

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

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

---

**A thesis presented in partial  
fulfilment of the requirements  
for the degree  
of Master of Science  
in Zoology at  
Massey University**

---

**Richard Adam Broadley  
1998**

*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 harvestman (*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 ( $\sim < 6^{\circ}\text{C}$ ) 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 ( $\sim 20$  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.

## Acknowledgements

---

Financial support for this research was provided by the (formerly) T.H.C. Waitomo Caves Hotel, Waitomo Caves Management Committee, Ruapuha Uekaha Hapu Trust, Department of Ecology at Massey University, and a graduate research award from the Massey University Graduate Research Fund.

Without the kind help of all of the following people this work would not have been possible - to all of you, thanks a lot: Bryson Anderson for showing me the glowworms up at Waituna West; Ian Andrew and Jay McCartney at Massey for identifying invertebrates. John Ash and Pete Chandler and guides of Blackwater Rafting for loaning me helmets, lamps, and an inflatable raft when needed, and also for granting me a free trip; Penny Aspin for taking cave photographs; Nick Broomfield at Massey for expertise in the editing of video tapes; Alan Carpenter and Case van Epenhausen for providing me with a bucket full of insect adhesive at short notice; Kate Banbury for information regarding lighting in Glowworm Cave; Stuart Burgess at the National Institute of Water and Atmospheric Research Ltd (NIWA) in Wellington for Waitomo rainfall data; Nicci Coffey for helping to lug equipment into Reserve Cave; Peter Dimond for his hospitality and for providing me with space for all my gear in the Museum of Caves and use of the workshop there; Allan Goss for allowing me to conduct research on his land at Piripiri Road Caves; Sacha Hall at the Carter Observatory in Wellington for various atmospheric data; Shane Hatcher for providing limitless supplies of *Drosophila* at a moments notice; Ian Henderson for much-needed help with statistical analyses; Dave Hurst for help collecting samples in the field and caving adventures; Jens Jorgensen for constructing various ingenious pieces of equipment from scrap material; Bruce Rapley, Dexter Muir, and Wyatt Page for their kind help with constructing the camera casing, infra-red light sources, light traps and various other pieces of equipment, and for teaching me some useful skills i.e. how to use a lathe and a soldering iron; Oliver Paskins for helping collect inverts off adhesive traps and insect collecting expeditions; Steve Pilkington for providing transport to get most of the gear up to Waitomo; Chris Pugsley for some brain-picking and use of his cave map; Ray Scrimgeour of DoC Te Kuiti for giving the all clear to conduct research at Reserve Cave; Ashley Shaw of the New Zealand Speleological Society for permission to use cave maps; Allan Singleton at NIWA for providing me with atmospheric data for Glowworm Cave; Dave Smith for a guided tour around several caves at Waitomo; Cam Speedy of Department of Conservation Taupo/Tongariro Conservancy for granting me permission to collect glowworm samples from Okupata; Robert Tahiri and guides of Glowworm Cave for advice and assistance; Tamsin Ward-Smith for her help and assistance; Dave Williams, former manager of the Waitomo Caves Hotel for allowing me to stay at the cottage for free throughout the field work and for much



needed local knowledge; and to the many travellers I met at the hostel and everybody else who took an interest in what I was doing, and lent a hand.

Thanks especially to my family for their support, and to my supervisors Dr Ian Stringer and Dr Alastair Robertson, who introduced me to a brilliant thesis topic.

---

	Acknowledgements	vii
1	<b>GENERAL INTRODUCTION</b>	<b>1</b>
2	<b>PREY ATTRACTION BY GLOWWORMS IN A CAVE AND IN THE BUSH-CLAD CAVE ENTRANCE</b>	<b>4</b>
	Introduction	4
	Materials & Methods	6
	Results	12
	Discussion	22
3	<b>ATTRACTION OF INVERTEBRATES TO GLOWWORMS AND ARTIFICIAL LIGHT SOURCES AT PIRIPIRI ROAD CAVES, POHANGINA</b>	<b>27</b>
	Introduction	27
	Materials & Methods	31
	Results	36
	Discussion	41
4	<b>PREY RECOGNITION BY GLOWWORMS</b>	<b>44</b>
	Introduction	44
	Materials & Methods	45
	Results	49
	Discussion	52
5	<b>OBSERVATIONS DERIVED FROM REMOTE RECORDING OF <i>ARACHNOCAMPA LUMINOSA</i> IN BUSH AND CAVES AT WAITOMO</b>	<b>55</b>
	Introduction	55
	Materials & Methods	57
	Results	64
	Discussion	92
	Appendix	96
6	<b>ARE <i>ARACHNOCAMPA LUMINOSA</i> IN BUSH GENETICALLY ISOLATED FROM THOSE FOUND IN CAVES? - AN INVESTIGATION USING ALLOZYME ELECTROPHORESIS TECHNIQUES</b>	<b>97</b>
	Introduction	97
	Materials & Methods	99
	Results	106
	Discussion	111
	Appendix	113
	<b>References</b>	<b>118</b>

