

Mating Behaviour of the Millet Headminer Moth, Heliocheilus albipunctella (de Joannis) (Lepidoptera: Noctuidae: Heliiothinae).

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ABSTRACT

The millet head miner moth, Heliocheilus albipunctella, is one of the most damaging pests of pearl millet in the Sahelian region. Its mating behaviour is complex but poorly understood. The present study describes the mating behaviour in detail, based on observations made both in the field and in the laboratory. For 2-3 hours after dusk, males generate a buzzing sound by the percussive vibration of their forewings, whilst simultaneously exposing their genitalia. This display is performed either singly or by groups of males, perched low down (<50cm) on millet stems or fieldside vegetation. Male groups, considered to be leks, are commonest in more open areas at the field margins, whilst single males predominate within the millet field. Females approach buzzing males directly from downwind, and mating occurs immediately on arrival, lasting approximately 1 hour.

KEY WORDS Heliocheilus albipunctella, Noctuidae, millet, Pennisetum glaucum, mating behaviour, bioacoustics, lek.

Introduction.

The millet head miner moth, *Heliocheilus albipunctella* (De Joannis) (syn. *Raghuva albipunctella*) is one of the most important agricultural pests of the Sahel. Pearl millet, *Pennisetum glaucum* (L.), is the predominant crop in this region, where it provides the staple diet of the population (Nwanze and Youm 1995). Damage caused by the larvae of *H. albipunctella*, which feed inside developing millet panicles, varies in intensity between years, but can result in yield reductions of over 50% (Nwanze and Sivakumar 1990, Krall *et al.* 1995).

Following the pioneering work of Vercambre (1978), a variety of potential management options have been subject to research (summarised in Nwanze and Youm 1995). These include the complex of natural enemies, soil management, planting of short-season millet varieties and use of pesticides. However, at present, Sahelian farmers still lack any effective control measures against this damaging pest. Here we begin to address the scope for management by means of behavioural manipulation (Foster and Harris 1997), providing a detailed description of the moth's mating behaviour.

Existing accounts of mating behaviour in *H. albipunctella* are sketchy, but suggest it differs substantially from the typical pattern found in noctuid moths, with females in this case approaching males prior to mating (Matthews 1987a,b). Males produce a buzzing sound, whilst perched on vegetation, by vibrating their structurally specialised forewings, and they are reported to do so in multi-male aggregations (leks). It was suggested that buzzing males also release a sex pheromone, and diethyl malonate was tentatively identified as a component of this (*ibid.*). Hence it appears likely that females could be guided during mate location both by acoustic and chemical cues.

An understanding of a species' natural mating behaviour, which is apparently complex in the case of *H. albipunctella*, is a prerequisite for developing a pest management strategy that would seek to exploit the moths' natural communication system (Boake *et al.* 1996). Previous accounts lack any quantitative information and mention no detail regarding the act of mating itself. The following study provides a more rigorous description of pair formation and mating in this species.

Materials and Methods.

The following account of *H. albipunctella* behaviour is based on observations made in the fields at night time, and an analysis of video recordings filmed under laboratory conditions.

Field Observations.

Nocturnal fieldwork was conducted in and around millet plots at the ICRISAT Sahelian Centre, Sadoré, Niger, and in neighbouring farmers' fields, during the moth's peak flight period, over four growing seasons (1996-99). The flight period here spans some 6-8 weeks, but usually the moth population peaks sharply at the end of August, coincident with the main period of emergence and flowering of millet panicles.

Observations of moth behaviour were made using red-filtered torchlight in most instances, although sometimes moonlight alone provided sufficient illumination. Bright red torchlight

can visibly disturb these moths, and so most of the present observations were made using a weak, wide-angle beam, directed to one side of the moths so that they were visible towards the periphery. In this way overt inhibition of moth behaviour was kept to a minimum, although disturbance did sometimes occur. In particular, the initial exposure to the torch beam could result in the moth(s) flying away, but provided this sensitive moment passed without disturbance then the subsequent behaviour seemed to be unaffected, and not noticeably different from observations made by moonlight. Mating was observed in the field under this dim illumination on several occasions (see below).

Laboratory Observations.

