Light, predation and the lekking behaviour of the ghost swift *Hepialus humuli* (L.) (Lepidoptera: Hepialidae)

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We examined the timing of the crepuscular lekking flight of male ghost swift moths in southern Sweden with respect to variations in: (i) the quality of the visual mating signal; and (ii) the behaviour of potential vertebrate predators (mainly bats). The moths' display flights started *ca.* 57 min after sunset, and occurred during 20–30 min at incident light intensities between 10.0 and 2.0 lux. Owing to the falling and more shortwave ambient light after sunset, the brightness contrast between the moth wings and the background (grass) increased steeply at the time of display onset. The silvery white male wing colour thereby seems to maximize conspicuousness, and may be a secondary adaptation that facilitates visibility at low light intensities. The display timing itself is probably determined by other factors, possibly predation. By displaying only for a short period at dusk, the moths seem to avoid most birds, which normally do not forage at these light levels, and gleaning bats, which typically do not start to feed until the light intensity has fallen even further. Nevertheless, aerial-hawking bats were often (54% of the evenings, $n=22$) seen at the leks, and one species (*Eptesicus nilssonii*) frequently fed on the displaying moths (22% of the moths observed, $n=83$). *H. humuli* represents an ancient clade among the Lepidoptera. By restricting its sexual behaviour to a short time window at dusk, when predation risk may be minimized (but still high), it may to some extent compensate for the lack of sophisticated predator defence systems such as aposematic or mimetic coloration, manoeuvrable flight, and ultrasonic hearing, which predominate among the more recent Lepidopteran clades. However, the time window solution restricts the moths' activities considerably and the lack of defence still carries a considerable cost in terms of predation.

Keywords: bats; echolocation; spectral contrast; vision

1. INTRODUCTION

Mating signals of crepuscular and nocturnal moths (Lepidoptera) are most often chemical (Svensson 1996), although there are also species in which the males announce their presence to females by acoustic (Surlykke & Gogala 1986; Spangler 1988; Bailey 1991) or visual (Mallet 1984) means. Several genera of crepuscular and nocturnal moths typically possess silvery white wings, which may make them conspicuous at low light levels. The colour may therefore be used for intraspecific communication, although it could perhaps also provide camouflage while at rest. There are many moths with silvery white wings among the Palaearctic Microlepidoptera. Examples include species belonging to the families Gracillariidae (e.g. *Phyllonorycter* spp., *Phyllocnistis* spp.), Coleophoridae (*Coleophora* spp.), Yponomeutidae (*Argyresthia* spp.), Elachistidae (*Elachista* spp.) and Pterophoridae (*Pterophorus pentadactylus* (L.)) (see, for example, Heath & Emmet 1985; Emmet 1996). In these examples, both sexes are generally of the same colour, suggesting that visual communication, if it exists, may not necessarily be sexual.

Silvery white wings are much less common among larger lepidopterans, perhaps because larger insects are generally more susceptible to visually guided, vertebrate predators. However, a well-known Palaearctic example of a large (wingspan 5–7 cm) moth with silvery white wings is the male ghost swift *Hepialus humuli* (L.) (Hepialidae). This species is interesting also because of the striking sexual dichromatism (the females are yellow–brown), suggesting visual epigamic signalling, and unlike the small moths listed in the previous paragraph, the behaviour of this species has been studied in some detail. The males are only active for a short period at dusk, when they aggregate on leks and perform a spectacular flight display, attracting females to the mating site, using both chemical and visual signals (Mallet 1984; Turner 1988).

Conspicuous signals intended for conspecifics often have the obvious drawback of also attracting predators, leading to opposing selection pressures on signal expression and signalling behaviour (Lloyd 1975; Tuttle & Ryan 1981; Burk 1982; Gerhardt 1983; Sakaluk 1990). In the case of the ghost swift, predators may be expected to include both birds and bats. At least some gleaning bats search for prey by vision (see, for example, Bell 1985).

