FURTHER BIOLOGICAL NOTES ON *RHYSSA* AND *IBALIA*, PARASITISING *SIREX CYANEUS*, FABR.

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1. Introduction.

The biology of *Rhyssa persuasoria*, L., and of *Ibalia leucospoides*, Hochenw., has already been sketched in a preliminary paper published in this Bulletin (xix, pp. 67–77, pl. iii, 1928) in collaboration with Mr. R. N. Chrystal, of the Imperial Forestry Institute. The following observations were made by the writer chiefly at the Farnham House Laboratory, during the spring and summer of 1928, and are gathered together in view of his departure from England. The work of collecting and rearing supplies of *Rhyssa* and *Ibalia* for shipment to New Zealand, for the biological control of *Sirex noctilio* (*juvencus*), has been continued on a larger scale. The present notes were made incidentally during this work and are arranged under nearly the same headings as in the previous paper, to which they are supplementary. One error needs correcting. It was stated (on p. 75) that the larch (*Larix europaea*, D.C.) is indigenous, though actually planted in the Oxford locality mentioned. As a matter of fact, of course, larch, though Palaearctic, is not indigenous to Britain.

2. Rhyssa persuasoria, L.

In his monograph on the parasitic Hymenoptera, Stellwaag* copies a figure from Hess & Doflein of *Rhyssa persuasoria* ovipositing *in* a *Sirex* larva, buried deeply in wood. The piece of wood is shown in section and the ovipositor is visible throughout its length. The position of the *Rhyssa* is markedly unnatural, and although the figure appears to have been reproduced from a photograph, it is obviously a fake. Moreover, as Mr. Chrystal will show in a later paper, it has now been definitely proved that *Rhyssa* lays its egg *on*, and not *in*, the host larva.

Mating.

Gade,† Champlain‡ and Barlow§ have recorded curious mating phenomena in North American species of *Megarhyssa*. Gade found a great congregation of males of the North American *Megarhyssa lunator* round a tree-trunk. On scraping away the bark he found a female ready to emerge. The males returned and copulation took place at once, but was of very short duration. Champlain states that males of *Megarhyssa atrata*, Fabr., also assemble at points where the female are about to break their way out. Thus early in May in Pennsylvania he found several groups of six to ten males. In every group one of the males had its whole abdomen inserted into the dead tree, through a hole gnawed either by the enclosed female or by the entering male. The hole was only large enough to admit the abdomen of one male, but the others crowded round and tried to force in theirs also. When the tree was split it was found that the male whose abdomen occupied the hole was actually *in copula* with the female.

A careful watch was kept this spring and summer for any similar behaviour in the case of *Rhyssa*, but no indication was found. Moreover, the following experiment seemed to show that females about to emerge have no particular attraction for males. A male which emerged from a gelatin capsule in sawdust on 24th February was placed in a

* Monogr. angew. Ent., No. 6, Beiheft 2, Zeits. angew. Ent. vii : 100 pp. 37 figs. 1921
† Bull. Brooklyn Ent. Soc., vii, pp. 103–104, 1884.
‡ Ent. News, Philadelphia, xxxii, p. 241, 1921.
§ Ent. News, xxxii, p. 291, 1921.

large cage in a warm room, with plenty of food in the shape of raisins and a feeding-tube of honey-water, both of which are readily eaten by both sexes of *Rhyssa*. On the 29th, this male was actually noticed feeding. On the 7th March I introduced three small, open boxes of sawdust. One contained sawdust only, as a control, the others a number of perforated gelatin capsules containing females just about to emerge. During the succeeding $2\frac{3}{4}$ hours the male flew about, fed occasionally, but showed no interest in any of the boxes. The capsules containing the females were barely covered by sawdust.

Mating took place readily in a large cage, which was later kept in the insect-room, illuminated by a Vita-glass lamp. A large female was liberated on emergence at 12·25 p.m. (12th March) in this cage with the above-mentioned male. She could not at first fly, though quite hard, but she began at once to climb upward and with some assistance arrived at the top of the cage at 12·30. There she cleaned herself, first rather perfunctorily her head and face with the first pair of legs, and later with much attention for three-quarters of an hour, the ovipositor and end of abdomen. The ovipositor was repeatedly drawn between the crossed apices of the posterior tibiae, with an upward strain of the abdomen and stretching of the dorsal intersegmental membranes, much as in the actual process of oviposition. When the sheath was separated it was always replaced by the hind pair of legs.