Video filming of *H. albipunctella* buzzing and mating behaviour was performed using a low light sensitive camera (Cohu) under dim red lighting, inside a windowless room at the ICRISAT Sahelian Centre, and under similar conditions at the Natural Resources Institute, UK. The moths were filmed inside a variety of wire-framed, fabric netting enclosures. In order to establish the pattern of wing movements during buzzing behaviour a stroboscopic red light was directed at buzzing males as they were filmed, and the position of the wing was then traced throughout the wingbeat cycle during video playback.

Sound recordings were made both in the field and the lab, using a UHER Report L reel-to-reel tape recorder and UHER microphone, and a Sony Walkman Professional cassette recorder with Sennheiser superdirectional electret microphone. Analysis was achieved using Avisoft SASLab Pro acoustic software. Ultrasonic components were also sought using an Ultrasound Advice U30 bat detector. Sound intensity was measured in the field using a Cel Instruments sound level meter (model 254).

Results.

Male Buzzing Behaviour.

H. albipunctella males generate a continuous buzzing sound, from a perched position, by vibrating their structurally specialised forewings. At the same time, the male abdomen is rhythmically extended, exposing the genitalia (see below). This conspicuous display, which can be sustained by individual males for periods exceeding 1 hour, will simply be termed 'buzzing' here.

Just before buzzing commences, the leading edge of each forewing is raised from the resting position (near horizontal, e.g. Plate 1) to an angle of approximately 30° above the longitudinal body axis (Plate 2). The forewings are then fanned through a restricted arc above this raised position, such that the costal thickenings repeatedly strike one another at the top of the upstroke in a castanet fashion, producing a continuous buzzing sound. During the upstroke the anterior half of the forewing bends along a longitudinal axis. The specialised region between vein Rs and the costa, which includes the membraneous "blister", becomes distorted to the extent that at the uppermost wing extension the costal thickenings of the two forewings briefly touch. The buzz consists of a repetitive train of short pulses (duration c.0.2msec), delivered at a steady rate of 136 pulses/sec (at 27°C). Most power is in the range 1-8kHz (Fig. 1). No ultrasonic component could be detected on our recordings, nor could any signal above 13kHz be detected using a bat detector whilst listening to buzzing males in the field.



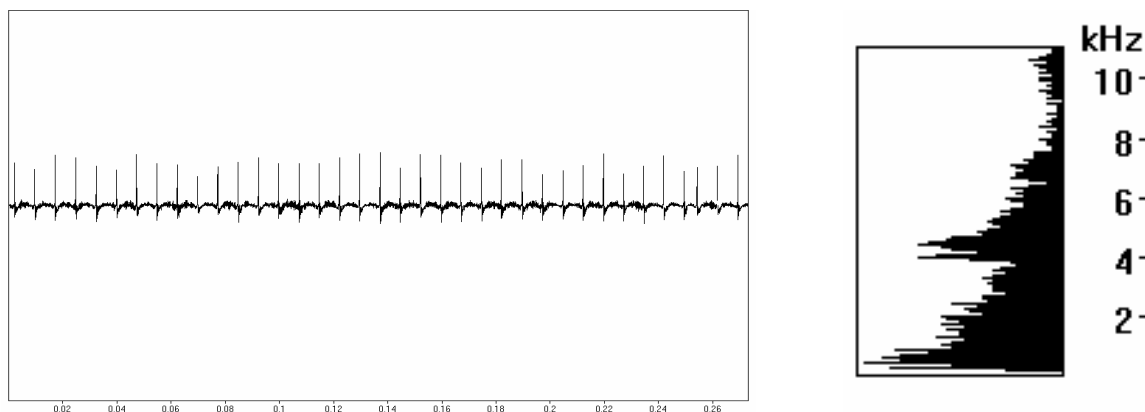
Plate 1. Male *H. albipunctella* in resting posture. Each wing's outer edge (costa) contains a thickened bolus at the apex of the bulge in the margin. Note the membranous region adjacent to this.



Plate 2. Male *H. albipunctella* in characteristic buzzing posture. The thickenings in the costal margins, which function as castanettes, are clearly visible here.

Figure 1. Acoustic characteristics of male *H. albipunctella* buzzing.