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We hypothesized that the epigamic coloration (silvery white wings) and the brief display time in ghost moths (Mallet 1984) represent a compromise between intra-specific sexual selection, which is likely to be strong in lek species (Andersson 1994), and constraints from predation. First, we investigated the temporal variation of the visual signal conditions, using spectroradiometry to measure the changes in ambient light and background radiance during the course of an evening. As the daylight fades at sunset and dusk, its spectral composition changes continuously (Lythgoe 1979; Endler 1993); the ghost moth colour might thus have evolved because it maximizes brightness contrast under the light conditions prevailing at the time of display. Second, we studied the occurrence, behaviour and timing of potential predators (birds and bats) at the leks. Adaptations against predation are particularly interesting in the Hepialidae, because this family represents a basal branch, the Exoporia, of the Lepidoptera (Scoble 1992). The Hepialidae have homoneurous wings and jugum rather than frenulum–retinaculum and therefore beat the fore- and hindwings independently, thus essentially lacking the adaptations that permit high manoeuvrability of most other moths (Mallet 1984). The Hepialidae also lack the predation defence systems which predominate among more recent lepidopteran clades, such as aposematic or mimetic coloration (against birds; Rothschild 1985) and ultrasonic hearing organs (against bats; Fullard 1987). They may therefore be expected to deal with predators either by avoiding them temporally (Yack 1988; Morrill & Fullard 1992) or perhaps by other means (Lewis *et al.* 1993).

2. MATERIALS AND METHODS

(a) *Moth observations*

The moths were observed between 18 June and 6 July 1995 in two areas of southern Sweden; near Ulricehamn in the province of Västergötland (57°N), and near Lund in the province of Skåne (55°N). Before this, observations had also been made in Västergötland 23–24 June 1982 and 20–24 June 1986 (by J.R.). The display sites were found by searching likely areas on foot or from a car. Each display site thus found ($n=11$ in 1995 and $n=1$ in 1982–1986) was then revisited one or several times during the following week (the moths normally displayed at exactly the same spot night after night; see next paragraph). Each site was thus observed during a maximum of five evenings, and in all but the first visit at each site, the observations started before arrival of the first males.

Throughout the observations in 1995, the incident light intensity was measured (directly in lux) every five minutes with a Gossen Mastersix digital light meter (with the diffuser on), directed towards the open sky. The number of displaying male moths at each site was recorded visually every minute during the first five minutes following the appearance of the first moth, then every five minutes, and again every minute as the number started to decline again. Any female appearing at the site as well as pairs in copula were also recorded. At each site, we also noted the type of vegetation (prominent species) and its height.

(b) *Signal quality measurements*

The ambient light conditions, background radiance and reflectance of the moth wings were measured with a PS1000 UV–VIS diode-array spectrometer (Ocean Optics Inc.,

Dunedin, Florida). Reflectance was recorded with a trifurcated fibre-optic probe, containing a measuring fibre surrounded by six illumination fibres, one of which was connected to an LS-1 tungsten-halogen lamp, and the other five to a deuterium lamp (Andersson 1996). These combined light sources provided light across the spectral measuring range 300–700 nm. Unidirectional illumination and measuring at 45° was acquired from a 3 mm wide spot, and reflectance was calculated in relation to a Spectralon (Labsphere Inc.) white standard. Using the average of five scans from the wing of a male *H. humuli*, the signal spectrum at time t , $p_{w,t}(\lambda)$, was calculated as the product of spectral irradiance at that time, $Q_t(\lambda)$ and the wing reflectance spectrum, $R_w(\lambda)$. As the distance between signaller and receiver is short (< 100 cm) and the air was clear, spectral attenuation was ignored (Endler 1990).

Irradiance, $Q(\lambda)$, and background (grass) radiance, $q_g(\lambda)$, was measured at a typical display site (a treeless pasture with grasses, knotgrass and nettles) near Göteborg, southern Sweden (Stora Askerön; 58°05'N, 11°45'E) on the evening of 6 July 1996. This day was clear (less than 5% cloud coverage) and still, and was therefore suitable for standardized measurements throughout the evening. From a point *ca.* 0.5 m above the vegetation the spectral radiance was measured by pointing a 400 μ m fibre end at 45° angle at the background and perpendicularly to the setting sun. The 28° solid acceptance angle of the fibre thus projected to an elliptic, approximately 0.4 m by 1.5 m measuring area of the vegetation. Irradiance, $Q(\lambda)$, was measured with a 400 μ m fibre, fitted with a flat (180° solid acceptance angle) 'cosine-correction' diffuser head (adjusting for the decline in intensity which is related to the increasing angle of incidence on a flat surface; see Endler 1993) assuming background and signal wing surfaces to be parallel with respect to irradiance.

