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Notes on pupal behaviour, eclosion, mate attraction, copulation and predation of the New Zealand glowworm *Arachnocampa luminosa* (Skuse) (Diptera: Keroplatidae), at Waitomo

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The behaviour of pupae and adults of the New Zealand glowworm *Arachnocampa luminosa* was observed in Reserve Cave and in the cave entrance at Waitomo, New Zealand, from remote video recordings made with infra-red light. One female pupa observed in the cave was videotaped for 111 h before the adult emerged and copulated with a male. This female took 13 h 23 min to eclose, during which she glowed intermittently on 17 occasions. The male alighted upon the emerging female 13 h and 8 min after eclosion commenced and 3 min 33 s after she last glowed. Copulation commenced 12 h 55 min later and continued for 12 h 36 min. Two minutes after the pair separated, both adults were caught and eaten by a predatory harvestman (*Megalopsalis tumida*). Most of the eclosion was recorded for a second female pupa observed, on a rock face in the bush-clad entrance to Reserve Cave after 97 h of videotaping. Prior to eclosion this pupa made flicking movements when small crawling invertebrates contacted it during the daytime; this is the first time this behaviour has been described for *A. luminosa*. A male pupa in the cave was videotaped for 94 h until the adult emerged. It glowed dimly for 45 min during eclosion and the adult flew off 42 h 39 min after eclosion commenced.

Keywords: bioluminescence, cave ecology, remote recording, sex pheromone, Opiliones

Introduction

The glowworm *Arachnocampa luminosa* (Skuse) inhabits caves and places in bush that are sheltered from wind and where humidity is high. The carnivorous larva occupies a mucous web suspended by threads from the substrate. Numerous fishing lines with sticky droplets hang from the web and form a snare for insects attracted to the light produced from the swollen distal tips of Malpighian tubules in the abdomen (Wheeler & Williams 1915; Green 1979). The bioluminescence has a maximum wavelength of 487 nm (Shimomura et al. 1966) which attracts mostly Diptera (Broadley & Stringer 2001). Prey caught in the fishing lines are hauled up by the larva and eaten (Edwards 1933; Gatenby & Cotton 1960; Richards 1960, 1964; Stringer 1967; Broadley & Stringer 2009). Much information has been published regarding the larva but less is known about the pupae and adults (see reviews by Kermode 1974; Meyer-Rochow 1990, 2007).

Pupae and adults also produce bioluminescence but the function of the light is not known. One suggestion is that the light of the female pupa and adult is used to attract male flies for mating (Hudson 1928,1950; Richards 1960,1964; Kermode 1974; Meyer-Rochow & Waldvogel 1979; Meyer-Rochow & Eguchi 1984; Meyer-Rochow & Liddle 1988; Meyer-Rochow 1990). Evidence to support this suggestion is based upon electrophysiological recordings of spectral responses from the eyes of male adults (Meyer-Rochow & Eguchi 1984). However, there is also evidence that pheromones may be involved because the antennae of male flies possess more and structurally different hair receptors than those of females (Stringer, personal communication; Meyer-Rochow & Waldvogel 1979).

Previous observations of pupae and adults were carried out both with captive specimens (Hudson 1890, 1926, 1950; Gatenby & Cotton

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1960; Richards 1960) and those in the field (Norris 1894; Hudson 1950; Gatenby 1959; Gatenby & Cotton 1960; Richards 1960; Meyer-Rochow & Waldvogel 1979), by means of artificial light sources visible to humans. However, anecdotal reports that these light sources affect the behaviour of *A. luminosa* (Hudson 1950; Gatenby 1959; Gatenby & Cotton 1960; Richards 1960; Gatenby 1960b; Stringer 1967; Meyer-Rochow 1990) call into question the reliability of these behavioural observations. Experiments conducted by Meyer-Rochow and Eguchi (1984) demonstrated that the eyes of adult male *A. luminosa* are maximally sensitive to light of 540 nm (green), with further response peaks at 460 nm (bluegreen) and in the near ultraviolet. Furthermore, Meyer-Rochow and Waldvogel (1979) reported that both larval and adult cave *A. luminosa* exhibit behavioural reactions to these light wavelengths. However, light of a wavelength longer than 660 nm does not elicit measurable responses (Meyer-Rochow & Eguchi 1984).

