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Prey attraction by larvae of the New Zealand glowworm, *Arachnocampa luminosa* (Diptera: Mycetophilidae)

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Abstract. The hypothesis that bioluminescence produced by larvae of the New Zealand glowworm, *Arachnocampa luminosa,* attracts prey was tested experimentally in Reserve Cave, Waitomo, New Zealand, and in its bush-clad entrance over a total of 200 days during winter, spring, and summer. We compared catches on transparent adhesive traps placed either over glowworms or over areas from which glowworms had been removed. Adhesive traps over glowworms caught significantly more invertebrates per trap per day than did control traps. Glowworms in bush attracted greater numbers and types of invertebrates than did glowworms in the cave. Diptera predominated in both bush (86% of the total catch) and cave (89%). Also caught were small numbers of Araneae, Coleoptera, Hymenoptera, Orthoptera, Trichoptera, Gastropoda, Acarina, and Neuroptera—listed in order of abundance—but no adults of *A. luminosa* were caught. Glowworms under adhesive traps survived with little or no food for up to 78 days.

Additional key words: bioluminescence, cave ecology

Bioluminescence is most common in marine animals, rare on land, and extremely rare in freshwater. It is probably used in defensive functions such as camouflage against down-welling light in the mesopelagic marine zone, to warn off potential predators, and in defensive maneuvers; in intraspecific communication such as maintaining contact within schools or in attracting mates; in obtaining food attracted to the bioluminescence, and to see by (Harvey 1952; Herring 1978). Few of these uses have been confirmed experimentally (Herring 1978). This applies to bioluminescence produced by larvae of the New Zealand glowworm, *Arachnocampa luminosa* (SKUSE 1890) (Diptera: Mycetophilidae: Keroplatinae).

Meyrick (1886) first suggested that glowworm larvae use their bioluminescence to attract prey, and this has been assumed to be so ever since. The light is produced at the posterior end of the body by the distal ends of the Malpighian tubules (Green 1979). The larvae live in caves and on banks in bush where the humidity is high and where they are protected from wind. Each larva constructs a horizontal web surrounding a ribbon-like gallery on which it lies. It suspends up to 30 vertical fishing lines from the web (Fig. 1). Each fishing line has small, sticky, regularly spaced droplets which snare small invertebrates that fly or fall into them. Invertebrates caught in the fishing lines are hauled up and eaten (see reviews by Kermode 1974; Pugsley 1983; Meyer-Rochow 1990).

The bioluminescence produced by another keroplatine, *Orfelia fultoni* FISHER, was shown experimentally to attract some arthropods, including a number of flying dipterans (Sivinski 1982). The larvae of *O. fultoni,* however, make horizontal webs over depressions in the ground and these nests lack vertical fishing lines (Sivinski 1982, 1998).

The only information on the potential prey of larvae of *A. luminosa* are reports of invertebrates found caught in the fishing lines (Norris 1894; Richards 1960; Stringer 1967; Pugsley 1984) or in traps placed near glowworms (Pugsley 1984; Oxenham 1985). Many of the prey are flying insects but immature isopods, ants, amphipods, millipedes, and small land snails are also caught, indicating that non-flying prey may jump or fall into glowworm snares.

We tested the idea that various kinds of invertebrates are attracted to glowworm bioluminescence, in a cave and in nearby bush. We compared the numbers of invertebrates caught on transparent adhesive traps that either surrounded live glowworms and their nests or surrounded areas from which glowworms had been removed.

