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Sex roles in the ghost moth *Hepialus humuli* (L.) and a review of mating in the Hepialidae (Lepidoptera)

"Vespere motu quasi in pendulo, in aëre fluctuans" (Linnaeus)

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Recently it has been found that female Lepidoptera belonging to diverse families actively court their males, rather than play a merely passive role. Male and female *Hepialus humuli* have been reported to come together in three different ways: (1) females are attracted to groups or 'leks' of white, hovering males by visual stimuli; (2) females are attracted to the males by olfactory substances produced on the hind-tibial brushes of the males; (3) males are attracted to sedentary females by olfactory stimuli. During my study I observed *H. humili* males flying on a total of 21 nights in two different parts of England. The males hovered in groups for about 20 min each evening, starting and stopping their flights in synchrony. Timing depended on light intensity, northern moths flying later in the summer evenings than southern moths. I observed a total of 18 matings. Normally, a female from outside a male lek flew into the group and up to one of the males. This male then usually followed her to a settling position, where mating took place. In a few cases females touched males; in one case a female struck a male in the air so that both fell to the ground and were copulating when examined. Photographs of hovering males show that their hind tibial brushes are fully everted in flight. The organs are folded against the body when the moth is mating, at rest or dead. Whilst hovering, the males are apparently emitting pheromones which function as primary attractants, rather than as the aphrodisiacs of many other lepidopteran males.

The mating behaviour of hepialids is reviewed. It is concluded that all studied hepialids which have male brush organs (some *Hepialus* and *Oncopera, Sthenopis, Zenophassus*) exhibit similar flight and mating behaviour: males hover, sit or loop back and forth on the spot in leks; females fly into male aggregations and mate there (although some published observations suggest otherwise). In contrast, hepialids such as *Fraus, Oxycanus* and other *Hepialus* that lack male brush organs have mating behaviour in which the males are the active partner, a more standard lepidopteran method. In view of the controversies surrounding mating in hepialids, future systematic and behavioural work on Hepialidae throughout the world will be worthwhile.

KEY WORDS:—Hepialidae – *Hepialus* – *Sthenopis* – *Zenophassus* – *Oncopera* - *Oxycanus* – *Fraus* – sexual behaviour – sexual selection – leks – flight behaviour – light intensity – male pheromones – scent organs.

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INTRODUCTION

Knowledge of the mating behaviour of Lepidoptera is important economically because of the possibility of using it to control pest species, as well as being of interest to evolutionary biologists. A standard view of lepidopteran mating behaviour has developed over the years, founded on field observations. Recent experimental work and the isolation and identification of pheromones, the chemicals which butterflies and moths use to communicate, has largely confirmed this view. In the standard pattern, lepidopteran males are the active partners, ranging over the countryside in search of females. Females of most nocturnal species 'call' males by emitting pheromones, while in butterflies, males are attracted to females visually (Roelofs & Cardé, 1977; Silberglied, 1977). Females are choosy; they can and do reject males. Males are usually indiscriminate maters (Silberglied, 1977), and often must subdue the female with aphrodisiacs (Pliske & Eisner, 1969; Birch, 1970a, b, c), or physically (Rothschild, 1978). This view fits comfortably with sociobiological and sexual selection theory (reviewed by e.g., Williams, 1966; Wilson, 1975; Dawkins, 1976). However, some recent results run counter to the prevailing model. In butterflies, females are sometimes attracted to males (Gilbert, 1969; Haber, 1978; Rutowski, 1980; Rutowski, Long, Marshall & Vetter, 1981). Females are attracted to the pheromones of sedentary males of some Pyralidae (Dahm *et al.*, 1971) and Arctiidae (Willis & Birch, 1982). These findings have led to the observation by Boppré (1983) that it is no longer useful to assume that the scent organs of lepidopteran males are purely aphrodisiac in function: they may have a variety of roles, including that of attracting females.

Hepialids are an especially interesting group in which to study mating behaviour: they probably represent an early branch from the line leading to the heteroneuran Ditrysia, which contain nearly all the lepidopteran species in which mating behaviour has been observed. Modern authors place the Hepialidae in the exoporian Ditrysia. The Exoporia are separated from the rest of the Ditrysia (Endoporia) by their external sperm canal which connects the two female genital openings, and by their similar (homoneurous) venation in fore- and hind-wings (Dugdale, 1974; Common, 1975; Kristensen & Schmidt Nielsen, 1981). The purpose of this paper is to review the scattered literature on the mating of hepialids, and to add my own observations on mating and flight behaviour in *Hepialus humuli* (L.) a species in which females are reported to fly to males.