Left: oscillogram showing buzz temporal modulation pattern (0.27sec shown); *Right:* power spectrum



On a relatively still evening, the human ear can detect the sound of a single buzzing male up to a distance of approximately 5m. Field measurements of sound intensity were rather variable, and were affected greatly by the male's immediate physical surroundings. Consistent readings were obtained from just two males whose positions were especially favourable for making measurements. A typical sound pressure level value under field conditions was 50dB at 15cm dorsally, set against a background sound pressure level of 35dB. Maximum sound intensity was measured above the buzzing male, perpendicular to the longitudinal body axis (Table 1).

Direction:	dorsal	lateral	posterior	anterior
Male 1	49.6 (0.32, 9)	43.0 (1.15, 3)	46.7 (0.54, 5)	46.5 (0.50, 2)
Male 2	52.6 (0.26, 8)	51.5 (0.42, 5)	51.8 (0.44, 9)	50.7 (0.46, 6)

Table 1. Field measurements of sound pressure level (dB) around buzzing male H. albipunctella. SPL measured at 15cm from male body; standard error and sample size in brackets.

At the moment of impact between the costal thickenings, the wings are in their position of maximum distortion, approximating a conical funnel, but this does not appear to function as a directional trumpet amplifier. Buzzing males cling to the edge of a leaf or stem, facing upward with the body raised at an angle of typically between 20° and 60° from vertical (Plate 2), hence the buzzing sound is projected upwards and backwards from the perch position.

During buzzing, the terminal segments of the abdomen, which are normally concealed, are everted and extended. This exposes patches of scales on the lateral posterior margins of the terminal two segments. The genitalic claspers are also periodically flexed, thereby exposing a profusion of hair-like scales on these appendages (Plate 2). At maximum extension, the male's abdomen could be stretched some 40-50% beyond its normal resting length. Typically, the end of the extended abdomen curves upwards such that the tip lies a short distance beyond the extreme sweep of the vibrating wings.

Moth Activity.

Females are evident in the fields before males, becoming active at around sunset (c.19.05h) as they fly between millet panicles to oviposit. Males emerge from the ground vegetation layer at around this time, but otherwise remain inactive until 15-20 minutes after darkness (c.19.45h) when they start to buzz, doing so either singly or in small groups. The transition period through twilight to night time (19.00h to 20.00h), when the moths become active, is characterised by a drop in temperature of 2-5 °C, stabilizing typically at 25-29 °C and a 20-30% increase in air humidity to >90% RH (measurements at 10cm above ground level). Frequently there is also a reduction in wind speed at this time, but this was not measured here.

Male buzzing activity was monitored throughout three nights of field observation by continuously patrolling a fixed circuitous route through a field plot and noting the time when each buzzing male was encountered. Buzzing was found to continue for approximately 2 hours before the males became silent (Fig. 2), by which time female activity had also declined markedly. Further field observations made throughout the night, and specifically patrolling the very same field plot from 04.30h until sunrise, failed to discover any further signs of moth acoustic activity.

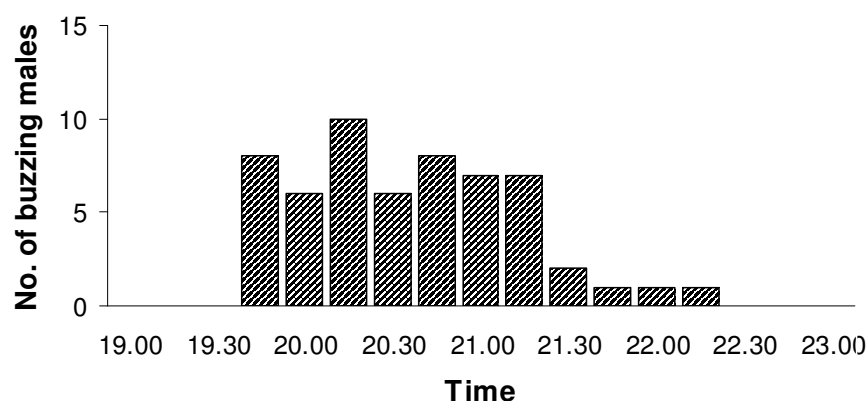


Figure 2. Temporal distribution of male buzzing activity. Number of buzzing males observed throughout 3 nights of continuous patrol through a field of 3/4HK pearl millet with emergent panicles (21, 22, 24 Aug 1996).