Methods

The adhesive traps were 3-litre clear plastic drink bottles with the bottom third cut off (Fig. 1). Each trap

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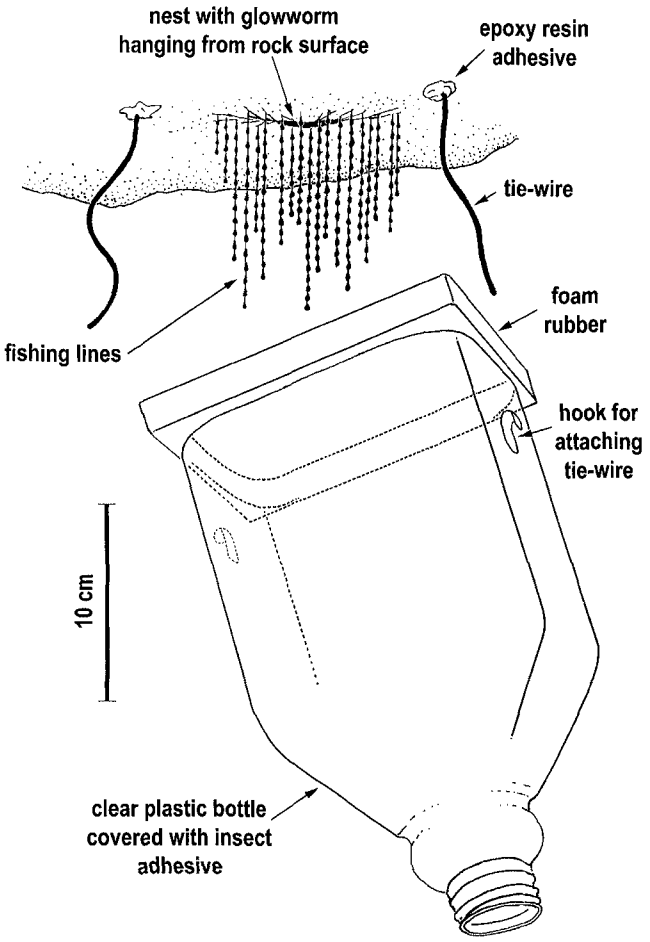

Fig. 1. Transparent adhesive trap used to determine what invertebrates are attracted to the bioluminescence of larvae of *Arachnocampa luminosa*.

was held in place with a pair of tie-wires cemented to the substrate with non-toxic "Emerkit" epoxy resin putty (S. Austin Carr & Co. Ltd., Auckland, New Zealand). Each wire was attached to an aluminium hook, a pair of which were riveted on either side near the base of the bottle. Foam rubber, glued to the cut edge of the bottle, sealed it against the substrate. The opening of the plastic bottle (32 mm diameter) was left uncapped to provide free exchange with the air outside. The outer surface of the plastic bottle was coated with a thin layer of "Tanglefoot" (The Tanglefoot Co., Grand Rapids, MI 49504, USA). All invertebrates caught in the adhesive were removed with forceps, then cleaned and stored in kerosene. Most were identified to family.

The adhesive traps were set simultaneously by the bush-clad entrance to Reserve Cave, Waitomo (38°16′S, 175°05′E) and about 500 m inside the cave (Fig. 2). Large populations of larvae of *Arachnocampa luminosa* were present at both locations. Each trap was placed so that it surrounded either a glowworm larva together with its entire nest or an area from which a glowworm and its nest had been removed. Glowworms used in the bush were 15–25 mm long and those used in the cave were 20–30 mm long. These were up to two-thirds the lengths of full-grown larvae to ensure that they would not pupate during the study. Of the 28 glowworms selected in the bush, 16 were chosen at random and removed. Of the 29 glowworms selected in the cave, 15 were chosen at random and removed. A trap was then fixed over each glowworm or over the site that a glowworm had occupied. The traps were first set on 4 July 1995 and left for 60 days during winter. Water runoff in the bush destroyed the invertebrates caught on 1 trap over a glowworm and on another 6 traps without glowworms, so these traps were removed and not set again. The remaining adhesive traps were set again in the same places for 62 days from 9 September 1995 (spring), and for 78 days from 10 November 1995 (summer). Four glowworms disappeared from within their traps in bush during summer, so data from these traps were discarded.