Here I present observations from remote recordings of *A. luminosa* pupae and adults in both a cave and its entrance at Waitomo, New Zealand, made with the use of infra-red light-sources apparently not visible to *A. luminosa*, and a TV camera sensitive to this light.

The antennae of male and female *A. luminosa* adults were also examined and scanning electron microscope (SEM) images of the antennae are presented here for the first time.

Methods

Remote recording was done in the Waitomo area (38°16'S, 175°05'E) in the bush-clad cave entrance to Reserve Cave and in the cave itself (Figure 1). This cave was chosen because it is seldom visited and it has a relatively large population of *A. luminosa* larvae both at the entrance and at the far end of the cave (c. 500 m in from the entrance) where there is a small stream.

Observations were made with an infra-red light-source (c. 900 nm light-emitting diodes) and a TV camera (Panasonic WV-BP504E) sensitive to this light. The camera in its waterproof housing was positioned so that the lens was as close to the *A. luminosa* individuals as possible (c. 5-10 cm), without touching them. The video recorder (Panasonic AG6040E) was set to record 24 or 48 h on a 3-h tape. Once set up, the equipment was visited to exchange batteries every 24 h and to replace cassettes.

Video cassettes were analysed with slow motion and frame-by-frame playback. Data recorded with observations were the date, time and duration of each behaviour to the nearest minute or second.

Conventional and SEM images of adults of both sexes of *A. luminosa* were captured and are included for comparison. A female was collected on 12 April 2011 from the Demonstration Chamber platform in Glowworm Cave, Waitomo, and a male was collected from beside the suspended walkway above Tomo Rapids in Ruakuri Cave, Waitomo, on 19 April 2011. The specimens were preserved in 70% ethanol, critical point dried, photographed and prepared for field-emission scanning electron microscopy. This involved sputter-coating the specimens with platinum and carbon and mounting each on a specimen stub holder with carbon paint, and then making observations with a JEOL JSM-6340F field emission scanning electron microscope (FESEM), operating at 5 kV.

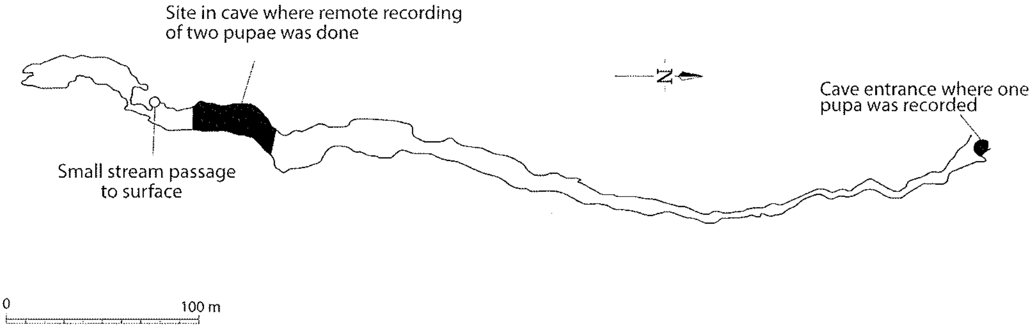

Figure 1. Map of Reserve Cave, Waitomo, where remote recording of *Arachnocampa luminosa* pupae and adults was done.

Results

Remote recording

One male and two female *A. luminosa* pupae were observed. Behavioural observations are described below and the time taken by each pupa to reach the stages of eclosion is presented in Table 1.

Notes made from incomplete observations of 2 pupae

On 21 June 1995 at 15:00 videotaping of a male pupa (c. 11 mm long) began in Reserve Cave. It appeared inactive until 09:35 on 26 June, when the posterior tip of the pupa began to move slowly. This movement was probably not noticeable to the naked eye. At 11:30 the pupa began to move from a vertical to a horizontal position while still hanging from its suspensory thread. The wings emerged 11 minutes later when the adult was horizontal. At 11:50 it was head-down. Legs began to emerge from the pupal exuvium at 12:40, and at 12:55 the abdomen appeared to glow through the pupal exuvium. This glowing was faint and continued for 45 min. By 14:00 both the head and the distal tip of the exuvium with the abdomen within were almost touching, so that the emerging adult and exuvium formed an inverted U. When videotaping recommenced following a loss of power to the equipment between 16:30 on 26 June and 14:40 on 27 June, the adult had emerged fully and was clinging to the empty pupal exuvium. It remained there until 06:19 on 28 June, when it flew away.

