Behavioural ecology and prey attraction of the New Zealand Glowworm *Arachnocampa luminosa* (Skuse)(Diptera: Mycetophilidae) in bush and cave habitats.

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To my father

Abstract

Larvae of the mycetophilid *Arachnocampa luminosa* (Skuse), known commonly as "glowworms", inhabit damp, sheltered and shaded places in bush, and caves. The glowworm is predaceous, and it lives within a mucus tube or gallery from which hang vertical "fishing lines" made from silk and sticky mucus. Invertebrates are captured on the fishing lines and hauled up by the larva and eaten.

Glowworms use bioluminescence to attract invertebrates. I tested the effectiveness of bioluminescence by comparing the numbers of invertebrates caught on transparent adhesive traps placed over glowworms with similar traps set over areas that glowworms had been removed from. Prey attraction was investigated in Reserve Cave, Waitomo, and in its bush-clad entrance over 200 days during "winter", "spring" and "summer." Traps placed over glowworms caught significantly more invertebrates overall per trap per day than control traps. Glowworms in bush attracted both greater numbers and types of invertebrates than glowworms in the cave. There were also significant seasonal differences in the numbers caught and types of invertebrates. Flying Diptera predominated in both bush (85% of the total catch) and cave (89%) habitats. Minor components consisted mainly of spiders (Araneae), Coleoptera, Hymenoptera, Orthoptera, Trichoptera, Gastropoda, Acariformes and Neuroptera. Confirmation that the attracted invertebrates were eaten by glowworms was demonstrated by collecting and examining glowworm faeces and identifying discarded material from their snares. This was done by placing blotting paper sheets under glowworms in cave and bush habitats during spring and summer. Most faecal material consisted of insect sensillae and spines, cuticle and compound eye cuticle, but discarded legs, antennae and wings were sometimes present either as parts or entire. Entire or fragmented millipedes were sometimes present, especially in the cave. Occasionally insect head capsules, thoraxes and abdomens were also discarded. Several small snail shells (Gastropoda) were found under bush glowworms and three entire insects were found under glowworms in the cave in summer. No adult *A. luminosa* were caught on adhesive traps, or identified in the material discarded from glowworm snares. Glowworms under adhesive traps appeared to be able to survive for long periods without food, especially those in the cave, which all survived with little or no food for 78 days.

At Waitomo, variation in light output by different glowworms affected the number of invertebrates that were attracted to the light and increased the variance in prey numbers between different glowworms. This was overcome at Waitomo by running the experiment for long periods of time in order to demonstrate attraction. Using live glowworms in such experiments was also labour intensive and time consuming. A light-emitting diode (LED) with a similar maximum wavelength to glowworms was used, to explore the possibility that it

could be used to sample the potential food of glowworms in areas where glowworms do not occur, such as some passages in caves. The suitability of these LEDs were tested by comparing catches in adhesive traps containing them with traps containing glowworms and traps without (controls). These were run in bush for 21 days and then a further 21 days in a cave passage at Piripiri Road Caves, Pohangina. Traps with LEDs caught a significantly greater total number of invertebrates overall than traps either with or without glowworms. However, there were no significant differences in the numbers of Mycetophilidae, other Diptera families and other invertebrates caught on the three trap types in bush or in the cave.

The prey recognition behaviour of *A. luminosa* larvae involves taste and/or smell. This was demonstrated by comparing the numbers of live and dead *Drosophila melanogaster*, and blotting paper that was both dry and soaked in crushed *D. melanogaster* juice, that were "hauled-up", "discarded", "left hanging" or "missing" the day after they were placed on the vertical fishing lines of larval snares. There were significant differences between responses of glowworms to dry paper, wet paper, and dry paper placed above *D. melanogaster* on fishing lines. Most (72%) of the pieces of paper with crushed *D. melanogaster* juice were hauled up into glowworm snares, and none were discarded, whereas dry pieces of paper were found hauled up 16% of the time but 40% of them had been discarded.

