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Observations on the adult behaviour and biology of *Histeromerus mystacinus* Wesmael (Hymenoptera: Braconidae)

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Introduction

Until recently the braconid group now generally accorded rank as the subfamily Histeromerinae had been considered to contain just two rather seldom collected species of *Histeromerus,* one Palaearctic and the other Nearctic (cf. Shaw & Huddleston, 1991). However, further species of *Histeromerus* have now been described from Taiwan (Chou & Chou, 1991) and Australia (Austin & Wharton, 1992), the genus has additionally been recorded from Papua New Guinea (Quicke & van Achterberg, 1990), and the Nearctic species has been found also to occur in Europe (van Achterberg, 1992). Attention has also been paid to the systematic position of the subfamily Histeromerinae, and Quicke & van Achterberg (1990) have concluded that it is one of the most basal groups within the Braconidae.

The systematic position of Histeromerinae raises a strong expectation that species of *Histeromerus* will be idiobiont ectoparasitoids, but knowledge of the biology of Histeromerinae, based almost entirely on fragmentary information on *Histeromerus mystacinus* Wesmael in Britain, is extremely vague. It is clear that *H. mystacinus* is a gregarious parasitoid of large beetles whose larvae inhabit decaying wood, but whether or not it also attacks small species as a solitary parasitoid, whether it is an idiobiont or a koinobiont, which host stages it can attack, and even whether it is ectoparasitic or endoparasitic, are all questions that have been addressed in the literature by conflicting statements and presumptions (briefly reviewed by Shaw & Huddleston, 1991).

An opportunity to make some observations on the behaviour of adult females of *H. mystacinus* (Fig. 1) in the field and subsequently to rear this species in captivity through one generation arose unexpectedly in June 1993. Its behaviour proved to be very unusual in several respects that are worth reporting. Partly because much of this was unanticipated, however, some opportunities to make crucial observations or to test possible interpretations were missed, and I have felt impelled to include circumstantial detail of uncertain relevance in outlining unanswered questions. The hope is that this account will help future workers to be better prepared when fresh opportunities arise to elucidate the behaviour of this interesting braconid.

Materials and methods

In the late afternoon of 4.vi.1993 a single female *H. mystacinus* was collected by A.J. Parsons as it crawled on the bark of an unidentified and moderately exposed ageing log, ca 80cm in diameter, that was infested with various species of beetle (including the cerambycid *Stenocorus meridianus* (L.)) at Silwood Park, Berkshire, UK, a vegetationally complex area consisting of open parkland, woodland, scrub, meadows, a lake and adjacent alder carr. In the carr a standing but nearly completely dead specimen of *Alnus glutinosa* (L.) Gaertner, ca 35cm in diameter near the base and more or less shaded and enclosed by other trees, was found to be heavily infested by the cerambycid *Leptura scutellata* Fabricius and also to contain fecund adult females of *H. mystacinus* tunnelling through the dead wood and beetle workings, evidently in search of hosts. The cerambycid was concentrated in an area of moderately dry and firm dead wood, lying between a narrow vertical strip of living wood and a much broader area of soft and wet-rotten wood that similarly ran vertically up the tree trunk, and the accessible part of this substrate between ground level and a height of ca 2m was gradually excavated with hammer and chisel on 5 & 6.vi.93. Several pupae and a few teneral adults of *L. scutellata* were encountered at relatively shallow depths, but larvae of various sizes were particularly abundant and also occurred deeper in the wood. About 20 females of *H. mystacinus* were encountered singly, well dispersed between a height range of ca 30cm and 200cm, and occurring at all depths excavated (to ca 10cm). They were found over the same range of substrate condition as the larvae and pupae of *L. scutellata,* but were not encountered in the more rotten wetter areas, nor near the living wood. These females, as well as the one collected by A.J.P., and parasitised and unparasitised larvae and pupae of *L. scutellata* removed from this tree, both in small blocks of wood around partially opened cells and *ex situ*, formed the basis for the experiments and observations undertaken. Further pieces of wood from the tree were kept in a closed polythene bag until being examined in detail on 25.ix.93. There was no indication that *H. mystacinus* had already bred in the tree.