Table 1. A comparison of the times taken by *Arachnocampa luminosa* individuals to reach stages of eclosion (hh:mm), commencing when each pupa began rotating from the vertical resting position (00:00); and timing of behaviour of the mating pair.

Stage or behaviour	Male - cave	Female - bush	Female - cave
Rotated to horizontal position	00:11	00:57	00:14
Wings visible	00:11	01:10	00:28
Head-down position	00:20	01:11	00:39
Legs visible	01:10	01:11	01:23
Inverted U shape	02:30	03:14	01:44
Male lands on female			13:08
Female emerges fully			13:23
Copulation commences			26:03
Copulation ceases			38:39
Pair separate			39:21

Videotaping of a female pupa c. 14 mm long (Figure 2a) began in the bush-clad entrance to Reserve Cave at 16:40 on 29 June 1995. The pupa glowed brightly for about 1 min at 21:41 when a spider moving over the substrate at night contacted the suspensory thread with one of its legs. It glowed again 3 min later and once more 7 min after that, glowing dimly for about 10 s each time. There was loss of power to the camera on 1 July from 16:22 onward, and recording recommenced at 16:16 on 3 July.

On two occasions during the daytime unidentified crawling invertebrates c. 1 mm in length were observed moving over the substrate, and contacting the suspensory thread and the pupa itself. The first invertebrate made contact several times from 16:25 onward on 3 July, 45 min before sunset. On three separate occasions during these contacts the pupa rapidly moved the distal part of its body in a flicking movement (Figure 2b). The pupa flicked once on two occasions and twice in succession on one occasion, each flick taking ca. 1 s to complete. The arthropod moved away 4 min later. At 08:25 on 4 July, 45 min after sunrise, another invertebrate contacted the suspensory thread several times over the following 45 min. The pupa made flicking movements with its abdomen on 17 occasions; then the invertebrate moved away. On each occasion the pupa made up to five successive flicks, each flick taking ca. 1-2 s to complete. The pupa did not glow during either of these daytime observations.

At night a cave weta (Rhaphidophoridae) contacted the pupa with one of its legs as it moved over the substrate at 18:19 on 3 July. The pupa glowed brightly for 4 min without moving and the

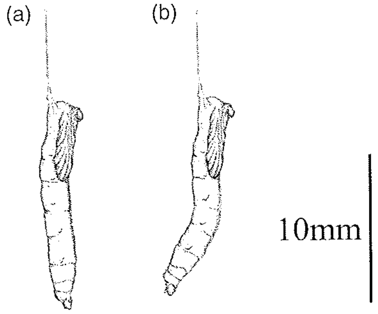

Figure 2. Illustrations depicting the female *Arachnocampa luminosa* pupa that was observed in bush. a) Pupa in resting posture, b) pupa flicking when disturbed during the day time.

weta moved away out of camera range 1 min 10 s after glowing commenced. The distal tip of the pupa began to twitch at about 18:20 on 5 July and the pupa glowed faintly for about 40 s starting at 01:31 on 6 July. It glowed faintly again at 01:56 for 1 min, and more brightly from 03:23 until 03:26. At 12:24 the pupa began to move from the vertical on its suspensory thread until it was horizontal at 13:21. The wings emerged at 13:34 and the legs emerged 1 min later. At this stage the emerging adult was vertical with its head facing downwards. At 15:10 the distal part of the exuvium, still with the abdomen in it, began to bend down towards the head of the adult, until it was adjacent to the head at 15:38. Power to the recording equipment was lost from 15:39 onwards, so the remainder of the eclosion was not videotaped.