The transmission of light through the traps was determined with a "Jenway" 6105 spectrophotometer (Jenway Ltd., Dunmow, England). Thirty pieces of the traps together with Tanglefoot were cut to fit into the spectrophotometer, and tested at 10 nm intervals between 420 and 600 nm. This covered the spectral range of glowworm bioluminescence (Shimomura et al. 1966).

Numbers of insects caught in individual traps were too low to perform a seasonal analysis so the total numbers of invertebrates caught over the entire 200-day sampling period were used to perform a two-way analysis of variance with *log(number of invertebrates caught + 1)* as the dependent variable and trap type (with or without glowworms) and habitat (bush or cave) as independent variables. In addition, for each habitat, single-factor analyses of variance were performed on each invertebrate group after log(n+1) transformation. Only invertebrate groups that occurred 5 times or more in the respective habitats were used in these analyses. All analyses were performed using generalised linear models with *S-PLUS* (MathSoft 1997).

Results

Traps placed over glowworms at both bush and cave sites caught significantly more invertebrates overall than control traps ($p<.01$, Table 1) even though the traps reduced the intensity of bioluminescence by 80–81%. Both glowworm-occupied traps and control traps in the bush at the entrance to Reserve Cave caught

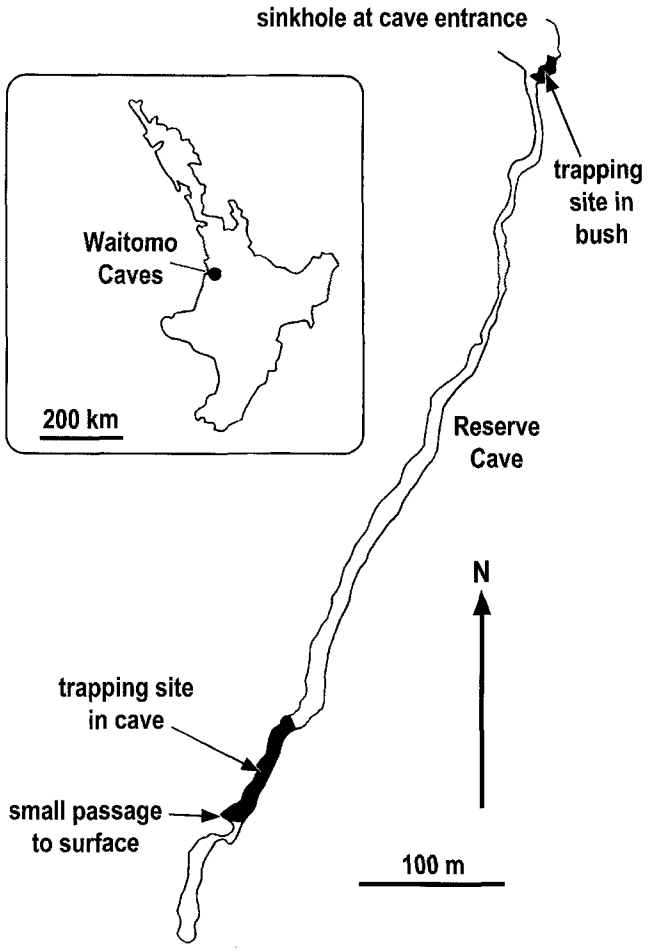

Fig. 2. Map of Reserve Cave, Waitomo, showing where adhesive traps were set in the cave and in bush at the cave entrance.

significantly more invertebrates per trap than traps within the cave ($p<.01$, Tables 1, 2). The difference between the numbers of invertebrates caught per trap on glowworm-occupied traps vs. control traps was greater in bush than in the cave (Fig. 3) and a greater variety of invertebrates was caught in bush (32 taxa) than in the cave (16 taxa) (Table 2). There was also an indication that traps in bush caught more in spring than in winter or summer, and that traps in Reserve Cave caught more in summer than in winter or spring (Table 2) but the numbers caught were too low to analyse statistically.