SUMMARY OF PREVIOUS WORK ON MATING AND FLIGHT BEHAVIOUR IN *HEPIALUS HUMULI*

Hepialus humuli, the Ghost Moth, is in colour the most sexually dimorphic British hepialid. The male wings are white above and black below, while the female has a brown, mottled wing-pattern. There is also a behavioural dimorphism: in two samples of 37 individual *H. humuli* coming to light traps there were only 22% males, even though sweep net samples gave an approximate 50 : 50 sex-ratio (Williams, 1939; Edwards, 1964). In contrast, males predominate in most species of moths caught at light. This is also true of two other species of *Hepialus*; 67% of *H. sylvina* (L.) ($n = 72$) and 83% of *H. lupulina* (L.) ($n = 151$) were males (Williams, 1939).

Two species of *Hepialus* in Britain, *H. humuli* and *H. hecta* (L.), have mating behaviour that is very different from the usual moth pattern. Males of these species hover in groups or 'leks' at dusk, and mating takes place in the groups. It is probably the lack of horizontal movement in male *H. humuli* that reduces their likelihood of being attracted to light. Both of these species have peculiar brush organs on the hind tibiae of the males (see discussion for details), and it is not clear how these organs function in mating behaviour. The three other species of *Hepialus* in Britain have more 'normal' mating and flight behaviour: they fly for longer periods into the night and the males fly wildly over the terrain, earning them their English common name 'swift moths'. Males of these species do not have metatibial brush organs.

The exact mechanism by which the males and females of *H. humuli* come together to mate is controversial. Essentially two hypotheses have been advanced by observers of the mating behaviour.

(1) The females are attracted to hovering males. The female may either bump a male or fly near him, whereupon the male follows the female to nearby vegetation where she settles. The male may then lose her, and return to hovering. The female may take wing again and repeat the process. Eventually the male follows the female to her settling position, settles on the back of the female, manoeuvres to a ventral–ventral position and copulates, the male finally hanging by his claspers from the female abdomen (Chapman, 1876, 1886; Robson 1887a, 1892; Barrett, 1892; McArthur, 1895; Manders, 1908; Cockayne, 1912; Ford, 1955; Kettlewell, 1973; Reynolds, 1973). Recent, highly detailed observations in York (Turner, 1976) showed essentially the same pattern. The females are thought by some to orient to the males' white colour (Chapman, 1876, 1886; Robson, 1887a, 1892; Ford, 1955); and Reynolds (1973) was able to attract a female using a white paper model near a swarm of hovering males. Others felt that the females were attracted to males by olfactory substances produced by the metathoracic tibiae of the males (Barrett, 1982; Michael, 1949; Edwards, 1964). The excised brush organs of male *H. humuli* can sometimes attract both male and female *H. humuli* (Cadbury *in* Kettlewell, 1973). Kettlewell (1973) suggests that females are attracted to males by both olfactory and visual stimuli, and that males also use these stimuli to aggregate at dusk.

(2) Males are attracted to sedentary females by olfactory stimuli (Carolsfeld-Krausé, 1959; Harper, 1960; Abdelrahman, 1966; Leuschner, 1970). There is some doubt about this second possibility: Carolsfeld-Krausé (1959) did not actually observe mating, but did find a resting female near a hovering swarm of "an estimated 1600 males". When he returned 20 min later, the swarm had gone and a pair of *H. humuli* were "in cop". Harper's (1960) observation was second hand, and both his, Abdelrahman's (1966) and Leuschner's (1970) observations are characterized by a lack of detail which suggests that they may have seen the final stages of type (1) courtship.

NEW OBSERVATIONS ON *H. HUMULI*

The aims of the present study were to secure further data on the flight and mating behaviour of *H. humuli*. I observed 18 copulations of the moth in two different parts of England. Some experiments were performed to determine the means of attraction of the sexes, but the results were inconclusive (Mallet, 1978). The first in-flight photographs of *H. humuli* were taken. These observations help to clarify the controversy surrounding mating in this species.

Methods

Observations were made in late May and June 1976 in Iffley Meadows, Oxford (grid ref. SP523052); and in late June and July 1978 at three sites in Newcastle: an industrial tip in Derwenthaugh (NZ211624), Heaton Park (NZ267656) and Leazes Park (NZ230653). Records of male flying periods were made from when the first male rose from the vegetation to the time when the last male stopped flying and burrowed back into the herbage. Photographs were taken using a macro lens and two electronic flashes. Light intensity was measured using a Corning–Eel portable photoelectric photometer. The programme 'SUNSET', on the Hewlett-Packard 2000E computer library at the University of Newcastle upon Tyne, was used to calculate exact times of 'civil twilight' (the time at which the sun is 6 degrees below the horizon), for given latitudes, longitudes and dates.

Results

I observed the hovering behaviour of male *H. humuli* on a total of 21 nights in Oxford and Newcastle, during which I saw 18 copulations. Times of initiation and cessation of male flight (where measured) are shown in Fig. 1, together with times of mating and civil twilight times.