With spectral conversion files (from calibration against a light source with known spectral output), radiance and irradiance measurements (recorded in Watts) were transformed in 1 nm steps to units appropriate for vision, i.e. quantal flux (irradiance, $Q(\lambda)$, in $\text{mmol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$; radiance, $q(\lambda)$, in $\text{mmol m}^{-2} \text{s}^{-1} \text{sr}^{-1} \text{nm}^{-1}$; Endler 1990).

A background radiance measure at 20.00 (in good light and temporally close to the irradiance scan at 20.01) was used to estimate background reflectance, $R_g(\lambda) = q_g(\lambda)/Q(\lambda)$. As for the moth wing, background signal spectra for each time, $p_{g,t}(\lambda)$ was then calculated as $R_g(\lambda) \times Q_t(\lambda)$. We considered only brightness contrast, not colour. To obtain a value of total signal brightness, p_T , wing and background spectra were integrated over the measuring range 300–700 nm for each time point. Finally, brightness contrasts between the moth and the background were calculated as p_{wT}/p_{gT} for each of the measuring times during the evening.

(c) *Observations of predation*

We looked for bats and listened for their echolocation calls through either a Pettersson D-960 or a QMC S-100 ultrasonic detector which was operated continuously throughout the observation periods. While observing, we stood 1–5 m from the edge of the display site. We noted the species of bat (those dealt with here could easily be identified in flight from their echolocation calls, flight style and size; Ahlén 1981) and its behaviour including its approximate flight height (to the nearest 1 m) while searching for prey. Attacks on moths were categorized as either successful or unsuccessful (from the bats' point of view). In 1995 we also recorded the approximate flight height of the moths in relation to the vegetation and the ground (to the nearest 0.1 m),

Table 1. *Observations of displaying male ghost swifts* *Hepialus humuli* *and their main predators, northern bats* *Eptesicus nilssonii* *at leks in (a) Västergötland (57° N) and (b) Skåne (55° N), southern Sweden, 1982 and 1995*

site	day	max number of male moths at the lek	northern bats observed	max. number of bats exploiting the lek	number of moths attacked	caught
<i>(a)</i>						
1	23/6/82	16	yes	3	—	11
	24/6/82	24	yes	3	16	6
2	19/6/95	6	yes	2	0	0
	20/6/95	6	yes	1	0	0
3	21/6/95	1	yes	0	0	0
4	23/6/95	2	yes	1	0	0
5	24/6/95	3	yes	1	2	1
	26/6/95	2	yes	1	1	1
6	25/6/95	2	yes	0	0	0
7	28/6/95	1	yes	0	0	0
<i>(b)</i>						
8	18/6/95	4	no	0	0	0
	22/6/95	3	yes	1	1	0
9	19/6/95	2	no	0	0	0
	27/6/95	1	no	0	0	0
	4/7/95	0	no	0	0	0
10	20/6/95	3	yes	1	1	0
	25/6/95	3	yes	1	0	0
	28/6/95	0	yes	0	0	0
	3/7/95	1	yes	0	0	0
	6/7/95	2	yes	1	1	0
11	29/6/95	1	yes	1	0	0
12	1/7/95	3	yes	0	0	0

and also whether moths being attacked by bats seemed to perform any defensive reaction.