Adhesive traps caught a range of invertebrates (Table 2). Most were spread over the flat surfaces of the traps and few were caught on the neck of the traps near the trap opening. The majority of invertebrates caught (86% of total bush catch; 89% of total cave catch) were small flying dipterans 1–4 mm long. No adults of *Arachnocampa luminosa* were caught in any adhesive traps.

Four glowworms disappeared from within their traps in the bush during summer, but no glowworms disappeared from the traps in Reserve Cave (Table 2). No discarded fecal material from glowworms or rejected parts of prey were found when the insides of the traps were examined.

Potential prey in bush

In bush, the only taxa that were caught significantly more frequently on traps occupied by glowworms vs. traps without glowworms were total Diptera, and the dipteran families Dolichopodidae, Psychodidae, and Teratomyzidae (Fig. 4). Other dipteran families that were important numerically but not significantly attracted to glowworms were Heleomyzidae, Mycetophilidae, Sciaridae, Tipulidae, and Trichoceridae. Of the non-dipteran invertebrates, spiders (Araneae) were the most frequently caught on all traps, followed by Coleoptera and Hymenoptera. Ground-dwelling invertebrates such as small snails (Gastropoda), the predatory harvestman *Megalopsalis tumida* (FORSTER) (Opiliones), mites (Acarina), millipedes, Collembola, cave weta (Orthoptera: Rhaphidophoridae), and isopods contributed less than 4% of the total number of invertebrates caught in all traps (Table 2, Fig. 4).

Potential prey in Reserve Cave

Glowworm-occupied traps in Reserve Cave caught significantly more invertebrates overall than traps

Table 1. Results of ANOVA for the effect of trap (occupied by glowworms vs. no glowworms) and habitat (bush vs. cave) on the numbers of invertebrates caught per trap. Adhesive traps considered were all those in Reserve Cave (14 over glowworms, 15 controls) and those not affected by water runoff in bush (7 over glowworms, 10 controls).

Source	DF	Mean-square	F Value	P	% Variance explained
HABITAT (bush vs. cave)	1	8.564780	83.0647	.000	90.62
TREATMENT (glowworms vs. control)	1	0.871215	8.4494	.005	9.22
HABITAT × TREATMENT	1	0.014810	0.0144	.707	0.16
RESIDUALS	42	0.103110			

Table 2. Invertebrates captured on all traps placed over larvae of *Arachnocampa luminosa* and over areas where larvae had been removed.

	Traps in bush with glowworms (without glowworms)			Traps in cave with glowworms (without glowworms)		
	Winter	Spring	Summer	Winter	Spring	Summer
Gastropoda	3	(1)	2	—	—	—
Isopoda	1 (1)	—	—	—	—	—
Araneae	6 (2)	18 (5)	3 (7)	(1)	(1)	—
Opiliones	(1)	—	1 (1)	—	—	—
Acarina	1 (1)	1 (2)	(1)	—	—	—
Diplopoda	1	—	(1)	—	—	—
Collembola	1 (1)	—	—	—	—	—
Orthoptera	(3)	2 (1)	2	—	—	1
Homoptera	—	—	1 (3)	—	—	—
Hemiptera	—	—	1 (1)	—	—	—
Plecoptera	—	—	—	2	—	—
Neuroptera	—	(2)	2 (1)	—	—	—
Trichoptera	—	—	1 (1)	—	1	2 (3)
Coleoptera	2	6 (1)	5 (10)	1	1	2 (2)
Hymenoptera	7 (2)	3 (4)	2	—	—	3
Diptera	123 (111)	208 (148)	121 (54)	20 (18)	29 (16)	49 (30)
Calliphoridae	—	—	—	1	—	—
Cecidomyiidae	1 (4)	—	—	4 (4)	—	—
Chironomidae	1	—	—	—	—	—
Culicidae	1	—	—	—	—	4 (1)
Dolichopodidae	18 (20)	51 (48)	42 (20)	—	—	—
Empididae	2	(1)	—	—	2	12 (22)
Heleomyzidae	10 (18)	15 (14)	3 (4)	—	—	—
Muscidae	—	(1)	—	—	—	—
Mycetophilidae	18 (21)	7 (16)	8 (1)	—	4 (7)	3
Phoridae	(1)	—	(2)	—	—	—
Psychodidae	5 (2)	21 (8)	14	—	2	(3)
Rhagionidae	—	1	—	—	—	—
Sciaridae	17 (12)	71 (41)	27 (8)	11 (13)	20 (9)	20 (4)
Simuliidae	1	—	—	—	—	1
Stratiomyidae	—	1	1 (1)	—	—	—
Tanyderidae	6 (2)	1	2 (4)	—	—	—
Teratomyzidae	—	13	8 (3)	—	—	—
Tipulidae	4 (3)	13 (11)	14 (9)	3 (1)	—	3
Trichoceridae	37 (24)	10 (5)	2 (2)	—	—	2
Unidentified	1 (5)	4 (3)	—	1	1	4
Total invertebrates	145 (122)	238 (164)	141 (80)	23 (19)	31 (17)	57 (35)
No. traps set	12 (16)	11 (10)	7 (10)	14 (15)	14 (15)	14 (15)