Flight time of H. humuli *and its correlation with light intensity*

Both males and females begin to fly at dusk. Males started to fly 15–30 min before civil twilight and settle 6 min before to 10 min after civil twilight. Total flight period was 17–27 min (Fig. 1). Male settling time is correlated with civil twilight time ($r = 0.973$, d.f. = 11, $P < 0.001$). Light intensity therefore seems to play an important part in determining the rising and settling times of male *H. humuli*. Table 1 shows the light-meter readings of rising and settling times of male *H. humuli* in Newcastle. Good evidence that light intensity has an influence on hovering behaviour is shown in Fig. 1, marked 'under sodium lamp'. On 19 June 1978 at Derwenthaugh, two male *H. humuli* were hovering at 23.05 hours (all times BST)—16 min after civil twilight—on the central reservation of a dual carriageway road. These males were directly beneath a sodium streetlamp. One male settled at 23.07 hours, but the other continued until the slipstream of a large van buffeted it to the ground at 23.12 hours. This was 23 min after civil twilight, nearly three times the number of minutes after civil twilight of any other male recorded. The mean time of settling is 2.92 min after civil twilight; 99.9% confidence limits of samples being 15.85 min before to 21.69 min after civil twilight. Thus there is a probability of less than 0.001 that this roadside

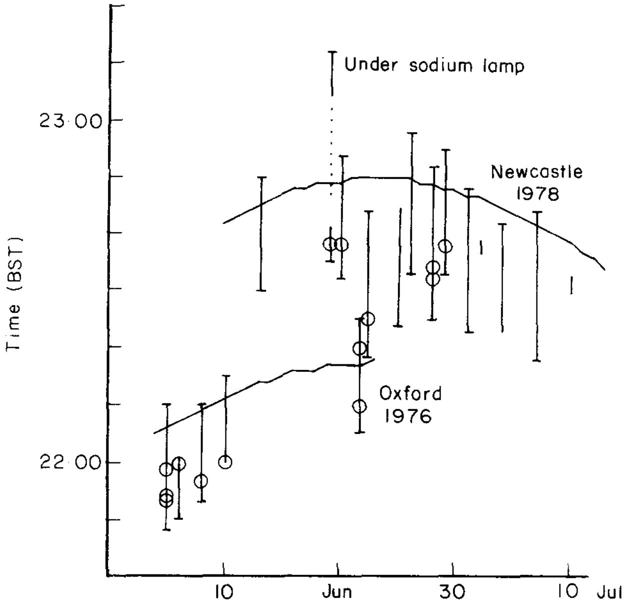

Figure 1. Flight and mating times of *H. humuli*. Vertical bars represent flight periods from the beginning of the flight of the first male to the termination of flight of the last male. If a vertical bar is uncrossed at its ends, rising and/or settling was not observed. Circles represent matings observed. The curves are fragments of the annual sinusoidal variation in time of 'civil twilight' in Oxford and Newcastle, to the nearest minute.

observation would occur by chance in a sample of the other males, and it can be concluded that the streetlight caused the behavioural deviations of these male *H. humuli*. Extremely bright conditions, however, cause settling; male *H. humuli* in flight always dropped to the ground (and rested for a while before resuming flight) after being photographed with electronic flash. This is also true of other species of moths that I have photographed, e.g. *Deilephila elpenor* (L.) (Sphingidae) but is not true of any diurnal butterflies that I have photographed in flight.

The drab females are more difficult to see during their dusk flight. They begin flying at a similar time to the males, and egg-laying females stop flying at about

Table 1. Overhead light intensities (lux/8.9) and times (BST) at which males of *H. humuli* rise to begin hovering, and settle finally. Newcastle, 1978

	Male flight period			
	Beginning		End	
Date	Light	Time	Light	Time
26 Jun	1.7	22.33	0.4	22.58
28 Jun	1.7	22.25	0.4	22.58
29 Jun	1.2	22.33	0.3	22.55
1 Jul	—	—	0.0	22.48
7 Jul	1.1	22.24	0.2	22.44