Females of *H. mystacinus* that had apparently not yet found hosts were enclosed singly with living unparasitised *L. scutellata* pupae in corked glass tubes (naked in 5 x 1cm tubes, or over crumpled tissue or partly within wood in 7.5 x 2.5cm tubes), or if the hosts were *in situ* in larger pieces of wood then in ca 13 x 18 x 6cm plastic boxes. Hosts collected in an already parasitised state were treated similarly, and opened cells were roughly closed with small pieces of wood and rubber bands. The adult female parasitoid was in each case kept with the host it had parasitised for the remainder of its life, though given the freedom to disassociate itself and kept under observation for signs of doing this. Minor variations and manipulations are referred to in the Results section.

Following a ten hour journey on 7.vi.93, when much of the material became overheated (with considerable losses), all livestock under observation was kept indoors in Edinburgh, at first in a cool room in a closed cupboard — from which, however, it was regularly removed for observation and flash photography. After

8.vii.93, by which time all wild and laboratory broods had pupated and adults were on the point of emerging, the cocoons had to be taken to a warmer laboratory, where limited observations on the behaviour of the resulting adults were made on my behalf by S.I. Baldwin during my absence. Unfortunately the adults proved difficult to keep alive and they had all died by the time I returned on 4.viii.93. The bagged wood was kept exposed to daylight in the cool Edinburgh room until being opened on 25.ix.93.

Results and Discussion

Summary of biology

H. mystacinus was found to be fully ectoparasitic, and to attack the larval, pupal and possibly teneral adult stages of its wood-inhabiting beetle host, in this case the medium sized cerambycid *L. scutellata*. It is gregarious and it was clear that in all seven reared broods males were much smaller than females and sex ratios were highly female dominated, although (owing to major escapes of adults, and the difficulty of seeing all around hosts *in situ* and of finding all emerged cocoons following the wide dispersal of larvae from opened cells) exact brood compositions can be given for only three. A brood of 43 females and three males developed on a large female pupa of *L. scutellata* that had been parasitised in the wild, all the females being at the upper end of the size range of wild-collected females. The other two complete broods, each of six females and one male, developed unobserved on part-grown larvae in the bagged wood, and the females in these broods were at the lower end of the size range of wild-collected females. Brood sizes on final instar larvae and pupae seemed usually to be in the range of 20-35. The host is paralysed by the female parasitoid before eggs are laid, and development is then quite rapid. In the midsummer generation (at ca 18-22°C) eggs (Fig. 2) hatch in about 75 hours; larval development (Figs 3&4) takes about ten days; and the cocoon stage (Fig. 5) lasts about 21 days. The larvae feed by sucking fluids through minute lesions in the host's integument without causing discolouration. The host does not putrefy and its integument is left more or less intact, though collapsed. Cocoons are spun individually in a more or less compact mass but without particular order. In the abnormal surroundings of a glass tube, a weak communal outer web was evident (Fig. 5). Emergence from the cocoon is through a ragged subapical hole.