without glowworms but there were no significant differences among any of the other taxa caught (Fig. 5). Dipterans comprised 89% of the total catches and the most frequently caught families were, in order of numbers caught, Sciaridae, Empididae, Mycetophilidae, and Tipulidae (Fig. 5, Table 2).

Discussion

We have demonstrated that bioluminescence produced by larvae of *Arachnocampa luminosa* does attract potential prey and that most of them are small flying dipterans. We also showed that glowworms and their nests were not releasing an attractive odour because few insects were caught near the openings of the traps. In addition, we showed that there were significantly more potential prey invertebrates for glowworms in bush than in the cave. Our results may underestimate the importance of bioluminescence because the traps covering the glowworms reduced the light intensity by about 80% and because the traps

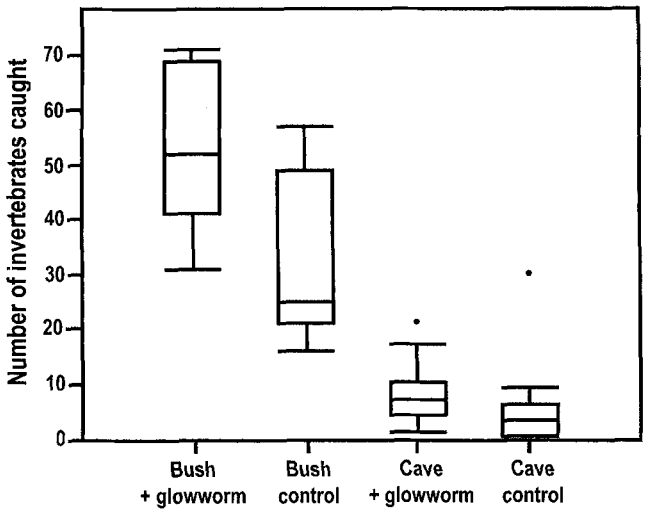

Fig. 3. Total numbers of invertebrates caught in transparent adhesive traps in Reserve Cave and in bush at the entrance to Reserve Cave, Waitomo. Traps were set over glowworms and where glowworms had been removed (control). Means, quartiles, and ranges are shown. Dots indicate outliers. The upper outlier (cave control) was due to numerous empidids (Diptera) that were caught on several control traps in Reserve Cave.

were larger than the snares of the glowworms they enclosed. Broadley (1998) used an infrared video camera and time-lapse recorder to observe a glowworm in Reserve Cave and reported no prey capture during 11 days whereas we found that glowworms there catch 1 potential prey every 19.2–36.5 days. We also found that glowworms in bush catch 1 potential prey every 2.9–5.0 days but the only other information on capture rates in bush is by Broadley (1998), who reported an actual capture rate of 1 insect every 12.8 days using infrared time-lapse video. However, his observations were made by a stream in Ruakuri Scenic Reserve, Waitomo, about 1.5 km away from the entrance to Reserve Cave, and in February and May.