The male meanwhile took no notice at all until 1 p.m., when he was seen on the glass roof, six inches away, walking straight towards the female, with his antennae vibrating. An inch from her he stopped. The female gave no sign of noticing him, but continued to draw her ovipositor between her legs. The male veered and walked past, but returned again and just avoided her. This circling manoeuvre was performed several times, in the intervals of flying occasionally to other parts of the cage. Still the female took no apparent notice. They were watched thus till 1.35, when the female was cleaning her wings and legs, with occasional rests.

On the 14th March at 1.0 p.m. the male was seen flying about, but at 1.5 the pair were copulating. Unfortunately the preliminaries, which must have been short, were missed. The female was clinging to a horizontal bar in the top of the cage with her abdomen hanging limply. The male was clasping her abdomen with his first pair of legs, while his third pair were free and stretched out laterally, the female's wings being pinned to her sides. One middle leg was hooked in the crook of one of the female's hind-legs, or occasionally free. His head and thorax were closely appressed to the side of the female's abdomen, while his abdomen was curved round and forward in a perfect U, to the genital opening at the base of the ovipositor. The antennae of the male were sticking upward and outward, rigid, immobile or slightly vibrating. At 1.10 the female was kicking occasionally and scraping at the male rather violently with her third pair of legs, as though to dislodge him, but he clung like a leech. At 1.15 she had flung him free, though he wrestled violently on her back and curved his abdomen round to copulate again. She very violently squirmed her abdomen and curved it up as though to avoid his. He was thrown off and fell to the ground. At 1.25 he began to crawl up towards the female again. As he approached, the antennae of both vibrated extremely rapidly but with small amplitude—about the same in male and female. Their antennae nearly touched. The female hung in the same position, swinging her ovipositor slightly up and down. The male diverged and walked away at 1.30, his antennae no longer vibrating as he turned, but waving normally. The female's antennae, directed towards him, continued several minutes to vibrate, as at first. Three minutes later there was another tentative approach, but the male veered off again when their antennae almost touched. Again at 1.36 the same thing happened. At 2.5 the female still hung in the same place and position, nearly motionless save for a slight jerking of the ovipositor ; her abdomen not quite so pendant as when mating.

Another female copulated with this same male (26th March) soon after emergence and only half an hour after liberation in his cage, before she had fed. It took place

essentially as described above, but the male clung with all three pairs of legs and thus clasped the females' wings still more closely to her sides. The pair were quiescent for four minutes, save for a rhythmical slow swaying up and down of the tip of the female abdomen. Then the female began to struggle violently and, disengaging her wings, attempted to fly, but fell to the ground with the otherwise dislodged male clinging to a rag of pupal exuviae which still adhered to her ovipositor.

This female was a large specimen, and very active, dashing all over the cage. About 20 minutes after copulation she exuded from the abdomen a drop of clear liquid on the glass.

Observations on a number of additional females confirmed the notion that there is a definite pre-copulatory position, in which the female clings to the horizontal roof of the cage, with the wings somewhat spread and depressed and the abdomen hanging limply and almost vertically, still or waving gently. A very small female, which apparently never succeeded in mating, adopted this position for long periods right up to a few days of her death. The case of this undersized female is extremely interesting. All the females with which copulation occurred were large, fine individuals, and we have seen that one at least was mated within about half an hour of liberation. The small one, on the second day after liberation, approached the male on the gauze side of the cage. Both were vibrating the antennae quickly and shortly, as when about to mate. When near the male she veered round, writhing her abdomen in a curious manner. This manoeuvre was repeated once. The next day she approached the male as before, but when close to him, instead of veering, she flew suddenly on his back. He struggled momentarily as though to throw her off, and she flew away only, however, to draw near again with intensely vibrating antennae. Again she sprang or flew—so quickly, I could scarcely see how— on to his back, and was again thrown off at once. I believe she was never mated, for whereas the other females, after pairing but usually not before, examined with minute attention logs containing *Sirex* larvae, she scarcely visited them once, but spent long periods in what I consider the pre-pairing position.