Hosts attacked in the wild

During the excavation of the tree on 5 & 6.vi.93 two pupae and three larvae of *L. scutellata* (one not fully grown) were found in a paralysed state, each with a single female *H. mystacinus* strongly associated with them, and eggs or early instar larvae were present at the time of collection on all of these. Eggs are laid loosely in untidy batches on the host, very often in the neighbourhood of the wing cases and/or hind legs of pupal hosts (Fig. 2). Eggs are not stuck down and are easily lost if the host is disturbed. One larval host and its female parasitoid were too badly damaged during
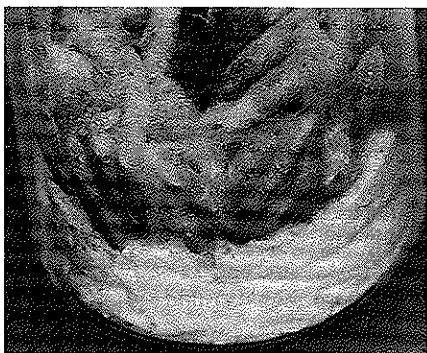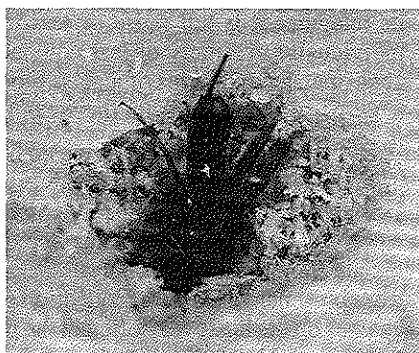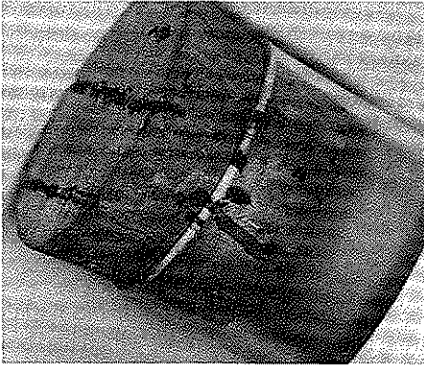
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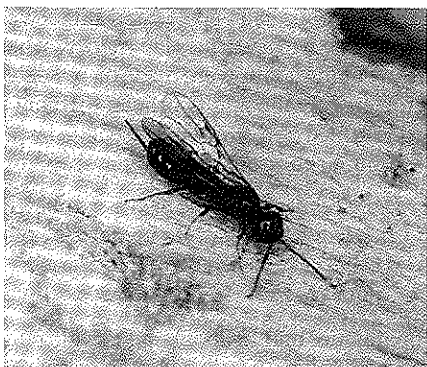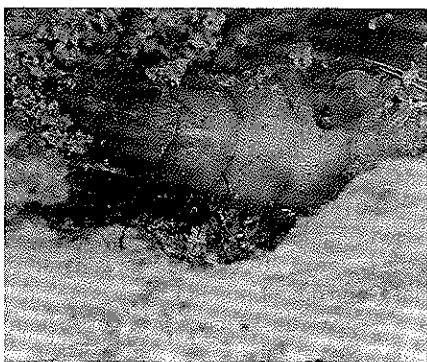
Figures 1-9. Biology of *Histeromerus mystacinus* (not all to same scale).

Fig. 1. Adult female on wood.

Fig. 2. Eggs on pupa of *Leptura scutellata.*

Fig. 3. Adult female attending brood developing on pupa of *L. scutellata.*

Fig. 4. As Fig. 3, five days later (to same scale).

Fig. 5. Cocoons being spun individually beneath a flimsy communal outer web.
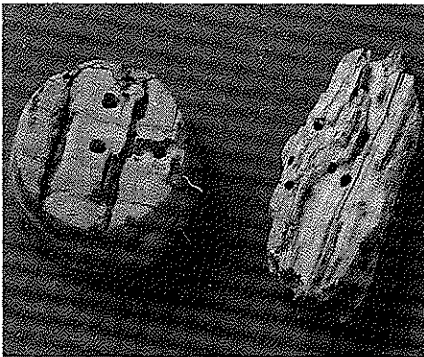
Fig. 6. Adult female re-entering its resting site.

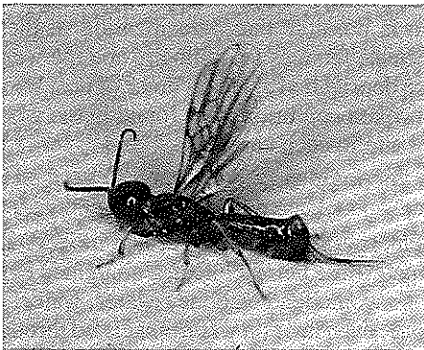Fig. 7. Tunnel through cork made by a freshly emerged escaping adult.

Fig. 8. Entry holes in cork and wood made by recently emerged adults.

Fig. 9. ''Probing stance'' adopted by females as they back towards the host.

the extraction process to provide further data, and another larval host was removed apparently before the female had laid many eggs: the few eggs became detached and lost before they hatched and the paralysed host larva was subsequently used in a variety of tests. This larva lived for over 3 months: although its paralysis was initially flaccid, it gradually became much firmer and after several weeks it was capable of slight movement though it never regained the ability to feed. Adult parasitoids resulted in due course from the broods on the other larval host and from both pupal hosts.