Remote recording of *A. luminosa* in both bush and cave habitats at Waitomo was done between 18/1/95 and 19/11/95. Observations were made using infra-red light and a TV camera which was sensitive to this light. A total of 934 individual "larva-hours" of activity were recorded, including 308 "larva-hours" of 4 glowworms in bush; 345 "larva-hours" from 4 glowworms in Demonstration Chamber of Glowworm Cave; 233 "larva-hours" from one glowworm in Reserve Cave; and 48 hours of several glowworms in Waitomo Waterfall Cave. Observations were also made of three adults emerging from their pupal exuviae. A male adult was observed alighting upon a female which had not glowed for about 53 minutes, and the pair copulated. This provides evidence to support the suggestion that adults may use olfactory organs in mate attraction. After copulating they were both eaten by a large predatory harvestmen (*Megalopsalis tumida* Forster). As a result of video-taping *A. luminosa* many observations were made and many types of behaviour were identified. The most obvious ones were production of bioluminescence, "fishing line construction", "defecation", "fighting" between pairs of larvae, "prey capture", and attempted capture of invertebrates by larvae. Behaviours recorded rarely were the eclosion of both male and female adult *A. luminosa* from pupae, mate attraction, and copulation. Glowworm larvae in bush glowed only at night. They usually became active late in the afternoon when they began to make fishing lines, repair snares, and void defecatory droplets. They started to glow up to an hour and a half after becoming active, and they turned on their bioluminescence relatively quickly, from less than 15 seconds to about 1 minute for a bright light to be visible. At dawn, glowworms in bush took several minutes to fade out their lights, but on cold nights (~ < 6°C) they glowed only intermittently or not at all. Larvae in the Demonstration Chamber appeared to be disturbed by cave lights and wind currents apparently generated by the activities of humans in there. When cave lights were switched on for more than about 30% of the time (~ 20 minutes per hour), larvae did not glow brightly and spent little time making fishing lines (< 5% of time per hour). However, there is no way to be certain if this disturbance was detrimental to their overall well-being. The larva in Reserve Cave glowed on average only between 13:00 and 02:00 on only four out of eleven days, and did not appear to glow brightly compared with glowworms either in bush or in Glowworm Cave. However, it was not possible to determine whether this behaviour was typical of other glowworms living in the cave. Only one observation of prey capture was made, and this occurred in bush. It appeared to be a small winged dipteran. Three other partial observations were made of insects being hauled-up. Observations were made in bush at night of spiders which appeared to move accidentally through glowworm snares, breaking the delicate fishing lines. However they were not caught and eaten by glowworms. On one occasion, a spider was attacked by a glowworm when it touched its snare, but it was strong enough to break free. Fighting between larvae usually occurred when a larva moved part-way out of its gallery to search the substrate for new points of attachment for its snare and fishing lines, and then accidentally touched the snare of its neighbour. This indicates that larvae fight to increase the size of their territory or to protect their own territory. Fighting larvae glowed brilliantly and would snap at each others heads with their jaws, and occasionally tried to pull each other out of their snares. These fighting episodes usually concluded when one of the larvae retreated, but often the fights would resume some time later. Larval cannibalism was not observed, although on one occasion a larva was bitten on its body by an intruder which had moved completely out of its snare. Defecation was observed on ten occasions. In bush, larvae either voided excretory droplets out of the snare or produced them so they hung on fishing lines. In the latter case the larvae then lengthened the fishing lines until the droplets made contact with the substrate. In caves the glowworms cut and dropped entire fishing lines with droplets on them, or they left them hanging within the snare.

Starch-gel electrophoresis of allozymes showed that populations of glowworms tend to be genetically discrete but with no particular geographic or ecological structuring between them. This was demonstrated by collecting *A. luminosa* larvae from many cave and bush sites in the North Island. Average Standard Genetic Distances between populations were determined (Nei, 1975) and the results were subjected to cluster analysis using average pair group clustering with the package M.V.S.P. This showed that geographically adjacent glowworm populations did not tend to be more similar genetically than distant populations and that glowworm populations did not cluster into bush and cave populations. However, the high degree of polymorphism (range ~ 38% to ~ 86%) and heterozygosity (range ~ 3% to ~ 18%) suggests gene flow occurs regularly between glowworm populations, and does not support the notion that cave and bush forms should be regarded as distinct species or subspecies.

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Overleaf *A boat-load of visitors gaze up at hundreds of pinpoints of bioluminescence produced by* Arachnocampa luminosa *larvae in the famous grotto of Glowworm Cave, Waitomo (Printed by permission Waitomo Museum of Caves).*

I wish I was a glowworm
For they are never glum
How can you be unhappy
When the sun shines out your bum?

- Ricardo Palmer, Entomologist, Museum of New Zealand