It is possible that some crawling invertebrates such as millipedes escaped from the adhesive on our traps. Conversely, some that were caught on the traps might not necessarily have fallen into the glowworm snares. Non-flying invertebrates that drop into glowworm snares from above can comprise a large proportion of the invertebrates found in the snares of glowworms in bush (Norris 1894; Stringer 1967; Pugsley 1984) but most of the prey reported from glowworm snares in caves are flying insects (Richards 1960; Pugsley 1980, 1984). However, non-flying potential prey species

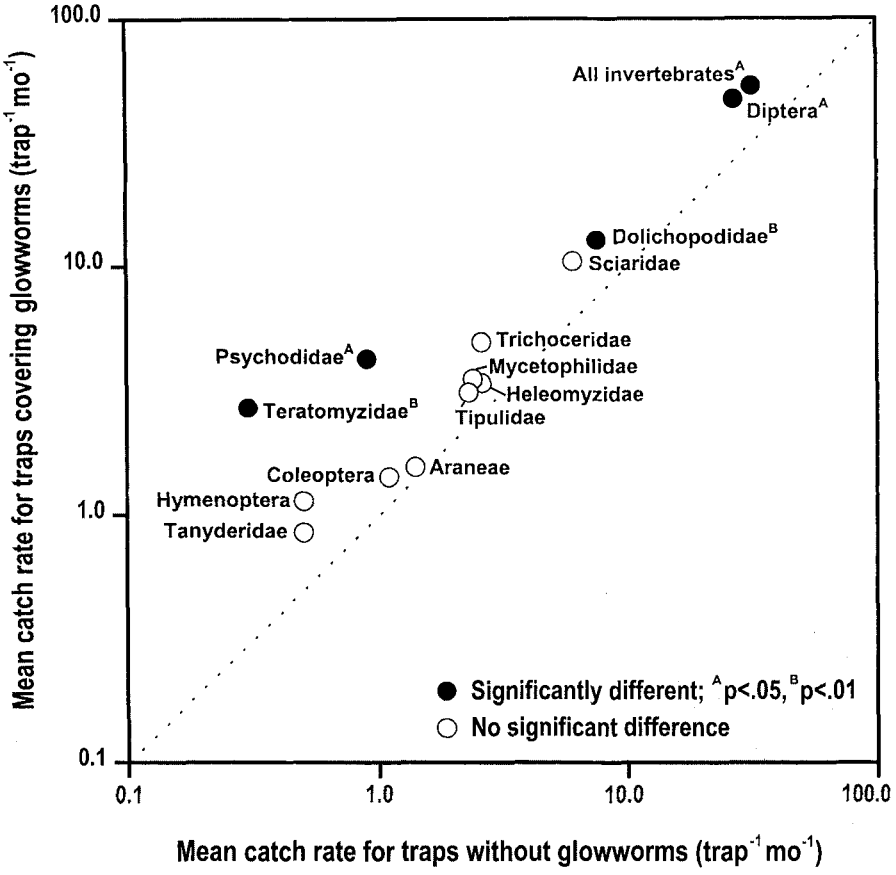

Fig. 4. Comparative catch rates of invertebrates on traps surrounding glowworms and control traps (no glowworms) in bush at the entrance to Reserve Cave, Waitomo. The dotted line indicates equal numbers of invertebrates captured on adhesive traps surrounding glowworms and control traps.

