. Magnified part of Fig. 4, showing the falling parabolic trajectory of expelled liquid. The liquid stream is bracketed by two straight yellow lines.

adminicula on its rear segments lose their grip on the inner wall of their cocoon so that, as the rear of the pupa bends for another thrust, grip is lost and the pupa retracts to its previous position.

Predation

As already described, the 2014 cohort of *S. apiformis* mainly fell prey to patrolling birds. Our observations were that Great Tits were the main culprits, but Blue Tits may also have been responsible. We did not see Magpies in the vicinity, but they have been reported as predators in the past (Northfield, 2014). Although we cannot be certain, our impressions are that predation by birds did not occur in 2013, or certainly it did not occur to the same extent.

It is interesting to consider the reasons why such heavy predation occurred in 2014. One possible explanation is that the earlier than usual emergence of *S. apiformis* was unfortunately within the normal time span for nesting Great Tits and Blue Tits, which were still engaged in feeding fledglings during the first two weeks of June 2014.

However, according to the theory of Batesian mimicry, *S. apiformis* should be protected by their resemblance to Hornet wasps (*Vespa crabro* Linnaeus, 1758) and related species even if their adult stage overlaps with active scavenging by birds. With the exception of birds described as Bee-eaters, *Merops apiaster* (Linnaeus, 1758) (which are only occasional visitors to Britain and Ireland), birds do not usually eat wasps. When Bee-eaters do eat them, they protect themselves by hitting their prey against a hard object until the sting has been pulled or ripped away. Only then do they swallow the remains.

Batesian theory is known to break down when the model species on which protection depends (in this case any wasp species, Vespidae spp.) is absent. Mimics are only expected to occur when their model is present. 'The first law is, that in an overwhelming majority of cases of mimicry, the animals (or the groups) which resemble each other inhabit the same country, the same district, and in most cases are to be found together on the very same spot.' (extract from the classic review of mimicry by Wallace, 1867).

A discussion of why there should be mimics without co-existing model species is given in a recent study (Pfennin & Mullen, 2010), but in the case of *S. apiformis* we normally expect there to be native wasps of the Vespidae family on the wing from May to October carrying a healthy sting that is likely to deter most birds. However, during 2014 there was almost a complete absence of Vespidae in the Cambridge area. Why this occurred is at present unknown. Whether the absence of wasps was a factor in the high level of predation of *S. apiformis* by birds remains a fascinating subject for speculation. Once predators have established that *S. apiformis* adults are harmless and provide suitable food, their prominent colouring and enforced waiting time in the open make them 'sitting ducks' for their attackers.

Acknowledgements

We are grateful to Dr Barry Henwood who drew our attention to observations of *S. bembeciformis* in Abbotskerswell, Devon, and to Mr John Walters who kindly made available his video of a moth emerging from a willow tree there; also to

Mr Adrian Russell who informed us about observations of *S. apiformis* in Rutland and sent photographs of a pupal case and cocoon that he had retrieved. We again thank Professor Roger L. H. Dennis for his helpful comments and suggestions after reading a first draft of this paper.

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Appendix

Approximate calculations for the extrusion of meconium by a newly emerged *S. apiformis* moth

These calculations relate to the situation shown in Fig. 6 in which a newly emerged insect expels liquid rapidly in a narrow stream. In the absence of gravity, this stream would travel in a straight line until it hits an obstacle. But gravity causes linear movement of the fluid stream to be deflected downwards.

By measuring how much the fluid stream is deflected downwards, it is possible to estimate the velocity of the fluid stream (i.e. the velocity with which the insect emits fluid) and the intra-abdominal pressure that must have been exerted to generate this velocity.

In time T , the total downwards deflection Δ of a droplet in the fluid stream is $\Delta = \frac{1}{2} g T^2$ where g is the acceleration of gravity.

If the total distance S travelled by the droplet in time T is $S = VT$ where V is the stream's velocity (assumed constant), time T can be replaced in the above expression by distance S . Substituting $T = S/V$, gives

$$\Delta = \frac{1}{2} g (S/V)^2$$

which allows the velocity to be expressed in terms of S and Δ as

$$V = S (g/2\Delta)^{1/2}.$$

In Fig. 6, by measuring on the original video still, and determining its scale by later measurement of the pupal casing after it had been retrieved, it was concluded that

$$\Delta \approx 1.2 \text{ mm and } S \approx 17 \text{ mm.}$$

Substituting those values into the above formula gives

$$V \approx 1.1 \text{ m/s.}$$

The intra-abdominal pressure that must have existed, measured as the height of a static column of liquid is h where

$$h = \frac{1}{2} V^2/g$$

which, for $V = 1.1 \text{ m/s}$, gives

$$h \approx 6 \text{ cm.}$$

This figure neglects the fluid-flow losses that would have been caused by viscosity, which would increase h , but indicates the order of magnitude of the pressure that a moth would have to exert to expel its meconium liquid at the urgent rate that it does.