Eclosion of a female pupa, mate attraction and copulation

Videotaping of a female pupa c. 14 mm long in Reserve Cave commenced on 23 March 1995 (Figure 3a). At 18:34 on 24 March a cave weta contacted the pupa with its antennae and then moved out of camera range. The pupa glowed brightly when first contacted and continued glowing for 3 min. The distal tip of the pupa began to twitch slightly and slowly move from about 07:00 onward on 29 March, but it did not glow. By 13:00 its abdomen began to move more noticeably. The pupa started its rotation from the vertical head-up position at 14:27 and was approximately horizontal by 14:41 (Figure 3b). The adult wings were visible at 14:55. Eleven minutes later the emerging female was head-down and vertical with the distal tip of the abdomen inside the pupal exuvium bent over at an angle of about 45° (Figure 3c). The insect glowed faintly for 3 min at 15:13. By 15:50 the legs were clearly visible, and 5 min later the distal empty part of the exuvium began to move down towards the head so that at 16:11 the emerging adult and pupal exuvium formed an inverted U shape (Figure 3d). The adult glowed intermittently and faintly on 16 occasions between 16:01 and 03:31 on 30 March, for periods of a few seconds to 6 min, and glowed for a longer time when cave weta made contact three times with their antennae and once when what appeared to be a harvestman's (*Megalopsalis tumida* Forster) leg brushed against it.

Three minutes and 33 s after the emerging female last glowed, at 03:35, a male *A. luminosa* adult alighted upon the pupal exuvium (Figure 3e). Five minutes later the male commenced glowing for 20 min. The female and exuvium remained in the inverted U-shaped position until 03:50 on 30 March, after which the adult emerged fully and orientated herself so that the pair were vertical, clinging head-up to the empty pupal exuvium and facing each other with their wings extended (Figure 3f). The pair changed positions several times before climbing up the suspensory cord to the cave roof where copulation subsequently appeared to start at 16:30 on 30 March (Figure 3g). From then on both insects glowed intermittently, although the female usually glowed longer and brighter than the male. The couple ceased copulation at 05:06 on 31 March after a copulation period of 12 h 36 min, but remained next to each other. The male then stopped glowing, but the female glowed intermittently on 14 occasions for 10 s each time. At 05:48 the pair separated and the female alighted upon the cave wall and glowed faintly for 10 s. The male dropped down a short distance and remained clinging to the empty pupal exuvium (Figure 3h).

Predation of *A. luminosa* adults

After the pair separated from each other, 133 s later a fast-moving predatory harvestman (*M. tumida*) snatched the female, and then 10 s later the pupal exuvium with the still-clinging male, in its chelicerae and moved away along the cave wall. However, when the harvestman moved off with its prey the pupal exuvium pulled free and swung like a pendulum from its suspensory cord. One of the harvestman's legs appeared to brush against the suspensory cord, which caused the harvestman to snatch the exuvium again in its chelicerae, but the exuvium was then discarded in favour of the two adults already held in its chelicerae, and it then proceeded to consume them (see frontispiece) The harvestman appeared to finish eating the adults 40 min later because its chelicerae no longer moved. The harvestman subsequently appeared to attempt to pull the empty pupal exuvium from its attachment to the cave wall but I could not determine if this was successfully accomplished.