---

1.1	Glowworms and their snares.	2
1.2	An adult <i>A. luminosa</i> male clings to a female pupa.	3
2.1	Location of Reserve Cave and the bush sites in Ruakuri Scenic Reserve, Waitomo.	7
2.2	A view from inside Reserve Cave, Waitomo, of the bush-clad cave entrance.	8
2.3	Location of both bush and cave adhesive trap sites at Reserve Cave, Waitomo; and location of blotting paper sheets used to collect glowworm faeces and discarded material.	9
2.4	Diagram of a transparent adhesive trap.	10
2.5	Log numbers of invertebrates collected per day from adhesive traps in Reserve Cave and in the bush-clad entrance to Reserve Cave, Waitomo, over winter, spring and summer.	12
2.6	Relative numbers of invertebrates caught per day on traps containing glowworms and control traps in the bush-clad entrance to Reserve Cave, Waitomo, during winter, spring and summer.	16
2.7	Relative numbers of invertebrates caught per day on traps containing glowworms and control traps in Reserve Cave, Waitomo, during winter, spring and summer.	18
3.1	The light sensitive photoswitch setup used to switch LEDs on at dusk and off at dawn at Piripiri Road Caves, Pohangina.	29
3.2	Circuit diagram of the light-sensitive photoswitch used in Figure 3.1.	30
3.3	Location of both bush and cave sites at Piripiri Road Caves, Pohangina, where invertebrates were collected from adhesive traps containing 470 nm LEDs, glowworms and from areas where glowworms had been removed from.	33
3.4	Diagram of watertight LED tube used to attract invertebrates at Piripiri Road Caves, Pohangina.	34
3.5	Bush location at Piripiri Road Caves, Pohangina, showing all 18 transparent adhesive traps wired onto the rock face.	35

---

3.6	Time exposure of the bush location at night, showing the location of both LEDs and some of the glowworms within adhesive traps.	35
4.1	Map of Glowworm Cave, Waitomo, showing the location of the tunnel ceiling site where glowworms were removed for prey recognition experiments	46
4.2	Diagram of an observation chamber, constructed from an inverted 1.5 litre transparent plastic soft-drink bottle with its top cut off, used to house a glowworm larva while conducting prey recognition experiments	47
5.1	Equipment used to record <i>A. luminosa</i> at both bush and cave sites at Waitomo	58
5.2	Location of the site in Demonstration Chamber, Glowworm Cave, Waitomo, where remote recording of <i>A. luminosa</i> took place	59
5.3	Location of both bush and cave sites at Reserve Cave, Waitomo, where remote recording of <i>A. luminosa</i> pupae, adults, and a single larva took place	60
5.4	Location of the site in Waitomo Waterfall Cave, where remote recording of <i>A. luminosa</i> took place.	61
5.5	Location of Glowworm Cave, Reserve Cave, and the bush sites in Ruakuri Scenic Reserve, Waitomo, where remote recording of glowworms took place.	62
5.6	Mean hourly percentage of time two larvae spent glowing in bush at Ruakuri Scenic Reserve, Waitomo, between 23 and 25/2/95.	65
5.7	Mean hourly percentage of time two larvae spent glowing in bush at Ruakuri Scenic Reserve, Waitomo, between 9 and 15/5/95.	66
5.8	The possible effect of temperature on the percentage of time per hour <i>A. luminosa</i> larvae were observed to spend glowing in bush at Ruakuri Scenic Reserve, Waitomo. Temperature measurements were taken each hour in bush outside the entrance to Glowworm Cave approximately 2.5 kilometres away.	67