3. RESULTS

(a) *Location and size of leks*

The lek observed in 1982 contained 16 and 24 males on the two evenings of observation, respectively. However, such large leks were not found in 1995, despite intensive searching. Instead, the 11 sites that we found contained only one to six males each (mean=2.7, s.d.=1.5, $n=11$ sites; no significant difference between the two areas; table 1). The much lower numbers in 1995 could have been owing to the unusually cold and rainy weather in early summer that year. We also searched intensively for leks in summer 1996, but found only a few single males (not included in the analysis), again possibly an effect of bad weather in early summer. In total, we made observations of 40 moth-evenings in 1982 (1 site) and 46 in 1995 (11 sites).

All the sites were situated at least 10 m away from trees, but in one case next to the wall of a large building (a

barn). The vegetation at the display sites varied from short (a few centimetres) knotgrass *Polygonum aviculare* L., or grazed or even mowed grassland to relatively high (up to 1 m) herbaceous vegetation at roadsides, including stands of meadowsweet *Filipendula ulmaria* (L.), nettles *Urtica dioica* L. and ground-elder *Aegopodium podagraria* L. Despite this variation, the vegetation at the display sites were in all cases uniformly green and never included any white or otherwise prominent flowers (which perhaps could be confusing for mate-searching females). Such stands sometimes occurred in abundance adjacent to the sites, however. The lek sites were very predictable from day to day, as, on the seven display sites that were revisited, displaying males were normally still present at the same spot in similar numbers (table 1).

(b) *Timing of display flights*

In Västergötland (57° N), the first male appeared at the display site on average at 23.04 (Central European summer time), or 57 min after sunset (s.d.=8 min, $n=7$), at an incident light level of 9.9 lux (s.d.=2.1 lux, $n=5$), and the last one disappeared on average 27 min later

Figure 1. The spectral change in the light during the course of an evening (6 July 1996), together with the reflectance of the background consisting of grass (dots) and the male *H. humuli* wings (squares).

(s.d.=9 min, $n=7$) at an incident light level of 2.0 lux (s.d.=1.0 lux, $n=7$). In Skåne (55°N), the first male appeared a little earlier at 22.46, or 48 min after sunset (s.d.=8 min, $n=7$), and the last one disappeared 25 min later (s.d.=5 min, $n=5$).

The timing of the display flights was closely correlated among the different individual males on a given lek. The time between the appearance of the first and the last individual was always less than five minutes, usually between one and three minutes. For example, on the largest lek observed (24 June 1982), 20 males appeared during one minute and all the 24 males were on the wings two minutes later. The disappearance of males from the leks appeared to be just as abrupt as the onset, although some of the males had already stopped flying earlier because they were courted by females or caught by bats.

(c) Display behaviour

The males typically displayed in a peculiar, nearly stationary, hovering flight immediately above the vegetation, now and then making brief vertical movements as they shifted display position (see Mallet (1984) for a more detailed description). While displaying, they sometimes moved slowly horizontally, but typically stayed within an area of ca. 10 m × 10 m, only very occasionally shifting position by much faster flights. The estimated mean flight height of displaying males varied from 0.1 m to more than 1 m above the ground. However, the height relative to the vegetation was much less variable. At every site ($n=11$), they spent most of the time within 0.5 m above the plants (mean=0.2 m, s.d.=0.14, $n=35$) but occasionally as high as 1–1.5 m. We observed eight flying females at the lek in 1982 and a total of nine in 1995. In 1995 we also found four mating pairs.

(d) Signal quality

Figure 1 shows the reflectance of the moth wings and grass background together with seven of the 11 measured

irradiance spectra (peaks normalized to 100%) during the course of the cloudless evening of 6 July 1996. At the scans –162 min and –72 min, the measuring location was directly illuminated by the setting sun, which then ‘sank’ behind treetops 100 m to the west, leaving the site in shadow. The figure illustrates how the medium wavelengths (green–yellow) first were depleted from the spectrum, creating a purple light (blue and red) during a period just after sunset (see also Endler 1993). Thereafter, the long wavelengths, and later also the medium wavelengths, disappeared completely, narrowing the (measurable) light spectra to a peak around 450 nm. After +78 min (23.30), the light was too dim to be recorded with our instruments.