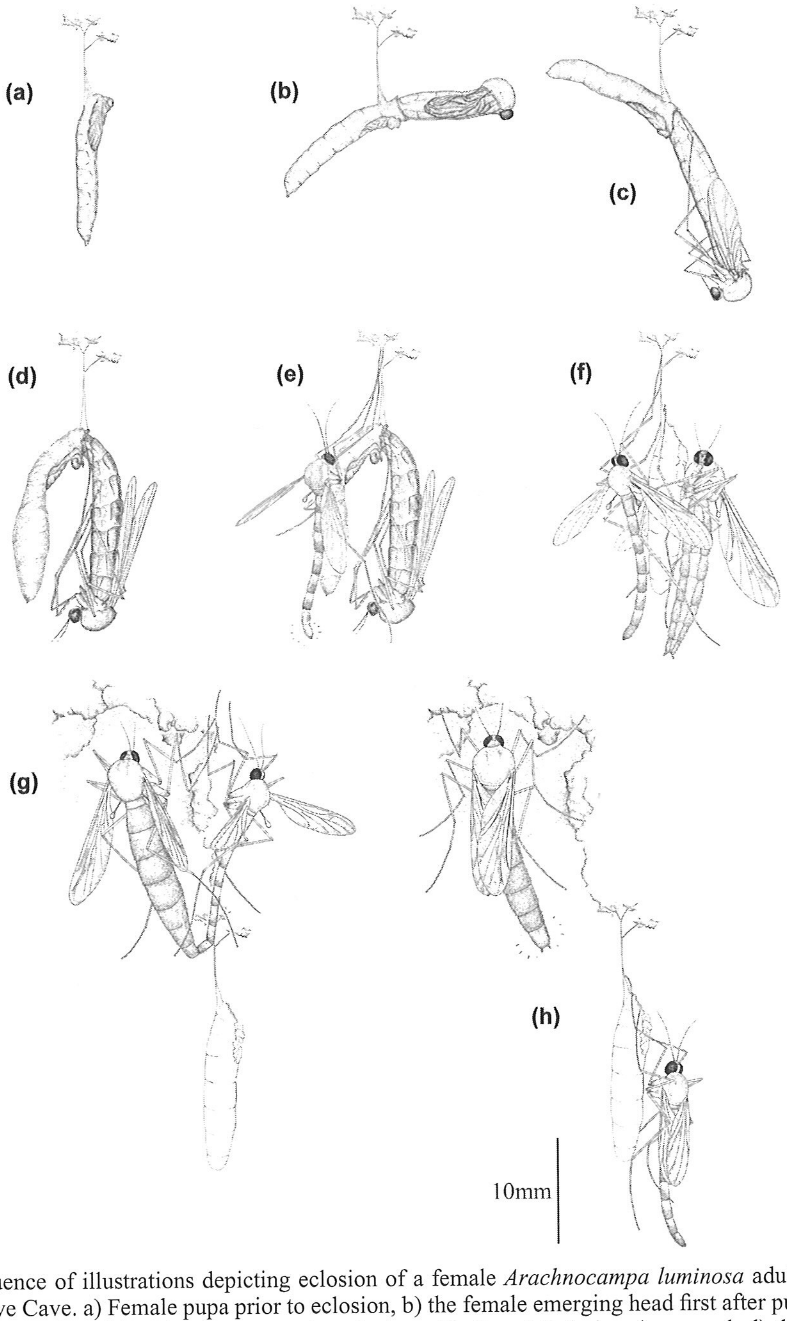

Figure 3. Sequence of illustrations depicting eclosion of a female *Arachnocampa luminosa* adult and subsequent mating in Reserve Cave. a) Female pupa prior to eclosion, b) the female emerging head first after pupal rotation from a vertical to horizontal position c) a later stage in eclosion with the adult facing downward, d) the pupal exuvium and emerging adult in the inverted U-shaped position with only the tip of the female abdomen remaining within the pupal exuvium, e) a glowing male *A. luminosa* adult after alighting on the eclosing female, f) the fully emerged female and the male, both insects with wings extended, clinging to opposite sides of the empty pupal exuvium, g) the mating pair after moving up to the cave roof, h) the female after flying to the cave wall and glowing briefly, with the male that has moved down onto the pupal exuvium. (Figures drawn from infra-red video footage, with some fine details added from the following sources: a) and g) sources include photographs by S.A. Rumsey (Plate 30, Figure 2 and Plate 33, Figure 2, respectively) in Richards (1960); c) and d) sources include Plate 11, Figures 15 and 16 in Gatenby & Cotton (1960). Sources used with permission from the Royal Society of New Zealand under Creative Commons Attribution - Non-Commercial 3.0 New Zealand Licence. Retrieved 18 February 2011 from http://creativecommons.org/licenses/by-nc/3.0/nz/deed.en)

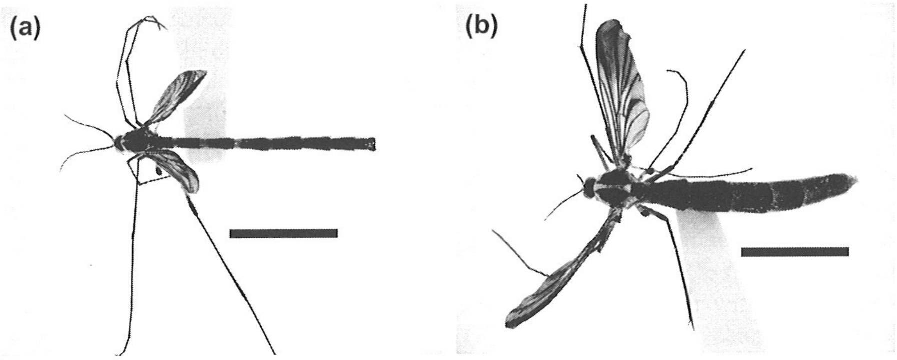

Figure 4. Dorsal view of *A. luminosa* adults. a) Male, b) female. Note one antenna on the female is broken off near the base. Images courtesy of Museum Victoria. Scale bars = 5 mm.