Hosts attacked in captivity

Eggs were obtained on at least three pupae in captivity, but one of the females concerned deserted its host soon afterwards, and the eggs (some of which had been laid beside rather than on the host) failed to hatch. A further host offered as a pupa had become a teneral adult by the time eggs were laid on it: again the female deserted and the eggs failed to hatch. While these observations are interesting, they are unfortunately much too limited to disentangle cause from effect. Broods were raised successfully from the other two pupae, the females remaining in attendance. A number of females provided with other hosts (mainly larvae) in partially closed cells evidently did paralyse hosts, but none remained with them until death and no broods resulted (it is uncertain whether or not eggs were laid). These and other females spent much of their time tunnelling more deeply into the wood and apparently ignored the potential hosts that were present. Females persisted in both kinds of behaviour when they were visibly in poor nutritional condition (with the ventral part of their gasters laterally shrunken as though compressed). Unfortunately, however, the realisation that females were neither feeding nor willing to oviposit on successive hosts dawned late, and the nutritional status of females at the time of first offering the hosts had not been adequately recorded. As far as could be ascertained, no female oviposited on more than one host, although the two females that had deserted their first hosts both paralysed others.

The small broods that resulted from part-grown hosts in the bagged wood should be regarded as laboratory rearings as it is possible that parasitization of these relatively small larvae only occurred because females searching inside the wood when it was collected on 6.vi.93 were then deprived of a wider choice of host sizes. On 25.ix.93 the dead female parent, in broken condition, was found in the wood within 2 cm of her brood's development site in each case.

Nutrition of females

All females found tunnelling, and the female collected at large, had moderately distended gasters. Some that were damaged while being collected contained eggs that seemed to be mature at that time. None would feed on honey-water, water, or haemolymph taken from *L. scutellata* pupae, even later on when emaciated through having laid their eggs or having aged apparently without doing so. Freshly emerged

adults from a captive brood similarly refused honey-water but laid eggs nevertheless (see ''oviposition''). No feeding on paralysed hosts was seen under any circumstances, although admittedly observation was not continuous.

When the bagged wood was opened on 25.ix.93, by which time it was very dry, three of the females from the broods that had developed in it were found alive, though more or less emaciated, in what appeared to be resting sites of their own excavation inside the wood (cf. Fig. 6). Three other females were found dead in similar sites, but some of the females (and the two males) were found dead loose in the bag. The least and the most emaciated of the living females were offered honey-water, which they refused, and were then dissected. Their ovarioles contained respectively 21 and 23 eggs that were fully sized in outline. However, the eggs graded in appearance and content, the more basal ones being more or less flattened or collapsed (and swelling the most strongly when dissected into water) and only the most apical eggs looked possibly fully nourished. There were no smaller eggs developing, and the 23 eggs in the more emaciated of the two females were much more profoundly collapsed. The putative gland at the end of the tubular venom reservoire (cf. Quicke & van Achterberg, 1990: Fig. 121) was distended in the better nourished female but collapsed and somewhat crumpled in the more emaciated one. These findings are consistent with resorption of nutrients (or perhaps largely water) from formerly mature eggs, and also suggest a proovigenic rather than synovigenic system, but the question of what the females were waiting for in their retreats remains unanswered. The rather rapid death of some of them would seem to argue against a seasonal diapause.

As *H. mystacinus* is fairly regularly collected in suitably sited Malaise traps it probably disperses from the tree in which it bred to seek new sources of hosts, and the possibility that it may feed during such a phase cannot be ruled out. An alternative possibility that it may derive some nutrition from the wood in which it tunnels was rather rudimentarily tested by giving emaciated females wood that was variously wetted and/or clearly fungus-infested but, although the females chewed into such substrates, their gasters ventrally remained flattened and shrunken. The preliminary conclusion that the adult female is proovigenic and does not feed is in need of verification, although it does seem consistent with its apparent behaviour of attacking only a single host in its lifetime.

Tunnelling behaviour

The head of *Histeromerus* is highly modified and the females use their powerful mandibles to bite through dead wood, making particularly rapid progress when it is soft or when moving through frass-packed tunnels. Each particle is bitten off, and passed under the body by the legs. The forelegs were seen not to be involved in more than providing a forwards thrust and moving the bitten-off particles backwards: even in relatively loose frass *H. mystacinus* seems to move literally head first. Freshly emerged females chewed through cork bungs very rapidly (Figs 7 & 8) — indeed, brood composition data were lost from all broods except for three

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because of this — and were keen to burrow into fragments of dead wood from the original tree when enclosed with them in a plastic box, even when escape would not result (Fig. 8). Wild-collected females that had not oviposited on hosts, or that had deserted hosts they had attacked, spent much time resting inside wood, usually reappearing occasionally for no evident reason and then returning to a favoured previous excavation. In view of the capacity of females to bore into woody substrates and to reappear, it would be wise to regard even supposed substrate rearings with considerable suspicion and to accept only rearing records that are supported by cocoons with adjacent host remains as proof that a female had developed in the substrate from which it emerged. In particular some of the citations concerning very small host species in substrates such as bracket fungi (cf. van Achterberg, 1984) are strongly at variance with the behaviour of *H. mystacinus* in relation to its large hosts reported here — especially the fact that hosts are not attacked successively.