In a plot of the relatively short millet variety 3/4HK (heading at approximately 1.5m), males buzzed from positions relatively low down on the millet plants, averaging at approximately 50cm above ground level (1996 data $x=52.0\text{cm}$; $n=60$; $SE=\pm 2.99$; 1997 data $x=48.0\text{cm}$; $n=21$; $SE=\pm 5.02$). Twenty three millet plants selected by males as buzzing sites were marked during one evening of observation, and these were measured the following morning and compared with 30 further millet plants selected at random. The buzzing site plants were significantly smaller than the population median (Mann Whitney U test: $U=255$ ($n=23,30$), $P<0.05$). Areas of less dense crop foliage, e.g. near to gaps within the field, also appeared to be favoured, but attempts to map buzzing positions in the field plots were confounded by the moths' tendency to fly away and then buzz on a new plant when disturbed by observers moving nearby. Buzzing behaviour was often observed amongst short grasses and weeds around the edges of fields, particularly on the locally abundant *Hibiscus sabdariffa*. These non-crop plants were typically much shorter than the millet, and males' buzzing perches were at a much lower elevation (1996+1997 combined average $x=20.1\text{cm}$; $n=20$; $SE=2.72$) than usually observed on millet plants. Males were significantly more likely to buzz in small groups in this more open situation than within the plot, where they tended to buzz singly (Table 2).

Buzzing site	Buzzing male group type	
	Single buzzing male	Multiple male group
Crop millet	116	47
Weeds at field margin	23	23

Table 2. Association between observed male buzzing group size (single vs multiple) and buzzing site (millet vs weeds at field margin). Combined data from 1996, 97, 98.

Contingency χ^2 (1 d.f.) = 7.22, $P<0.01$

When there was any noticeable air movement, buzzing males consistently orientated themselves with their abdomens pointing downwind. Single males are capable of buzzing continuously for extended periods: on two occasions a male, in each case already buzzing

when first observed, continued for more than 60 minutes. On another occasion, two males were observed to continue buzzing for at least 20 minutes during a heavy storm, doing so by adopting sheltered positions on the downwind side of their millet plant.

Male-Female Interactions.

On most nights during the peak flight period mating pairs could be located in the field, but the behaviour occurring immediately beforehand proved very difficult to observe.

Over the four years during which observations were made, 11 natural matings were witnessed, plus a further three involving virgin females which emerged from pupae in the lab and were released in the field. The timing of the natural matings (*i.e.* when they started) was spread fairly evenly throughout the buzzing period, with the latest taking place at 21.36h. In the majority of these matings, the female was observed to locate the buzzing male by means of a rather direct, horizontal approach flight from downwind, and mating ensued almost immediately upon her landing next to the male. The brief duration of the pre-mating interaction would explain the difficulties experienced in making such observations. One mating, observed on a completely still evening, involved the female flying past the millet plant on which the male was buzzing, and subsequently following a spiral flight path back around the plant before alighting close to the male.

In most cases the receptive female approached a solitary buzzing male (5 on millet, 4 on weeds), but two of the observed matings involved multi-male groups. One of these occurred amongst a lek of 5 males, in an open area of weeds and wild grasses between two millet fields, on a completely still evening. In this case the female walked erratically amongst the males, fluttering her wings, and approached several different males before coupling successfully with her eventual mate. In the second case, the female alighted on a millet plant with two males, of whom one was buzzing whilst the other, perched 3cm below the first, had stopped buzzing 26 minutes earlier. The female landed just below the buzzing male but was instantly clasped by the silent male, and copulation ensued. Such lek matings are probably rather more common than the findings presented here would suggest, since in this study most field observations were made at the edge of millet plots, where single buzzing males predominated. Pairs observed *in copula* were frequently observed with one or several buzzing males in attendance, and on two occasions two mating pairs were found on the same millet stem separated by just 2-5cm, with other buzzing males in close attendance (Plate 3). Such attendant males were never observed to physically interfere with the mating pair, but often they buzzed very vigorously, and usually continued to do so when the mating pair eventually separated. In such cases however, subsequent remating was never observed, although it is known that during a female's lifetime a second mating sometimes does occur since females may contain two spermatophores (Bayoun *et al.* 1995). The location and height above ground of observed mating pairs is illustrated in Figure 3.