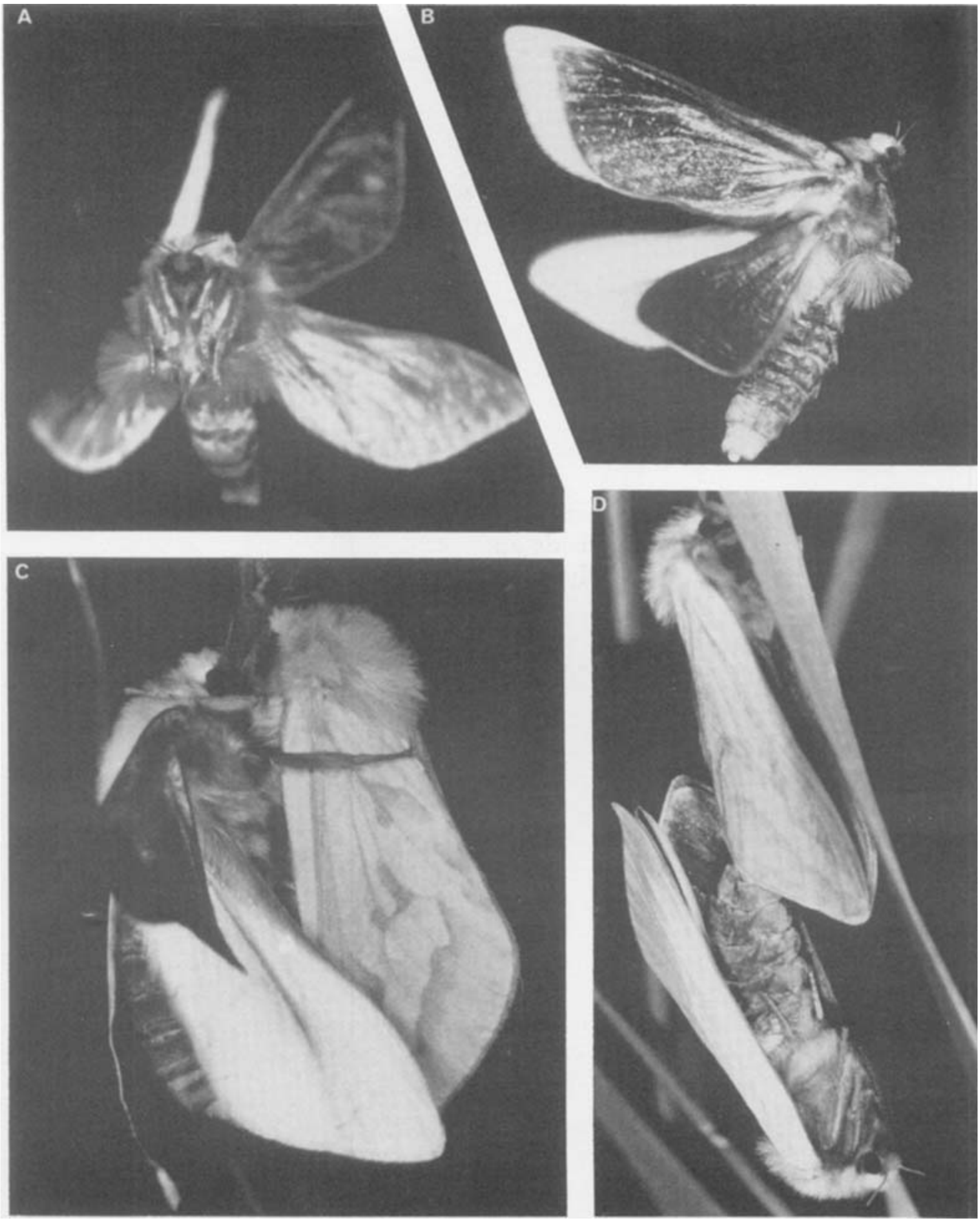

Figure 2. Flight and mating behaviour of *H. humuli*. A & B, Males of *H. humuli* hovering, showing how the wings beat semi-independently. The rosette organs are everted, and originate from the hind tibiae; C, after alighting next to a female, the male adopts a ventral–ventral posture with her, and begins copulation. The male (left) is fluttering his wings, the forewing is pointed directly towards the camera, independently of the hindwing. The male's rosette organs are apparently folded; D, after intromission is achieved, the male hangs limply from the female, attached to her only by his genital apparatus. His rosette organs are folded against his abdomen.

half an hour after the males. Females of this and other species of Hepialidae are known to drop their eggs during flight (Chapman, 1886; Robson, 1892; Illidge & Quail, 1901; Williams, 1905; Cunningham, 1955; Barton Brown, Soo Hoo, Van Gerwen & Sherwell 1969; Hardy, 1973). The only known exceptions are *Hepialus pyrenaicus* Donzel which has brachypterous females, and in the genera *Oncopera* (Lea, 1908, Hill, 1929; Evans, 1941; Martyn, 1960; Barton Browne *et al.*, 1969) and *Oxycanus* (Dick, 1945) in which egg-laying is by females fluttering or resting on the ground.

Description of mating and flight behaviour

At the beginning of the flight period males rise up from the vegetation and after an initial short flight they take up a position and hover about 0.5 m from the ground (Fig. 2A, B). If there are a number of males they chase each other for a while, turning around each other in the air, until they eventually hover, spaced 1–5 m from each other. During this hovering flight, they face upwind and bob up and down, and from side to side like pendulums. Viewed from upwind the males appear dark as they hover, tail down, a few inches above the vegetation, because their undersides are heavily dusted with black scales. Their uppersides are white so that, seen from downwind, they are extremely conspicuous. Usually the moth twists and turns as it hovers, so that it appears to vanish and reappear as the underside and upperside are alternately presented to the viewer. The males seem to fly in all weather, including during very heavy rainfall at Heaton Park on 1 July 1978. *Hepialus humuli* were common in Oxford in 1976, where the males formed distinct groups, or 'leks' of up to about 10 males. The males would interact with each other, flying near each other and then separating again. These interactions were more common towards the beginning of the nightly flight periods.