Copulation with the large females sometimes occurred more than once, and periods spent in the pre-pairing position alternated with intervals of searching and boring in logs. I have, however, no evidence of polyandry. The males, of course, are polygynous.

Though no females kept indoors in the early spring betrayed any interest in logs until after pairing, several virgin females, which were liberated in a still larger cage outdoors in the summer, oviposited freely in larch logs containing *Sirex* and *Ibalia* and produced offspring, the sex of which is not yet ascertainable.

Oviposition.

The process of oviposition in *Rhyssa* resembles less that in *Ephialtes* than we were led to suppose (*l.c.*, p. 69) by Dingler's figures. In a species ovipositing in larch, the whole instrument with its sheath is brought down and directed to the desired spot in the same way as in *Rhyssa*, but the tip of the sheath guides the terebra only momentarily and is then flicked entirely away, to take up its usual caudal (and thus nearly skyward) position even before penetration has actually begun. The thin hair-like terebra, buckling and bending thus performs all the boring unsupported save by the coxae—an extraordinary feat.

In *Rhyssa* there is a certain amount of individual variation. Thus one female was observed in the usual oviposition posture, inserting its instrument into a crack, but instead of passing *between* the hind coxae, it was outside them and to the right of the right leg. This specimen, perhaps through cramping in the gelatin capsule from which she emerged, had her ovipositor bent slightly but permanently to the right, which probably explains this divergence and incidentally throws light on the great

difficulty *Rhyssa* seems to experience in managing her ovipositor. This boring was only a tentative one, lasting a minute or two. Sometimes the ovipositor is slewed round to the point of application with the help of all the legs (more or less in succession) of one side.

Unremitting attempts were made throughout the spring and early summer to see the actual deposited egg of *Rhyssa* in the cages at Farnham Royal, but entirely without success. The few cases in which eggs were laid in large logs were not discovered till after hatching. Mr. Chrystal and his assistant finally succeeded at Oxford, using logs abundantly supplied with large larvae of *Sirex gigas*.

At Farnham Royal, thinking that the logs might contain insufficient material, I had holes bored a few inches apart in small logs and pieces of wood, inserted *Sirex* larvae and corked them tightly. In many cases the *Sirex* larvae continued to feed and remained healthy for many weeks. These artificially infested logs were kept in the cages for months at a time, and the larvae examined at intervals, but with no result. *Rhyssa* females spent long hours examining these pieces of wood, and were often seen boring, even to the hilt of the ovipositor, at points close to the buried larvae. In one particularly striking instance, a fairly thin split piece of wood was used, the holes being bored in its edge, where corks indicated their positions. Thus on the face of the piece there was nothing to show where the larvae lay. A female was observed walking along the face, tapping in the usual way with her antennae. She stopped and bored, not deeply, exactly over the site (as indicated to me, in side view, by the cork) of a larva. She crawled along further and lingered over another buried grub, curving the antennae more abruptly at the tip and tapping more meticulously. In neither case was an egg laid, but this behaviour, coupled with that of the other females found boring exactly where larvae were buried, renders it clear that olfaction or audition (or both) are involved in the process of immediately locating the host.

A *Sirex* larva inserted in a shallow crevice, which exposed part of it to view, was visited several times by different females, one of which actually touched it first with her antennae and then with her probing ovipositor, but no egg was laid.

Dr. Thompson then suggested a technique which had been eminently successful, even with strange and unaccustomed hosts, in the case of *Pimpla* (*Exeristes*) *roborator*, Fabr., parasite of the corn-borer (*Pyrausta nubilalis*). The host larva was enclosed in a corn-pith cell, strongly perforated and smeared with the body fluids of the host larva. As no pith was available, two cells were made, one of polyporus and the other of peat slabs, both perforated so that the larva was almost visible. The outside was smeared copiously with the body contents of another *Sirex* larva. *Rhyssa* females, even when actually placed on these baits, betrayed but a languid interest, and no oviposition took place. The enclosed *Sirex* larvae even pupated and one eventually emerged. This experiment succeeded no better in a large insectary, where the insects flew freely, than in the cage.