---

5.9	Mean percentage of time per hour that four <i>A. luminosa</i> larvae spent glowing brightly in Demonstration Chamber of Glowworm Cave, Waitomo. Observations were taken between 2 - 5/4/95 and 19 - 23/5/95.	68
5.10	Relationship between the mean percentage of time per hour spent by four <i>A. luminosa</i> larvae glowing brightly in Demonstration Chamber of Glowworm Cave, Waitomo, and the mean hourly percentage of time that the cave lights were switched on. Observations were made between 2 - 5/4/95 and 19 - 23/5/95.	69
5.11	Mean percentage of time one <i>A. luminosa</i> larva spent glowing per hour in Reserve Cave, Waitomo. Observations were made between 7 - 19/11/95.	70
5.12	Mean hourly percentage of time spent by two <i>A. luminosa</i> larvae constructing fishing lines in bush at Ruakuri Scenic Reserve, Waitomo, between 23 - 25/2/95.	73
5.13	Mean hourly percentage of time spent by two <i>A. luminosa</i> larvae constructing fishing lines in bush at Ruakuri Scenic Reserve, Waitomo, between 9 and 15/5/95.	74
5.14	Mean percentage of time per hour spent by four <i>A. luminosa</i> larvae constructing fishing lines in the Demonstration Chamber of Glowworm Cave, Waitomo, between 2 - 5/4/95 and 19 - 23/5/95. The mean percentage of time when the cave lights were switched on is also shown.	75
5.15	<i>A. luminosa</i> larva constructing a fishing line in Demonstration Chamber of Glowworm Cave, Waitomo.	76
5.16	Relationship between the mean percentage of time per hour spent by four <i>A. luminosa</i> larvae constructing fishing lines and the mean hourly percentage of time cave lights in Demonstration Chamber of Glowworm Cave, Waitomo, were switched on, between 2 - 5/4/95 and 19 - 23/5/95.	77
5.17	Mean hourly percentage of time spent by one <i>A. luminosa</i> larva constructing fishing lines in Reserve Cave, Waitomo, between 7/11/95 and 19/11/95.	78
5.18	In bush at night a small flying insect is caught in glowworm fishing lines.	82
5.19	In bush at night a spider is attacked by a glowworm.	83

---

5.20	A pair of <i>A. luminosa</i> larvae fighting in Demonstration Chamber of Glowworm Cave.	85
5.21	Glowworm voiding an excretory droplet onto the substrate below the snare.	88
6.1	Location of sites in Glowworm Cave, Waitomo, where glowworms were removed from for allozyme electrophoresis experiments.	100
6.2	Location of the site in Ruakuri Scenic Reserve, Waitomo, where glowworms were removed from for allozyme electrophoresis experiments.	101
6.3	Location of the site in Frazers Bluff Cave, Okupata, Tongariro, where glowworms were removed from for allozyme electrophoresis experiments.	102
6.4	Location of the site in a tunnel passage at Piripiri Road Caves, Pohangina, where glowworms were removed from for allozyme electrophoresis experiments.	103
6.5	Location of the bush site near Totara Reserve, Pohangina, where glowworms were removed from for allozyme electrophoresis experiments.	104
6.6	Cluster analysis of Average Standard Genetic Distances (D) between seven bush and cave glowworm populations.	110

---

2.1	Analysis of Variance of the numbers of invertebrates caught per trap in bush and cave habitats, using traps occupied by glowworms or no glowworms (controls) during winter, spring & summer.	13
2.2	Invertebrates captured on traps placed over <i>A. luminosa</i> larvae and over areas where larvae have been removed from.	14
2.3	Means, ranges and standard errors of numbers of invertebrates caught per day in glowworm-occupied traps.	19
2.4	Means, ranges and standard errors of numbers of droplets collected per day per glowworm from beneath glowworms.	20
2.5	Material identified from blotting paper sheets placed under bush and cave glowworms.	21
3.1	Invertebrates captured on adhesive traps placed over 470 nm LEDs, glowworms and over areas where glowworms have been removed.	36
4.1	The status of prey items the day after they had been placed upon glowworm fishing lines.	49
4.2	The status of live <i>Drosophila melanogaster</i> , dead <i>D. melanogaster</i> and live <i>D. melanogaster</i> hanging below pieces of paper the day after they had been placed on glowworm fishing lines.	50
4.3	The status of pieces of dry paper, paper crushed in <i>D. melanogaster</i> juice and dry paper hanging above live <i>D. melanogaster</i> the day after they had been placed on glowworm fishing lines.	51
5.1	Time (minutes) spent making fishing lines by glowworms in bush, Glowworm Cave and a glowworm in Reserve Cave, Waitomo.	72
5.2	Means, ranges and standard errors of the lengths of time (h:mm:ss) that pairs of glowworms were observed fighting for.	84
5.3	Means, ranges and standard errors of the lengths of time (h:mm:ss) glowworms recorded at each location took to dispose of excretory droplets.	87

---

6.1	The 10 enzymes and their standard abbreviations, which glowworm samples were run successfully in.	105
6.2	Frequency of alleles derived from running glowworm extract from several bush and cave populations in starch-gel electrophoresis, for 10 enzymes.	107
6.3	Percentage of polymorphic loci (P) and average heterozygosity (H) for each glowworm population.	108
6.4	The average standard genetic distance (D) between each glowworm population, based on allele frequencies from the 10 loci (enzymes).	109

*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