Mating ($n = 18$) usually occurred near the beginning of the male flights. For example, on 19 June 1978 two males were found hovering at 22.35 hours at the Derwenthaugh site. At 22.38 hours a female approached one of these from more than 25 m downwind, and circled round him for *c.* 30 s, before flying down to the vegetation just in front of the male. The male responded by following the female, but when she settled on a stalk of grass, he appeared to lose her and continued hovering. The female then took to the air again, and again located the male and flew down near him. This time the male followed the female to the position where she had settled, and settled beside her. After achieving copulation in a ventral–ventral position (Fig. 2C), the male relaxed his grip with his legs and hung suspended, by his claspers only, from the female moth (Fig. 2D). The whole procedure was over by 22.40 hours. Another mating was observed on 20 June 1978 at 22.39 hours: a female approached one of the males after circling the area for about a minute, and touched the hovering male twice in flight before leading him down to vegetation where copulation took place. I observed a similar mating in Oxford on 27 May 1976 (the time was not recorded): a female had twice descended in the vicinity of the male and the male had both times apparently lost the female, and resumed hovering. The female arose from the vegetation for the third time, and struck the male in the air, causing both to fall in the grass. When the couple were examined closely, they were found to be already copulating in the manner shown in Fig. 2D. All 15 other matings observed confirmed to a simpler pattern than those above: the female flew towards a hovering male, which then followed her to a stalk of vegetation upon which copulation took place in the sequence described by Fig. 2C, D.

Details of male flight

I took a total of five interpretable photographs of male *H. humuli* hovering during their dusk flights (Fig. 2A, B). These reveal two hitherto unknown features.

Firstly, in all photographs there is a rosette-like brush organ extruded from the metathoracic tibia (Fig. 2A, B). These organs are normally folded back on the tibia in resting or dead male *H. humuli*. The in-flight photographs show that the rosette organs are normally everted during hovering flight, even though no females were nearby when the photographs were taken.

Secondly, the photographs show that the flight of this hepialid is more disorganized than the flight of the 'higher' Lepidoptera. Figure 2A shows the hindwings down while forewings are at the top of the upstroke. Figure 2B shows both hindwings and forewings raised but not obviously overlapping, while another photograph shows the forewings overlapping while both are raised. The photographs suggest the forewing and the hindwing perform downstrokes together, but that the hindwing upstroke is delayed until after the forewing has completed its own upstroke. My photographs of *H. humuli* in flight look more similar to photographs of Neuroptera and Mecoptera in flight (Dalton, 1975) than to similar photographs of heteroneurous Ditrysia. Blair (1918) had previously observed the forewings of sedentary female *H. sylvinus* beating independently of the hindwings during 'calling' behaviour (see also Hanson (1938) for observations on sedentary, fluttering *H. hecta*). These observations confirm Philpott's (1925) finding that the 'jugum' of hepialid wings rarely, if ever, links the fore- and hindwings together during use.

DISCUSSION

Mating behaviour in H. humuli

My observations show that female *H. humuli* fly up to hovering males, although I was not able to show the nature of the attractant. The usual sequence is as follows: (1) female flies to the 'lek' of males from some distance away; (2) female approaches one of the 'lekking' males; (3) male follows female while she slowly flies down to nearby vegetation and settles; (4) male lands on back of female, moves to a ventral–ventral position and copulates; (5) male releases hold of substrate and hangs, suspended only by his genital organs, from the quiescent female. In all of the 18 matings I observed, I never saw a male attracted to a sedentary female as reported by Carolsfeld-Krausé (1959), Harper (1960), Abdelrahman (1966) and Leuschner (1970). I did see two matings in which males apparently had difficulty following the female (see also Chapman, 1886; Manders, 1908; Martyn, 1960). It would be interesting to know whether receptive females are initially attracted to males visually or by means of pheromones. The literature is confusing on this issue also: small-scale experiments have shown alternative types of attraction (Cadbury *in* Kettlewell, 1973; Reynolds, 1973). In my own experiments I failed to attract female moths with paper models (Mallet, 1978). I suggest that the solution lies in the combination of the two (Kettlewell, 1973), with long-range attraction mediated by means of pheromones, but with the visual attraction to the white males taking over at close range. If this is true, then the white colour of males would have evolved by means of Darwinian sexual selection. While I observed females flying to males on 18 occasions, it is still possible that males will on occasion fly to females. Males of the Arctiid *Estigmene acrea* are attracted to females, as well as females being attracted to males, depending on the time of night (Willis & Birch, 1982). It is possible, for example, that male *H. humuli* aggregate in areas where females are likely to emerge, perhaps attracted initially by a long range female pheromone, and that the females are then attracted by male pheromones and colour pattern. There is also the possibility of a female close-range pheromone, since Kettlewell (1973, quoting Cadbury, unpublished) cites an observation of a male following a female through very thick vegetation through which the female was not visible. This disagrees with my own observations. It is clear that female *H. humuli* frequently fly to males, but not much more can be said until pheromones are isolated and assayed. The lack of detail presented in contrary observations suggests that some behaviours may have been presumed rather than observed.