From about the time when the display flights started, the irradiance spectrum was gradually deprived of the wavelengths corresponding to the 550 nm peak of the grass reflectance (figure 1). As this disproportionately decreased the background radiance compared with that of the moth wings, which reflected uniformly, brightness contrast of the moth started to increase at this time. Figure 2 shows the change in computed brightness contrast along with the decrease in the absolute radiance of the moth wings. The contrast remained nearly constant until it started to increase slowly at +33 min, and then more abruptly from +57 min, which corresponds to the onset of the display flight. On average, the contrast was nearly twice as high during the moths’ display window as compared with earlier in the evening.

(e) Predator–prey interactions

On 23 June 1982, a group of seven common gulls *Larus canus* L. were observed to exploit an *H. humuli* lek containing about 12 males. In this case the attack was observed at a distance of ca. 50 m, so the number of moths involved could not be estimated accurately. The birds hovered among the moths for 15 min (23.10–23.25), and caught at least some, perhaps all, of them in flight. No

Figure 2. The time window of the *H. humuli* flight display in relation to the brightness contrast of the moth wings against grass (open squares), and moth wing quantal radiance (filled circles), during the course of an evening (6 July 1996).

moths were visible at the lek immediately after the birds had left. With this exception, we did not observe any birds at *H. humuli* leks during this study (but gulls feeding on *H. humuli* leks have also been observed by others; R. Å. Norberg, personal communication). Apart from bats (see next paragraph) the only other predator observed at a lek was a house cat, which caught and immobilized one male.

While observing moth leks, we detected three species of aerial-hawking bats: common pipistrelles *Pipistrellus pipistrellus* at two sites, noctules *Nyctalus noctula* at three sites and northern bats *Eptesicus nilssonii* at all sites. The latter species was the only one that we observed attacking the moths. Northern bats were observed at, or close to, the leks on 82% of the evenings ($n=22$; table 1). During 12 evenings (54%), the bats were observed patrolling over the leks for extended periods, flying in circles or back and forth at a height of 3–5 m—above the ground (a habit otherwise untypical of this species; Rydell 1989). On evenings when no northern bats were observed at the leks, there were usually very few (none to four) moths present (table 1). The number of bats patrolling the large lek (1982) was either three (23 June) or two to three (24 June), and the total number of bat minutes observed at this lek amounts to 225. At the smaller leks (1995), bats were not present continuously but came and went, so the time bats were present was more difficult to estimate. Gleaning bats, such as *Myotis* and *Plecotus* spp. were not observed at any of the leks.

We observed 23 successful captures of displaying *H. humuli* males by northern bats, and in addition 22 cases when the bat attacked but missed the moth (table 1, and four additional observations from 1986). When attacking a

displaying moth, a northern bat typically made a rapid vertical dive towards it and in every case it also increased its echolocation pulse repetition rate, i.e. to a 'feeding buzz'. Successful attacks were on moths flying relatively high above the vegetation (7 m and 2.5 m in 1995), while missed ones were on moths flying lower (0.2–0.5 m, $n=4$, in 1995; flight height was not quantified in 1982 and 1986). Hence, successful attacks appeared to be associated with the moths changing their position and not with their 'normal' display flight. The observations of bat–moth interactions were distributed among four different sites but, naturally, most (59%) were made at the large lek in 1982 (table 1). We never observed any defensive reaction from the moths in response to attacks by bats.

4. DISCUSSION

The timing, location and design of visual signals in relation to signal conditions (ambient light, background, and so on) is a research programme that was clearly outlined 30 years ago (Hailman 1977), and recently re-emphasized (Endler 1991). However, perhaps owing to a preoccupation in past decades with information content (benefits of female choice, honesty of threat signals and so on) rather than transmission optimization, much of the tremendous variation in animal signals and signalling behaviour remains unexplored (but see Endler 1991; Endler & Thery 1996). Here we have described, albeit not tested, some potential selection pressures behind the epigamic white coloration and very precise timing of the lek-displaying ghost swift. That visual signals in dim light should maximize brightness contrast through strong total reflectance, is certainly not a novel observation (Hailman

1977), and it seems an intuitive explanation for the white coloration of the male ghost swift, most likely driven by sexual selection (Mallet 1984; Turner 1988). It is, however, probably less generally appreciated that there are colour changes in the ambient light after sunset (see also Endler 1993), which might affect achromatic brightness in different signal and background colours. In this case, as the green wavelengths of the grass background began to disappear about an hour after sunset, the contrast of the uniformly reflectant moth wings started to increase. This coincided well with the onset of the display, and could in principle be the main selective pressure on display timing.