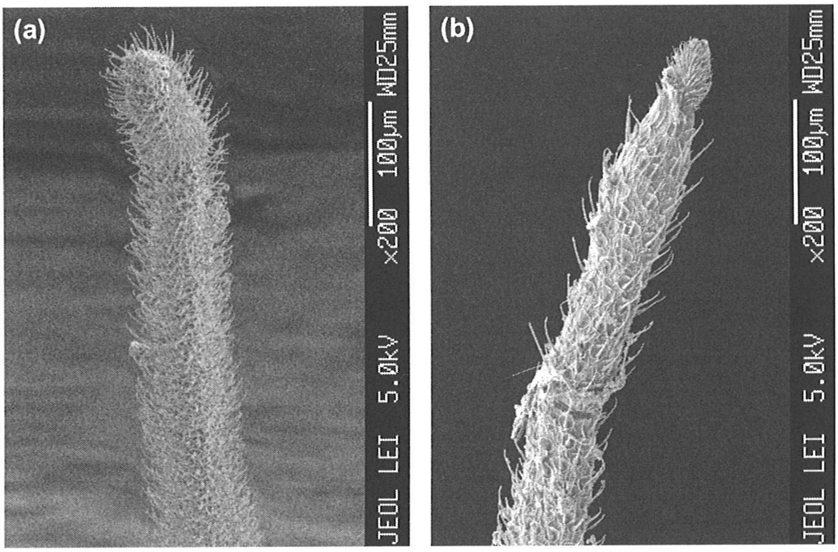

Figure 5. SEM images of the apical antennal segments of a) male and b) female, showing comparatively more sensilla on the male antenna. Scale bar = 100 µm.

Comparison of male and female *A. luminosa* antennae

The antennae of male *A. luminosa* adults are longer than those of females (4.0 mm in the male and 3.1 mm in the female shown (Figure 4)). In addition, there are more sensilla on the male antenna (Figure 5a) and those of the female appear morphologically more diverse, although the functions of none of them have been determined.

Discussion

Some authors have suggested that the light of the female pupa and adult could be used as a mate-attraction device (Hudson 1928, 1950; Richards 1960, 1964; Kermode 1974; Meyer-Rochow & Waldvogel 1979; Meyer-Rochow & Eguchi 1984; Meyer-Rochow & Liddle 1988; Meyer-Rochow 1990), but the time lag I observed between an emerging female ceasing to glow and a male *A. luminosa* alighting upon the female in the darkness of the cave (other than infra-red light) provides strong evidence that vision was not used and that, instead, a different mechanism is involved for attracting mates of *A. luminosa* to each other. In the present case, the female, even if it did glow, would have been largely obscured from flying males by the recording equipment. Gatenby (1960a) similarly concluded that the pupal light is not likely to be involved in mate attraction after examining the antennae of male *A. luminosa*, and suggested that 'the male no doubt finds his mate by the use of sensillae in these comparatively very large antennae.' As I have shown, the antennae of male flies are indeed longer and do possess more sensilla than those of female flies and some of these sensilla are morphologically different from those of females, a finding that suggests sex pheromones could be involved. It also seems unlikely that bioluminescence could be used as a cue for sexual attraction unless it is used in some form of signalling that involves blinking or changes in intensity, because it is the same colour for all life-cycle stages. I found no evidence of such signalling behaviour during my observations, and it is worth noting here that only one early-stage female pupa and no adults of the Australian glowworm *Arachnocampa flava* Harrison were reported to glow whilst under observation in the laboratory (Baker & Merritt 2003).

If sex pheromones are involved in the attraction of *A. luminosa* males, it is tempting to speculate that vision could be used in another way, because the principal navigational mechanism used by flying insects to locate an odour source is to fly upwind while in contact with the odour (Cardé & Willis 2008). Many insects detect upwind direction by the 'optomotor anemotaxis' response, which involves visually maintaining a front-to-rear image flow of the ground pattern (Hardie et al. 2001). This mechanism is also necessary for controlling nocturnal insect flight (Warrant & Dacke 2011), e.g., in the mosquito *Anopheles gambiae* Giles, which shows behavioural optomotor responses to light intensities as low as or lower than one log unit of starlight (Gibson 1995). In the case of *A. luminosa*, the adults do have large dark-adapted eyes (Meyer-Rochow & Waldvogel 1979) and those of adult males are highly sensitive to light of a wavelength that corresponds closely to the peak emission spectra of conspecific larvae (Meyer-Rochow & Eguchi 1984). Therefore, if sex pheromones are involved, perhaps male *A. luminosa* flies use the only visual references available to them in the darkness of caves – the glows of nearby larvae – to help them track odour plumes upwind to reach waiting females. Even in caves with relatively still air, other mechanisms such as casting and counterturning (zig-zagging flight) could be used by adult males to help them locate a pheromone plume.