Adult behaviour towards hosts

In the wild *H. mystacinus* presumably comes upon hosts in entirely enclosed spaces. The many observations summarised here involved hosts in partly opened cells, allowing (or perhaps forcing) the female to operate at a greater distance. The first outward sign of host recognition was antennal contact, which arrested the female. Without further exploration she would turn around, raising her wings and exserting her ovipositor in line with the ventral fold of the well-developed hypopygium so that it extended posteriorly beyond the sheaths by about half its length, with the sheaths bent down in a curve so as still to support it. In this stance (Fig. 9) the female would back towards the host, sometimes rocking towards it, fairly gently poking her ovipositor into the host's cavity. This activity was very imprecisely directed, though strongly provoked by any slight host movement, and was sometimes maintained for periods of up to an hour without a direct hit being scored: in these prolonged bouts the female would often undergo many changes of position in relation to the host. It appeared that the impaling of the host may depend to a large extent on the host's own energetic movements that were intermittently provoked. The parasitoid's wings, held vertically, often became extremely bent and crumpled during these interactions, but were always settled again smoothly. The parasitoids also regularly entered spaces full of loose powdered frass, but stayed remarkably clean with very little need to groom (an activity that was hardly ever seen). The act of paralysing a host was not observed clearly enough to ascertain whether more than one insertion of the ovipositor took place, but one (larval) host took tens of seconds to subside to an apparently complete state of initially flaccid paralysis. (One host larva found in the wild in a similar state gradually recovered body tone and the ability to make very weak movements — see "hosts attacked in the wild".) All female parasitoids, whether they then oviposited or whether they were aged and emaciated, seemed prepared to behave towards hosts in the same way, and were capable of causing at least partial paralysis. The probing stance (Fig. 9) was some-

times also adopted by emaciated parasitoids in response to physical disturbance in the absence of hosts.

Oviposition

It was extremely disappointing that despite many hours of observation no ovipositions were witnessed. The freshly laid egg is relatively large for a parasitoid only 3-5 mm long, measuring 0.60 x 0.17 mm, and is of a normal translucent white colour and hymenopteriform shape for a cyclostome braconid, with no stalk or clear means of distortion.

Surprisingly, it was eventually found that oviposition could be induced in the absence of host stimuli. About 20 females resulting from one of the broods raised in captivity and transferred to a clear and clean plastic box were then placed by a colleague in a refrigerator (at 2°C) on or about 13.vii.93, within a day or two of their emergence, in an effort to keep them alive during my absence. By 4.viii.93 all the parasitoids were dead, but about 400 eggs had been laid haphazardly on the floor of the box. Because eggs were dumped by females of *Histeromerus* under conditions of cold stress, it seems possible that during the period of heat stress suffered by the experimental females on 7.vi.93 some of them may similarly have shed egg loads. Needless to say, this had not been investigated, but it could account for the subsequent failure of some of those females to oviposit when they were supplied with hosts.

"Cold stress" and "heat stress" may of course have little to do with egg dumping: no control experiments were undertaken to eliminate the effect of merely denying the females their natural substrates and hosts. The dumped eggs failed to hatch, but it was not clear whether they had simply been killed by chilling.