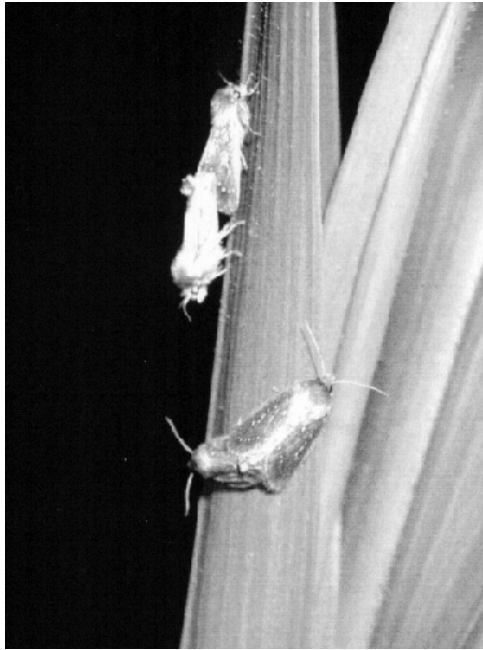


Plate 3. Two mating pairs of *H. albipunctella* on millet.

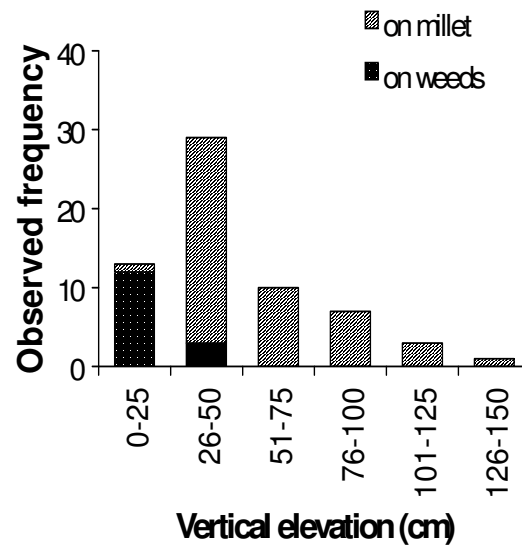


Figure 3. Resting elevation of mating pairs of *H. albipunctella* observed in field plots

Video Analysis of Mating Behaviour.

Low-light video recordings of 13 staged matings filmed inside netting enclosures, allowed an analysis of the behavioural events taking place just before genital coupling. After alighting close to the buzzing male, the female walks directly towards him, fanning her wings, and pushes past the region of the male's head. The male continues to buzz as the female approaches until, when she is very close, he reaches out either sideways or directly over his own head with his extended abdomen toward the female's abdomen tip, flexing his genitalic claspers and attempting to grasp her (Plate 4). The first attempted grasp was successful in 7/13 filmed matings, and in these cases copulation commenced almost instantaneous upon the female's arrival. A reliable indicator of successful genitalic coupling is when after 2-3 seconds the female's wings are lowered into the normal, sloped resting position.

In those cases where the male's first attempt to grasp the female was unsuccessful, a few seconds of frenzied clasping followed before proper genital contact was established, and in one exceptional case this did not occur until the eighth attempt. In 2/13 filmed matings the female walked beyond the male, turned and re-approached the buzzing male, wing-fanning as before. In both cases the male made an initial movement to follow the female, attempting to clasp her as he did so, but almost immediately returned to stationary buzzing rather than pursuit. The average copulation duration under filming conditions at 25-27°C, was 58 min. 30 sec (n=16; SE=4.20). Throughout copulation the mating pair remain motionless, and following separation males were never observed to recommence buzzing behaviour.