Male *H. humuli* are attracted to each other (Robson, 1892), to excised male tibiae (Cadbury *in* Kettlewell, 1973), and to white paper models (Mallet, 1978). It is probable that males use the same cues to form leks as the females do to find mates. Males are similarly attracted to 'leks' by male pheromones in *Estigmene acrea* (Willis & Birch, 1982).

Metatibial rosette organs and their function in hepialids

Of the British species of *Hepialus*, two have rosette organs on the metathoracic tibiae of males: *H. humuli* and *H. hecta*. The male of *H. humuli* has a swollen hind tibia to which are attached long setae; otherwise the leg is normal. In *H. hecta* and some American allies, the hind tibia of the male is grossly swollen, and the tarsus is almost completely absent and is functionless. From an opening in the distal portion of the tibia protrude papillae which are not at all like the setae of *H. humuli* males. Another peculiar feature of *H. hecta* is that the hind tibia of the male fits into an abdominal pocket, so that the hind legs often appear absent in museum specimens. These features were first described, in great detail, by Bertkau (1882). This work was summarized by Illig (1902), and the tibiae were again described by Deegener (1902), who corrected some errors made by Bertkau. *Hepialus hecta* has mating behaviour in which males hover or sit in groups and females perform the initial approach (Barrett, 1886; Robson, 1887a, 1892; Deegener, 1902; Deegener & Schaposchnikow, 1905; Cockayne, 1912; Cockayne & Jackson, 1913; Turner, 1976). Deegener (1902), Cockayne (1912) and Cockayne & Jackson (1913) report that males sometimes sit on vegetation and 'call' with outstretched tibial scent organs, and that females are attracted to these sedentary males. Hanson (1938) made some detailed observations that were similar; he noted sedentary individuals in small groups (which attracted females and males), but stated that they were females. Perhaps "Deras genitalier stucko ut som en liten mörk tub i bakkroppens spets" represents an observation, not of the abdominal tip of the female as Hanson thought, but of the protruding metathoracic tibiae of the male. Hanson (1938) also saw a female being attracted to a male, and concluded that in *H. hecta* each sex can attract the other. Otherwise only Carolsfeld-Krausé believes that females attract males: "I have seen thousands of *H. hecta* and their matings right from the start, . . . and in all cases it was the male which was the aggressive party" (Carolsfeld-Krausé, 1959). In some cases copulation of *H. hecta* apparently took place in the air (Deegener, 1902; but see Deegener & Schaposchnikow, 1905).

Males of both *H. humuli* and *H. hecta* produce a smell from their hind tibiae while in flight. Barrett (1892) described the smell of *H. humuli* as faint and goaty, but I was unable to detect this. Barrett (1882), Turner (1976) and other authors agree that male hind tibiae of *H. hecta* smell strongly of pineapple. The males of *H. hecta* lose their odour when boxed overnight (Turner, 1976), because their hind tibiae have been inserted into their abdominal pockets (Bertkau, 1882). *Zenophassus schamyli* Christoph has *H. humuli*-like rosette organs, described and figured by Deegener & Schaposchnikow (1905). In this species females are also attracted to groups of hovering males; after arriving, the female leads a male down to a resting spot where copulation takes place.

The males of the British species *H. sylvina, H. lupulina* and *H. fusconebulosa* De Geer, are without male brush-organs, are fast-flying and do not hover, and are unanimously reported to seek actively for females. The females of these species 'call' from a settled position by beating their forewings only, while keeping their hindwings folded (Robson, 1887b, 1891, 1892; Stainton, 1887; Blair, 1918; Harper, 1959). The brachypterous females of the French *Hepialus pyrenaicus* also attract males, and males of this species lack tibial scent organs (Donzel, 1838; Robson, 1887b; Bethune-Baker, 1913).