Only two subfamilies of Ichneumonoidea have hitherto been found to lay eggs in the complete absence of hosts, and both have highly specialised eggs and oviposition behaviours. The obligatorily hyperparasitic *Euceros* (Ichneumonidae: Eucerotinae) oviposits on vegetation in the wild, having a first instar larva adapted to make contact with the host, and it will readily lay its numerous stalked eggs in clean glass tubes although it is not clear exactly how it does this (M.R. Shaw, unpublished). The heavily sclerotised pedicellate eggs of *Netelia* (Ichneumonidae: Tryphoninae), in which only the pedicel passes down the ovipositor, are anchored onto host larvae in the wild, but eggs are freely dumped onto the sides of glass tubes if these synovigenic females are well fed on honey-water but deprived of hosts in captivity (M.R. Shaw, unpublished). The widespread use of the internal canal of the ovipositor as a precision delivery system elsewhere in the Ichneumonoidea has presumably evolved along with mechanisms for receiving and interpreting stimuli resulting from contact of the ovipositor with the acceptable host, and it is hard to imagine that if *H. mystacinus* used the ovipositor for exact egg placement it would be able to relax such a mechanism enough to allow it to dump large numbers of eggs onto clean plastic.

A second and more compelling piece of circumstantial evidence to support the

suggestion that *Histeromerus* may oviposit directly through the genital opening rather than via the ovipositor concerns the structure of the ovipositor itself. Not only is the dagger-like ovipositor very slender (with external dorsoventral and lateral cross-sectional diameters near the base respectively ca 0.4 and 0.2 times the diameter of the egg), but it has a structure that is unique in Braconidae, with largely separated dorsal valves joined only by a thin notal membrane, and which would appear to allow easy separation of the ventral valves (Quicke & van Achterberg, 1990: Fig. 7). Given this, it is hard to see how the ovipositor would remain integrated if a large egg were to start to pass down it. Although certainly requiring confirmation by direct observation, the tentative conclusion that *Histeromerus* does not use its ovipositor for egg placement seems tenable.

The loss of use of the ''sting'' as a means of oviposition has been regarded as a synapomorphy of Aculeata (Gauld & Bolton, 1988), and this clade within Hymenoptera is now generally accorded a sister-group relationship with Ichneumonoidea (Mason, 1983, unpublished: see Gauld & Bolton, 1988; Rasnitsyn, 1988). However, in one group of Ichneumonidae, the Adelognathinae, oviposition has been directly observed to take place onto exposed and temporarily paralysed larval sawfly hosts straight from the genital opening, without any part of the egg passing down the ovipositor (M.R. Shaw, unpublished). It is of some interest, too, that, like *Histeromerus* and many parasitoid Aculeata, one species of *Adelognathus* (*A. cubiceps* Roman) reaches its host by chewing into the substrate concealing it (Kopelke, 1987). If the suggestion that *Histeromerus* oviposits from the genital opening rather than down the ovipositor is upheld by direct observation, this habit will be known in both of the two extant families in the clade Ichneumonoidea (Sharkey & Wahl, 1992), and moreover in groups that appear to possess several primitive characteristics. While it remains unclear to what extent Histeromerinae and Adelognathinae are likely to reflect the ancestral biology of their respective families, this might raise the potential for an alternative view of the biological ground plan from which the different specialised uses of the ovipositor or sting have evolved in the sister-groups Ichneumonoidea and Aculeata. Rather than regarding Aculeata as having ''lost'' the use of the ovipositor for egg-laying, the possibility that using the ''ovipositor'' to immobilise the host or prey preceded its use for placing eggs in the ancestry of the clade Ichneumonoidea + Aculeata may be worth further consideration.

Maternal care

All five of the parasitised hosts collected wild were found with a female parasitoid in association. In at least one case the brood was already larval by the time it was collected. Six other parasitoids oviposited on hosts in captivity: two subsequently abandoned the hosts and the eggs failed to hatch, but the other four females remained with their host while the broods developed successfully. In all seven successful broods the female parasitoids remained in more or less close association with the host (Figs 3&4) in an active but progressively more emaciated state until they died,

by which time all broods had reached the cocoon stage.