In the field, the proportion of *Rhyssa* oviposition borings which yielded, not only no eggs, but often no sign at all of the host, was as great as in the preceding season. This, coupled with the behaviour above described, makes it evident that by far the greatest and " intrinsic limiting factor " (to adopt Thompson's term) to the increase of *Rhyssa* is its own innate inefficiency. Both in the field and in captivity it would seem that, at a generous estimate, three-quarters of its time is spent in fruitless boring, often where no host exists within a considerable radius. In parasitic Hymenoptera in general, as Dr. Thompson has suggested, there is probably very much more random thrusting with the ovipositor than is usually realised, but in those which, like *Rhyssa*, bore in solid wood, the apparently wasted effort is necessarily far more conspicuous, and the time lost considerably greater.

In one of the captive females, mated in the cage as described above, an egg was found on 12th March, entangled between the terebra and sheath of the ovipositor.

The insect itself eventually disengaged it by drawing the instrument between the crossed tips of her hind tibiae. This egg, which was recovered uninjured, agreed well with Bugnion's description. It was 13 millimetres long, of which the pedicel made up 10.

It appears that *Rhyssa* sometimes oviposits on pupae of the host. Thus on 10th July a first-stage larvae of *Rhyssa* was found on a newly formed *Sirex* pupa, which bore a number of blackish spots—one on the left hind wing-pad, three on the side of the abdomen near its tip, one on the base of the venter, one at the base of the right antenna, one just in front of right fore-wing pad—thus seven in all. The spots looked very like the seats of punctures, and it is difficult to suggest what else they could be. Moreover I could detect no signs of heart-beat, though this latter is less significant from the fact that the heart-beat is in any case difficult to see in a *Sirex* pupa. In a full-grown *Sirex* larva, however, which had been recently oviposited upon in one of Mr. Chrystal's cages, no heart-beat was discernible even under the highest magnification of a binocular, though a normal but similar larva showed a heart-beat of 24 per minute. This parasitised larva was kept in a gelatin capsule, packed in sawdust, in company with a number of normal ones, similarly encapsuled, which carried on their development. On 25th August, or rather more than two months after parasitisation, it was apparently unchanged, nor was any heart-beat perceptible. On 8th October the head and thorax had turned brownish, but the rest seemed normal and in excellent condition.

Evidently, then, *Rhyssa* stings the host larva before ovipositing upon it, and either kills it or paralyses it so thoroughly that even the action of the heart is stopped. I have shown elsewhere that the Braconid, *Alysia manducator*, when ovipositing in *Calliphora* larvae, stops their heart-beat for a period varying from some seconds to a quarter of an hour. If *Rhyssa* kills the *Sirex* larva it is difficult to understand how decay is so long delayed, for dead and injured larvae kept in similar capsules in sawdust have been found to discolour in a few days, and eventually they either dry up, or change into a deliquescent brown mass. If the number of punctures in the larva studied is at all typical, the stinging must be a very thorough process.

Thus Bordas (1917), who was astray in his supposition that the *Rhyssa* egg is deposited in the host larva, was perhaps not far from the truth when he suggested that the liquid from the " glandes venimeuses," " injected into the larva of the *Sirex* when the egg is laid, must be endowed with anaesthetic properties and also preserve from decay the larval tissues."

Movement and Resting Position.

In the Farnham Royal insectaries the gauze sides are fastened to the teak framework by smooth strips of sheet copper about an inch wide, one of which extends right round just at the top of the walls. It was curious that *Sirex cyaneus* and *S. gigas*, crawling up the gauze sides, were invariably baffled by this strip, and never learned to cross it, but would cling to the gauze for hours on end, pawing hopelessly at it with their front feet. *Rhyssa*, however, learned to negotiate it in a very short time, varying somewhat with the individual. For instance, a female that emerged on 12th March was liberated in a large cage, lined on the floor and for nearly an inch up the sides with zinc. She immediately ran jerkily and quickly across the floor and essayed in vain to climb up the side. I finally supplied her a blotting-paper ladder, by which she rapidly climbed to the gauze and up it to the top wood-work, where, however, the glass roof again baffled all her efforts. Yet the male, which had been liberated some weeks before was walking about with ease, upside down, across this glass roof. By the 20th this female was able to do the same with equal facility. This implies a considerable power, both of learning, and of adaptation to conditions not experienced in the natural environment.