The correlation between metatibial morphology and behaviour in these European hepialids suggests that the function of the hepialid rosette organ is very different from that of the hair-pencils, brush organs and coremata (Varley, 1962) of male heteroneurous ditrysian Lepidoptera. Male ditrysians are usually attracted to females from long distances. The males normally use pheromones from their brush organs or coremata as aphrodisiacs, to subdue the female in preparation for mating (Birch, 1970a, b, c; but see also Boppré, 1983). Closely-related species of heteroneurous ditrysians often differ in their possession of brush organs (Birch, 1970b). As an example, Watson (1975) found a pair of sibling species of the arctiid genus *Emurena*; one of these species has no less than three separate male scent-organs that are completely lacking in the other. The probably aphrodisiac role of the pheromones disseminated by these organs seems to be evolutionarily labile—a male can after all also subdue a female by physical means! In *H. humuli, H. hecta,* and *Z. schamyli* on the other hand, the brush organs and pheromones seem more important for primary attraction of the female. A brief survey of the Hepialidae of the world (using the collections of the British Museum (Natural History)) showed that presence or absence of metatibial brush organs is usually a generic character (Table 2). In fact only *Hepialus*, the polyphyletic (G. S. Robinson, pers. comm.) genus *Phassus*, and *Oncopera* had some species with, some without the rosette organs. The peculiar arrangement of scent-organ found in male *H. hecta* is only found in a few apparently related species of *Hepialus* from Europe and North America (Table 2).

In North America, Holland (1903) noted that individuals of *Sthenopis argenteomaculatus* Harris "dance in the air and perform very peculiar gyrations" (see also Keith, 1916). Males of *Sthenopis thule* Strecker are also reported to gather in swarms at dusk (Lyman, 1893; Winn, 1909). Forbes (1923) writes that *Sthenopis* spp. in New York "have the habit of swarming like midges, the males having a wavy, zigzag flight, and the females apparently entering the swarm of

Table 2. Presence of male brush-organs in some Hepialidae

Species	Brush-organ type	Notes
Abantiades spp.		
Antihepialus antarcticus		
keniae		
Callipielus spp.		
Charagia cyanochlora	hu	
daphanandrae	hu	
dulcis	hu	♂ is pure white
eximius	hu	♂s have white hindwings, females are brown
hampsoni	hu	
mirabilis	hu	♂s have white hindwings, ♀ are brown
lignivora	hu	♂s have white hindwings ♀ are brown
ramsayi	hu	♂ is paler, nearly white hindwings
scotti	hu	
splendens	hu	♂ very white and silver
virescens	hu	
Dalaca spp.		
Endoclita excrescens	hu	
sericeus	hu	
Eudalacina ammon		
*Fraus simulans**	—	
Gorgopis spp.	-	
*Hepialus humuli**	hu	
behrensi	he	
californicus	he	
*hecta**	he	
lenzi (= hectoides)	he	
*sequoiolus**	he	
carna		
fuscoargenteus		
*fusconebulosa**		
ganna		
gracilis		
*hyperboreus**		
*lupulinus**		
*macglashani**		
Hepialus macilentus		
mustelinus		
nebulosus		
*pyrenaicus**		
*sylvina**		
Leto spp.		
Metahepialus xenoctenis		
Neohepialiscus algeriensis		
Nevina spp.		
*Oncopera alboguttata**	hu	
brachyphylla		See Elder (1978) for with *O. parva*
*fasciculata**	hu	
*intricata**	hu	
mitocera	hu	
parva	hu	See Elder (1978) for with *O. branchyphy*
*rufobrunnea**	hu	
*tindalei**	hu	
*Oxycanus cervinata**		
spp.		
Parapielus spp.		
Phassus phalerus	hu	
"*Phassus*" *chilensis*	-	
Puermytrans chiliensis	hu	
*Sthenopis argenteomaculatus**	hu	
purpurascens	hu	
quadriguttatus	hu	
*thule**	hu	
Thitarodes variabilis	hu	
Trichophassus spp.	--	♂ has extremely long s wings and body
Trictena argentatus		♂ has antennae more p than ♀
Zelotypia stacyi	hu	♂ has long scales on and body
Zenophassus schamyli	hu	

* = mating and flight behaviour observed, see text for details.
hu = brush organ on swollen tibia, as in *Hepialus humuli*, tarsus present.
he = brush organ protrudes from inside grossly swollen tibia, as in *H. hecta*, tarsus vestigial, almost absent, tibia placed in pouch on abdomen when not in use.
= brush organs absent.

males one by one". Male specimens of *Sthenopis* have *H. humuli*-like brush organs and their behaviour, from the descriptions above, also seems similar. *Hepialus sequoiolus* Behrens, with *H. hecta*-like male brush-organs, is also reported hovering in all-male groups (Williams, 1905). David Wagner (in prep.) reports that *H. sequoiolus* and its relatives have mating behaviour that is very similar to that of *H. hecta* in Europe: males hover in groups, sometimes settling with scent organs exposed, and females fly to these groups. In two species without hind-tibial organs, on the other hand, the males fly to females that are sitting and vibrating their wings (*Hepialus macglashani* Edwards (Edwards, 1886) and *H. hyperboreus* Moschler (McDunnough, 1911)).