However, the fact that cryptically coloured hepialids sympatric with *H. humuli*, e.g. *H. hecta* (L.), *H. lupulinus* (L.) and *H. sylvina* (L.), also are crepuscular (Robson 1887; Hanson 1938; Mallet 1984; J. Rydell, unpublished data), suggests that the evolution of crepuscular activity patterns in hepialids in general preceeded the evolution of white wings in *H. humuli*. Therefore, the timing of the display flight in *H. humuli* is probably determined ultimately by factors other than the variation in signal quality. It may be that the onset and end of the display flight was triggered proximally at least by the rapid change in the light intensity after sunset (Dreisig 1980). It could also be that restrictions on the flight timing are imposed on the males by the behaviour of the female, i.e. display and mating must precede egg laying, or by an absolute threshold for visual orientation. These explanations are somewhat undermined, however, because the females normally continue flying for at least half an hour after the end of the display flight, while engaged in egg dispersion from the air (Mallet 1984). Another possible constraining factor is predation.

The combination of white wings, large size and lack of fast movements by the displaying males would seem to provide any visually oriented predator with very easy and highly profitable targets. Nevertheless, we rarely observed visually oriented predators at the leks, only one house cat and a group of gulls. Gleaning bats were not observed at all, although one such species, the brown long-eared bat *Plecotus auritus* (L.), is very common throughout southern Sweden, including the study areas (Rydell 1989). Although gleaning bats may not be detected by using a bat detector at distances of more than a few metres (Ahlén 1981), the light was always bright enough so that other bats which were present could be observed easily. It is therefore unlikely that gleaning bats were present at the leks but missed by us.

The scarcity of birds and gleaning bats at the leks could perhaps indicate that the moths managed to avoid these predators by temporal means (Morrill & Fullard 1992), by using a short but relatively predation-free window, when the light intensity is too low for efficient foraging by most insectivorous birds (Kacelnik 1979), but still too high for activity of at least some bats (Speakman 1991; Jones & Rydell 1994). In that case, the confinement of the display flight to a very brief period at dusk may be an evolutionary response to diurnal birds on one hand and a category of bats on the other. The available data are, however, insufficient to test this hypothesis conclusively. Nevertheless, gleaning bats such as *P. auritus*, which probably forage at least in part by visual means (Bell

1985; Anderson & Racey 1991), do not emerge and start to feed until the incident light intensity has fallen below 1.0–2.0 lux (Rydell *et al.* 1996), which corresponds well to the light intensity at which the male *H. humuli* flights ceased (2.0 lux).

One species of aerial-hawking bat, *E. nilssonii*, regularly exploited the leks and caught many displaying males. In contrast to gleaning bats, this species forages mainly by echolocation, an assumption that was substantiated in the present case by the consistent use of 'feeding buzzes' during attacks on moths. Aerial-hawking bats typically emerge from their roosts and start to feed half an hour or more before gleaning species (Jones & Rydell 1994), and the moths may therefore not have been able to avoid them temporally without simultaneously increasing the exposure to diurnal birds.

H. humuli represents an ancient evolutionary line among the Lepidoptera, which has survived encounters with later-evolving birds and bats at least since the Eocene or for more than 50 million years (Habersetzer *et al.* 1992). *H. humuli* males cram their sexual behaviour into a short time window at twilight, a behaviour which helps to compensate for the lack of hearing and the disorganized flight in comparison with most other main groups of crepuscular and nocturnal moths. However, the time window solution of *H. humuli*, and probably other hepialids, restricts the moths' activities considerably in space and time, and the lack of more sophisticated defence systems still carries a considerable cost in terms of predation, both by late-hunting visual predators and by early emerging echolocating ones.

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