The resting (and probably sleeping) position of *Rhyssa*, adopted in dull and cold weather or towards evening, is quite unlike the female's pre-pairing posture. The head and body are in one straight line, inclined at an angle of 30° to the surface—usually the wood-work of the cage-roof—on which the insect rests. The wings are folded, the antennae stretched in front, along the plane of the resting surface, and diverging from each other at an angle of about 45°. The first pair of legs are held close to the body, the others extended nearly parallel to one another and about at right angles to the body.

3. **Ibalia leucospoides,** Hochenw.

All stages of *Ibalia* larvae have now been found, and are being studied morphologically by Mr. Chrystal. The intermediate instars show a conspicuous tail like that of an Ichneumonid larva, and a body with distinct segmentation.

Larch logs cut at Oxford in the autuun, and sent to Farnham Royal by Mr. Chrystal, were cut up at intervals during the winter and early spring. These trees were quite green and were barely dying at the time they were cut. When the bark was removed every *Sirex* oviposition-bore was at once obvious, surrounded by patches of brown, discoloured tissue. Since, as indicated in the previous paper, the female *Ibalia* oviposits only in the egg tunnels of the host, the task of finding all the *Ibalia* material was simple.

It is proposed here only to give a few figures as an indication of the extent of parasitism, and to leave the intimate details of the structure and biology of the larvae to Mr. Chrystal's paper.

On 17th January, nineteen *Sirex cyaneus* egg tunnels were dissected out of a log which was still green and sappy. These yielded 13 young *Sirex* larvae, two of the tunnels containing two larvae each, and the remainder being empty or filled only with secretion. Only one larva, the further-in member of a pair, was parasitised, and this contained two relatively large *Ibalia* larvae. From 16th to 19th March no fewer than 64 *Sirex* egg-bores were dissected out of a two-foot larch log. Some of these were short, did not contain even secretion, and were evidently trial bores. There were three *Sirex* eggs, two in one tunnel and one in another, all unduly soft and probably addled, which would account for their non-hatching at such an advanced date ; 38 young larvae were found, ten of the tunnels containing two larvae, and one three ; 36 tunnels, including the trial-bores mentioned above, were empty or contained only secretion ; 8 of the larvae were dead, shrivelled and dried-up, possibly owing to some cause proceeding from the cutting and partial drying of the log. One larva in a tunnel by itself contained a first stage *Ibalia* larva, while another, in a burrow with a fellow, had an *Ibalia* egg. Adding together the results of these two examinations the parasitism by *Ibalia* was at the rate of 5·9 per cent.

With regard to the burrowing behaviour of parasitised larvae, a case was observed on 3rd April in which the host had followed an exceedingly winding course and when found was just completing a flat spiral, which brought it back just below an earlier part of its burrow. This was entirely within the superficial part of the trunk, in marked contrast to the course of a normal larva of the same age.

4. Inter-Relations of Rhyssa and Ibalia.

In the previous paper it was stated that the risk of superparasitism of *Rhyssa* upon *Ibalia* is probably absent. The possibility of direct hyperparasitism was not envisaged. Nevertheless a case has come to light in an outdoor cage containing virgin females of *Rhyssa* and larch logs infested with *Sirex cyaneus* and some *Ibalia*. On 16th July a *Rhyssa* larva 8·5 mm. long was found on a white *Ibalia* pupa. By the 21st merely the skin of the host remained.

Such hyperparasitism is perhaps not of frequent occurrence, but the larva or pupa of *Ibalia*, by virtue of the changed course of the parasitised host, is never out of reach of the ovipositor of even a small *Rhyssa*.

5. Technique.

The gelatin capsules packed in sawdust have continued to prove satisfactory for larvae and pupae which have finished feeding. The atmosphere in large containers may be kept sufficiently moist, without softening the capsules, if a reagent bottle be buried up to its neck in the sawdust, and supplied with a short wick of cotton-wool. *Ibalia* as well as *Rhyssa* has now shown its ability to cut its way out of the capsules when ready to emerge. Some individuals, especially undersized ones, do however occasionally fail. At Dr. Thompson's suggestion the task has been simplified by denting slightly the head-end of the capsule with the thumb-nail.