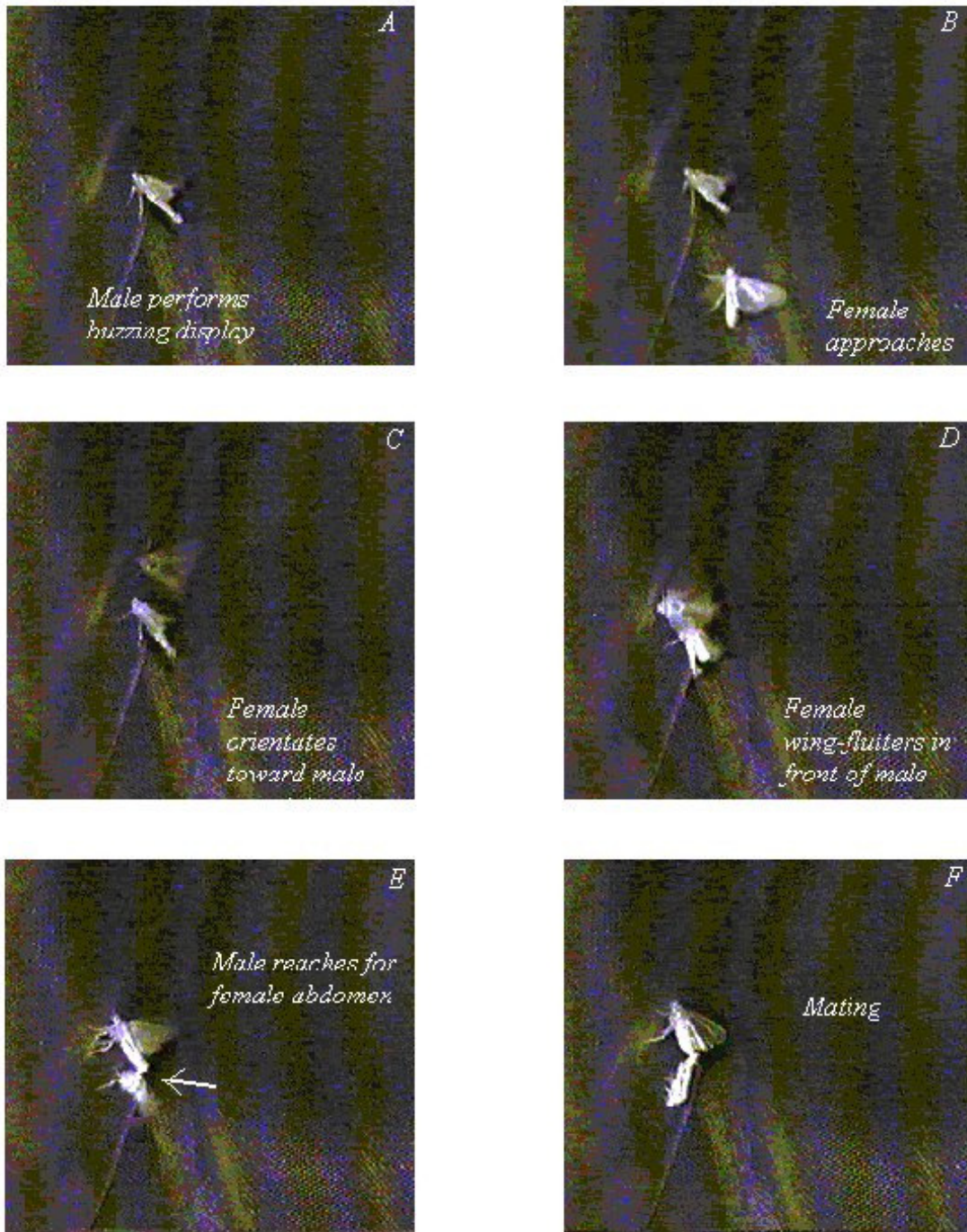


Plate 4. Mating sequence in *H. albipunctella*, filmed inside a net cage in the lab.

Male-Male Interactions in the Field.

Male groups, most frequently of just 2 males, but sometimes more (Table 3), formed early in the evening, and were frequently the source of the first buzzing to be heard. Males were sometimes observed flying to join or departing from existing groups, particularly during the early part of the buzzing period.

Buzzing group size	1	2	3	4	5
Observed frequency	142	79	9	2	1

Table 3. Number of males in observed buzzing groups. Combined data from 1996, 97, 98; in multiple-male groups not all males were necessarily buzzing.

Within groups, inter-male distance was typically less than 15cm, and was sometimes as little as 1-2 cm. Spacing was at least partly maintained by inter-male agonistic behaviour in which males attempted to clasp each other's abdomens. Whether such behaviour constitutes a misdirected mating attempt or an overtly aggressive act is not clear, but in any case the observed outcome was to increase spacing of individuals, and sometimes it even resulted in the departure of one of the males. With few exceptions, all males in such leks buzzed during the early part of the evening, but as time passed individuals gradually stopped buzzing, and towards the end of the buzzing period typically just one male remained acoustically active.

Discussion.