It was not possible to investigate whether air or substrate vibrational cues play any part in sex attraction, so future research is required to show unequivocally which mate attraction mechanism or mechanisms are employed by *A. luminosa.*

Some authors reported that *A. luminosa* pupae will glow when touched gently (Gatenby 1959; Richards 1960, 1964; Meyer-Rochow & Waldvogel 1979; Meyer-Rochow & Eguchi 1984; Meyer-Rochow 1990) and I also observed female pupae at night in bush and in the cave glow briefly when weta and a spider contacted them. However, the pupae glowed for no apparent reason on several other occasions. It is possible that this behaviour could be a defensive mechanism used by *A. luminosa* pupae in the dark to startle intruders such as weta. However, glowing seems unlikely to deter the only known predators of *A. luminosa* in caves: *M. tumida*, which eat large larvae, pupae and adults; and the smaller harvestman, *Hendea myersi cavernicola* Forster, which eat the eggs and early instar larvae, because both species are reported to be attracted to larval glowworm bioluminescence (Meyer-Rochow & Liddle 1988, 2001). For these reasons it also seems unlikely that this glowing behaviour could be an aposematic signal; e.g., as De Cock and Matthysen (2003) have shown for larvae of the firefly *Lampyris noctiluca* Linnaeus, which use bioluminescence as a signal to convey their unpalatability to toads. The many sticky fishing lines that hang from areas inhabited by *A. luminosa* larvae are probably more useful to the glowworm defensively, by physically segregating them from *M. tumida*, spiders and weta, as suggested by Richards (1960).

Overall, my observations support the suggestion by Broadley and Stringer (2001) that bioluminescence has no function in the pupal and adult stages of *A. luminosa*: it is, instead, carried over from the larval stage simply because the Malpighian tubules of Diptera are not affected by metamorphosis (Wheeler & Williams 1915; Ganguly 1960; Green 1979; Locke 1985).

My observations also show that pupae in bush during the daytime can flick their abdomens rapidly in an apparent attempt to ward off crawling invertebrates that contact them. As far as I am aware, this is the first time this behaviour has been described in glowworm pupae. Such flicking behaviour seems to be the only possible defence available to a pupa to deter the apterous female of the hymenopteran parasitoid *Betyla fulva* Cameron (Hudson 1892a,b), which has to walk to its host. Cole (1959) described similar defensive behaviour used in freely suspended pupae (chrysalids) of two species of nymphalid butterflies against attacking ichneumonid parasitoids. The circle of fishing lines that a glowworm larva surrounds itself with before pupating may also protect the pupa from some walking arthropods (Richards 1960; Meyer-Rochow 1990).

Richards (1960) first reported *M. tumida* as a predator of adult *A. luminosa* in Glowworm Cave, but it appears that the present study is the first time that actual predation has been recorded. It is possible that the attack was triggered by the female fly glowing briefly and moving when she separated from her mate and alighted upon the cave wall, because *M. tumida* is reported to exhibit a positive phototactic response to a dim artificial 'glowworm' light (Meyer-Rochow & Liddle 1988). However, light alone may not have been the only cue for the harvestman to orientate towards its prey because the pedipalps and the first and second pair of legs possess a variety of sensory receptors (Willemart et al. 2009); therefore both chemical and vibrational cues may have been involved.

Overall, my observations of the behaviour of glowworm pupae and adults undisturbed (other than possibly by the infra-red remote video recordings) have confirmed–similarly to the observations of larvae reported by Broadley and Stringer (2009) – that it is the same as most of the behaviour previously reported for these insects when they are illuminated by short periods of artificial illumination; e.g., the eclosion behaviour that I have described appears to be fairly typical for *A. luminosa* (see Gatenby & Cotton 1960; Richards 1960). The great advantage of using infra-red remote video recording is that I have been able to provide precise timing of the behaviours from observations extending over many days.

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