A number of hepialid pasture pests have been studied in Australia and New Zealand. In *Oncopera* that have *H. humuli*-like brush organs, males are said to fly to females. But once again, I feel it is possible that only the last stages of courtship were observed: in *H. humuli* also, the male does indeed usually fly to the female when she has arrived. For this reason it is worth reviewing these studies for similarities to those on *H. humuli.*

Adults of *O. intricata* Walker fly backwards and forwards for 40–55 min at dusk. The moths appear from the description to be aggregated, and the sex-ratio is male-biased on the wing (though emerging adults have a 1 : 1 sex-ratio; Hill, 1929). Hill (1929) stated that males are attracted to sedentary females. In his more careful study, Martyn (1960) showed that females always fly before attracting males, and that sedentary females are ignored by hawking males. *Oncopera fasciculata* (Walker) is also crepuscular, and flights begin after sunset at a time that is related to light intensity. Individuals disperse during the earliest flights, but this is soon followed by an aggregated flight during which individuals hawk rapidly back and forth. Males are again more commonly seen in the aggregations (Madge, 1954). Both Hill (1929) and Madge (1954) write that there is an equal sex-ratio at the beginning of the mating flights, but that females drop out after mating as the flight proceeds. A further three species of *Oncopera* (*O. alboguttata* Tindale, *O. rufobrunnea* Tindale and *O. tindalei* Common) were observed by Barton Browne *et al.* (1969), and their mating is very similar to that of *O. fasciculata* and *O. intricata.* One peculiar feature is that copulation is very brief in some species, lasting as little as 30 s. Van Gerwen, Barton Browne & Soo Hoo (1972) showed that take-off times of male *O. alboguttata* vary around the time of sunset, depending on light intensity changes caused by weather differences. In all of the three most recently-studied species, the males fly before the females, which apparently was not the case for *O. fasciculata* and *O. intricata.* Martyn (1960) found similar mating behaviour for *O. intricata* and *O. rufobrunnea.* The females of all the *Oncopera* studied fly before mating, though these authors unanimously reject any suggestion that females fly to males. It is therefore with some hesitation (never having seen the species flying myself!) that I suggest that "The female flies in a relatively straight line through the cloud of hawking males. . . ." (Barton Browne *et al.*, 1969) could mean that the female is orienting to the male groups. Males probably follow females, as in *H. humuli*, after the female has come very close to them. It will be interesting to find out if *O. brachyphylla* Turner (without brush organs) and its close relative *O. parva* Tindale (with brush organs) (Elder, 1978) have similar mating behaviour. Two other hepialid pasture pests, *Oxycanus cervinata* Walker and *Fraus simulans* Walker, lack male brush organs, and females do not fly before mating. The males fly directly to sedentary females (Dick, 1945; Hardy, 1973).

It would be fascinating to have a report on the mating behaviour of the giant green hepialids of the Australasian genus *Charagia*: they have male rosette organs and many are strongly dimorphic in colour (Table 2). It can be predicted that the females will fly to groups of hovering or hawking males at dusk. Apart from a few notes on the odour of the hind-tibial organs (Illidge, 1899; Dodd, 1902), I cannot find any relevant observations.

CONCLUSIONS

Of the hepialids studied so far, species with male brush organs (in the genera *Hepialus, Oncopera, Sthenopis* and *Zenophassus*) have unusual mating behaviour with a number of features in common: The moths fly during strict time periods determined by light intensity just before to soon after sunset; individuals either hover or loop back and forward over the same spot, or settle in groups; these hawking, hovering or sedentary groups are usually male-biased; and females fly before being mated.

In *H. humuli*, more females than males are attracted to light, suggesting that they are the more mobile sex. Also in *H. humuli*, aggregated males hover with brush organs fully everted (Fig. 2A, B), which suggests they are calling, and males and females are attracted to these males. This occurs in other hepialids (*H. hecta, Sthenopis* and *Zenophassus*) with brush organs. Other species which lack brush organs (in the genera *Hepialus, Oxycanus* and *Fraus*) do not show these traits, and appear to fly and mate in a way which is more standard for ditrysians. These studies should be expanded, especially in Australia where there is a high diversity of hepialids, and where an understanding of their pheromonal communication could lead to methods of controlling some important pasture pests. It will be most interesting to find whether the brush organs and associated mating behaviour are primitive or advanced traits within the Hepialidae, and whether they have evolved more than once. The existence of this 'reversed-role' mating behaviour in a basal branch of the ditrysian line raises the question: could mating where the female is the active partner be primitive in the Lepidoptera as a whole? We will be able to answer this question only when the systematics and the biology of basal groups like the Hepialidae are better known. David Wagner (pers. comm.) is at present performing just such a study of the systematics and behaviour of the Holarctic *Hepialus*, and is investigating the pheromones of Californian species. His results should help resolve many of the conflicting reports reviewed here.

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