The evolution of a lek mating system is thought to be favoured in situations involving abundant or evenly distributed resources for females (food or oviposition sites) which individual males cannot monopolise (Thornhill and Alcock 1983, Höglund and Alatalo 1995). Based on the present observations, there can be little doubt that the aggregations of buzzing male *H. albipunctella* meet all criteria that have been specified for a "classical" lek. Males contribute nothing but gametes, there is a discrete mating arena, males' territories within the arena contain no vital resources for the female, and the females are able to select a mate freely within the arena (Bradbury 1981, Shelly and Whittier 1997).

Parental investment theory predicts that the sex which makes the lesser parental investment will expend most energy and expose itself to greater risk during pre-mating activities (Trivers 1974). Species which have a lek mating system represent an extreme situation where effectively all parental investment is made by the female. In the present case, *H. albipunctella* females produce in excess of 800 eggs (Bayoun *et al.* 1995), which ultimately they must oviposit on exposed millet panicles in fields patrolled by bats and insectivorous night birds such as *Caprimulgus* sp. In order to mate they must also incur an energetic cost and predation risk during the mate-seeking flight. In contrast, males fly relatively little. Although the sex ratio obtained from field-collected pupae is 1:1, light trap catches of *H. albipunctella* show a female sex bias of 3.75:1 (Bayoun *et al.* 1995; trap height 3m). Instead, males channel their energy into acoustic display and, possibly, pheromone production. The energetic cost of prolonged buzzing is likely to be high, in addition to which pheromone production would also incur a metabolic cost. Field observations suggest that buzzing behaviour also involves a considerable element of risk because males were observed to fall prey to several species of spider (most notably members of the Solifugidae), and praying mantises.

In contrast to earlier accounts of this species' behaviour, here it was found that in areas of dense foliage within millet fields males are most likely to buzz singly, whilst the lek group

display predominates in more open areas, especially in low grass and weeds adjacent to fields. Hence this moth's mating system is variable, falling amongst relatively few recognised examples of facultative lek-breeding species (Höglund and Alatalo 1995). It is likely that the balance between costs and benefits for an individual male buzzing either alone or in a group is different in these two microhabitats. Leks are more conspicuous acoustically, and possibly so chemically, compared to single buzzing males, and out in the open where they might be perceived over long distances by many transient females it seems likely that such groups could attract more females per male than would a single male buzzing alone. Conversely, within the vegetation matrix of the millet field the male display is likely to be perceived less clearly and over a shorter distance. Hence the prospects of a lek achieving an improved mate attraction rate would be reduced and the cost:benefit ratio would favour males spacing themselves out and buzzing individually. Males are certainly capable of exercising choice over where they perform buzzing behaviour, since they were observed both joining and leaving leks, and although they are not strong fliers they are easily capable of moving between field and adjacent open areas.

Acoustic signals are now known to be produced by a wide range of moths (Scoble 1992, Conner 1999). In many cases the sounds play a role in predator deterrence or avoidance, but acoustic emissions are also known to play a role in the mating behaviour of several species (Bailey 1971, Heller and Achmann 1993, Surlykke and Gogala 1986). The acoustic display of H. albipunctella has similarities with that of the Australian agaristid moth Hecatesia exultans, whose males also generate sound using a castanet mechanism, whilst perched (Bailey 1971). In that species, however, the wings are held closer together and vibrated through a narrow arc at a rather higher frequency, and the vibration is modulated into a series of clicking sound. Bailey calculated that the dimensions of the cavity created between the vibrating forewings and hindwings in H. exultans are such that it functions as an almost perfect cavity resonator for sound of the wavelength that moth produces (*ibid*). In the present case, on the basis of rather limited data, the wings of H. albipunctella appear to serve as a directional amplifier, with the sound intensity greatest directly above the male's longitudinal body axis. Since receptive females were almost invariably observed to approach buzzing males from above and behind, this suggests they may use sound intensity as a guidance cue during mate location. However, because buzzing males always orientate themselves with their abdomen pointing downwind then the former observation is also consistent with female guidance by air-borne chemical cues.

The present observations confirm and elaborate upon earlier reports (Matthews 1987a,b) of a sex role reversal in mate location in H. albipunctella, compared to the typical pattern of pair formation in noctuid moths (Scoble 1992, Phelan 1997). In the present species, receptive females locate buzzing male conspecifics with a high degree of accuracy, and upon doing so mate straight away. If it were possible to mimic these signals then population monitoring, mating disruption or even trapping of females might be possible. The latter option would have a considerable impact by removing gravid virgin females from local populations.