Although this behaviour is clearly an example of maternal care in a broad sense, it was very difficult to work out its adaptive significance. As already noted, cause and effect surrounding the abandonment of eggs that failed to hatch cannot be ascertained from the available information, but there was nothing in the females' behaviour to suggest that their presence was necessary for eggs to hatch. Nor was the host's recovery from paralysis sufficient to suggest that the female may need to administer more venom from time to time (though it is possible that she does so, as slight movements seemed generally to provoke the probing stance). The females moved all around the host and made frequent contact with it and the brood throughout the association, and (at least under the conditions observed) the cells in which hosts lay gradually became filled with loose particles of frass as a result, but there appeared to be no benefit in this as other broods developed successfully on tissue paper in glass tubes without being buried in frass. When two females were enclosed with only one host they both interacted with the host and appeared to completely ignore each other, although in this case probably neither was capable of oviposition. Another female, possibly again incapable of oviposition, was put in with a female attending a host on which she had oviposited, and (despite approaching the host on occasion) the introduced female was completely ignored. Unfortunately it was not possible to introduce a fecund female in the vicinity of an attended developing brood to see whether the resident female would defend it against attempts to take it over or destroy the eggs of competitors, but nothing seen in the interactions between emaciated (yet still active) females gave real cause to suppose that this would happen. The associated female would move among the developing brood on the host from time to time, but it was not clear why. In future experiments it would be worth killing a developing larva to see if it was removed, or introducing bacteria or moulds to see if the female was capable of arresting their growth, but from the available evidence there is again nothing to suggest these capabilities. Owing to the openness of development sites, some broods dispersed quite widely as fully grown larvae, and isolated individuals were able to make cocoons satisfactorily in the absence of the female.

Among Aculeata very many systems of maternal care have been developed, with the behaviour seen in Bethylidae such as *Goniozus* most closely approximating to that described here in *Histeromerus*, and brood guarding has also been observed in several families of Symphyta (eg Kudô *et al.*, 1992, and references therein). However, maternal care seems to have been noticed in only one other ichneumonoid. This is the hormiine braconid *Cedria paradoxa* Wilkinson, a gregarious idiobiont ectoparasitoid of various leaf-feeding Pyralidae in India and China, that similarly remains with the parasitised host, apparently without feeding on it (although evidently having fed previously: cf. Mathur, 1959), until its progeny have developed (Beeson & Chatterjee, 1935; Chu, 1935; see Clausen, 1940 and Mathur, 1959 for summaries of its biology). In the case of *Cedria*, further hosts may then be attacked, though broods on them are small and it has been considered that normally only one

host is used in an individual's lifetime (Beeson, 1941), as seems to be the case in *Histeromerus*. Intraspecific competition was not investigated, and it was concluded (though with little supporting evidence) that the female *Cedria* guards her progeny from hyperparasitoids. In the pamphiliid sawfly *Cephalcia isshikii* Takeuchi maternal care has been shown to enhance the survival of eggs, probably by reducing predation (Kudô *et al.*, 1992). Neither of these explanations, however, seems likely to apply to *Histeromerus*, whose broods must surely be well protected from both hyperparasitoids and predators by virtue of their deep concealment.

Behaviour of freshly emerged adults

All captive broods emerged in my absence, and all adults that did not escape were dead by the time I returned (except for the few aged females found inside dry wood on 25.ix.93). However, some outline observations on freshly emerged females can be given (S.I. Baldwin, personal communication). In the only brood unable to escape, the males were reluctant to leave the cocoon mass: this observation, and the highly female biased sex ratio (noted in all broods notwithstanding subsequent escapes), indicates a sib-mating system. The females were strongly phototropic immediately after emergence, when they refused honey-water. Subsequently most individuals from all broods, except the brood confined in a plastic box, tunnelled through cork bungs 1-2 cm deep (Figs 7&8) and escaped. The death of freshly emerged females at 2°C suggests that the winter is not passed as an adult in diapause, despite the apparent resting behaviour of females in wood.

Acknowledgements

Summary

Fecund adult females of the primitive braconid *Histeromerus mystacinus* Wesmael tunnel through beetle-infested wood to find their hosts. Direct observations confirm that *H. mystacinus* is a gregarious ectoparasitic idiobiont, and broods were raised on both larvae and pupae of the cerambycid beetle *Leptura scutellata* Fabricius feeding in dead *Alnus glutinosa* (L.) Gaertner in southern England. The host is paralysed prior to oviposition. All wild and laboratory broods had highly female biased sex ratios, and brood sizes ranging from seven to 46 were obtained. Females do not seem to feed and apparently oviposit onto only a single host in their lifetime,

remaining with it while the brood develops. This suggests maternal care, although the functional significance of the behaviour was not elucidated. Although oviposition was not witnessed directly, circumstantial evidence suggests that eggs do not pass down the ovipositor. The possible phylogenetic significance of this oviposition behaviour is briefly discussed.

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