Behavioural and electrophysiological studies are currently under way, aiming to elucidate the mechanism of mate location in this species.

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References Cited

- Bailey W.J. 1971.** Resonant wing systems in the Australian whistling moth Hecatesia (Agarasidae, Lepidoptera). *Nature* 272, 444-446.
- Bayoun, I.M., Gilstrap, F.E. and Youm, O. 1995.** Assessment of the effectiveness of natural enemies of the millet head miner. *International Sorghum & Millets Newsletter* 36, 55-56.
- Boake, C.R.B., Shelly, T.E. and Kaneshiro, K.Y. 1996.** Sexual selection in relation to pest-management strategies. *Ann.Rev Entomol.* 41, 211-229.
- Bradbury, J.W. 1981.** The evolution of leks. In R.D.Alexander and D.W.Tinkle, eds., *Natural Selection and Social Behaviour*, pp. 138-169. New York and Concorde: Chiron Press.
- Conner, W.E. 1999.** 'Un chant d'appel amoureux': acoustic communication in moths. *J. Exp. Biol.* 202, 1711-1723.
- Foster, S.P. and Harris, M.O. 1997.** Behavioural manipulation methods for pest management. *Ann. Rev. Entomol.* 42, 123-146.
- Heller, K-G. and Achmann, R. 1993.** The ultrasonic song of the moth Amyna natalis (Lepidoptera: Noctuidae: Acontiinae). *Bioacoustics* 5, 89-97.
- Höglund, J. and Alatalo, R.V. 1995.** *Leks*. Princeton University Press, New Jersey, USA.
- Krall, S., Youm, O. and Kogo, S.A. 1995.** Panicle insect damage and yield loss in pearl millet. pp 135-145 *In* Panicle insect pests of sorghum and pearl millet: proceedings of an international consultative workshop, 4-7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger. (Nwanze, K.F. and Youm, O., eds). ICRISAT Patancheru, A.P. 502 324, India.
- Matthews, M. 1987a.** Moths make inroads into Mali's crop of millet. *New Scientist* 114 (1565), 50.
- Matthews, M. 1987b.** The African species of Heliocheilus Grote (Lepidoptera: Noctuidae). *Syst. Entomol.* 12: 459-473.
- Nwanze K.F. and Sivakumar, M.V.K. 1990.** Insect pests of pearl millet in sahelian West Africa. II. Raghuva albipunctella de Joannis (Noctuidae, Lepidoptera): distribution, population dynamics and assessment of crop damage. *Trop. Pest Man.* 36 (1): 59-65.
- Nwanze, K.F. and Youm, O. 1995** (eds) Panicle insect pests of sorghum and pearl millet: proceedings of an international consultative workshop, 4-7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger. ICRISAT Patancheru, A.P. 502 324, India.

Phelan, P.L. 1997. Evolution of mate-signalling in moths - phylogenetic considerations and predictions from the asymmetric tracking hypothesis. pp.240-256 In: The evolution of mating systems in insects and arachnids (J.C. Choe and B.J. Crespi, eds). Cambridge University Press, Cambridge, UK.

Scoble, M.J. 1992. The Lepidoptera. Form, function and diversity. Oxford University Press, London.

Shelly, T.E. and Whittier, T.S. 1997. Lek behaviour of insects. pp.273-293 In: The evolution of mating systems in insects and arachnids (J.C. Choe and B.J. Crespi, eds). Cambridge University Press, Cambridge, UK.

Surlykke, A. and Gogala, M. 1986. Stridulation and hearing in the noctuid moth Thecophora fovea (Tr.). J. Comp. Physiol. A 159, 267-273.

Thornhill, R. and Alcock, J. 1983. The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, Mass., USA.

Trivers, R.L. 1974. Parental investment and sexual selection. pp.136-179 In: Sexual selection and the descent of man, 1871-1971 (B. Campbell, ed.) Aldine-Atherton, Chicago.

Vercambre, B. 1978. Raghuva spp. et Masalia sp., chenilles des chandelles du mil en zone sahelienne. Agronom. Trop. 33: 62-79.