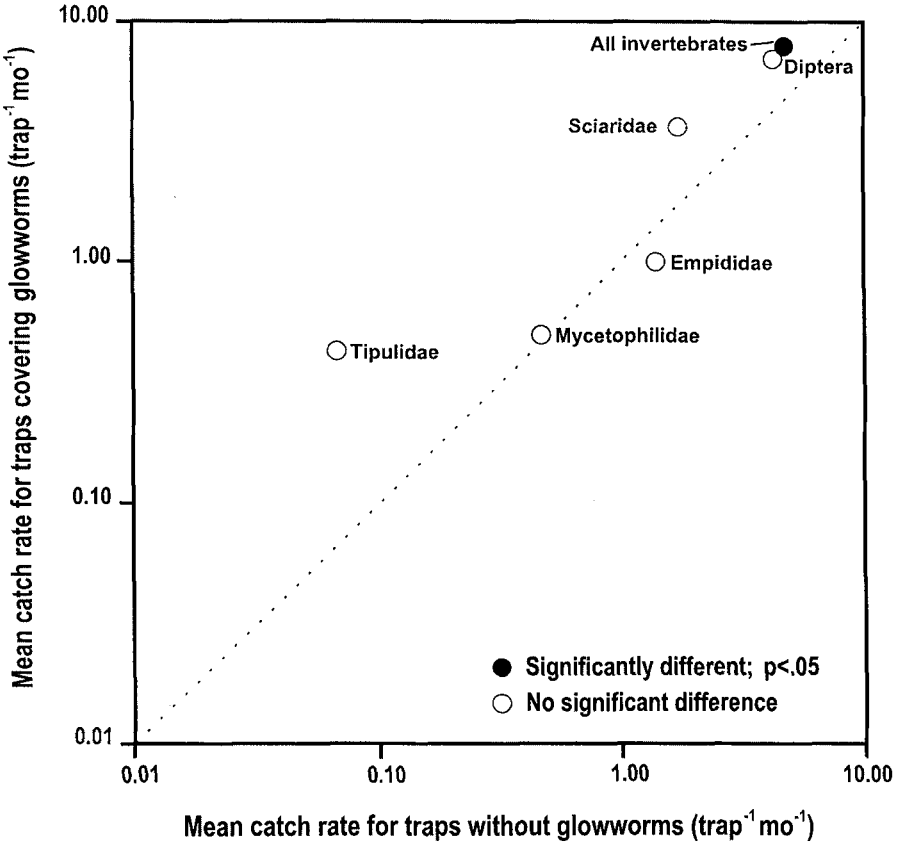

Fig. 5. Comparative catch rates of invertebrates on traps surrounding glowworms and control traps (no glowworms) in Reserve Cave, Waitomo. The dotted line indicates equal numbers of invertebrates captured on traps surrounding glowworms and control traps.

deep within caves in the Waitomo region of New Zealand are rare compared with the large numbers of adult insects that can emerge from the streams flowing through these caves (May 1963; Pugsley 1980, 1984; Oxenham 1985).

The only other experimental study of prey attraction with bioluminescent web-spinning mycetophilid larvae was that by Sivinski (1982), who studied *Orfelia fultoni* from the Appalachian Mountains of North America. The larvae of *O. fultoni* make webs over depressions in the ground that are suspended with sticky strands that trap arthropods (Fulton 1941). Sivinski (1982) used clear Petri dishes covered with adhesive and found that significantly more dipterans were caught on Petri dishes placed over larvae of *O. fultoni* than when no larvae were present. However, tipulids and wingless arthropods showed no significant attraction to bioluminescence (Sivinski 1982).

In our study in bush, spiders were the commonest non-dipterans caught on all traps, but there is no evidence that they prey upon glowworms. Broadley (1998) observed 7 instances of spiders moving through glowworm nests in Ruakuri Scenic Reserve, Waitomo, without attacking the glowworms even when 1 glowworm unsuccessfully tried to attack a spider. Harvestmen, however, do attack and eat glowworms in caves (Meyer-Rochow & Liddle 1987) although none were caught in our traps in Reserve Cave.

Spider webs were commonly observed in front of glowworm snares both by us and other authors (Meyrick 1886; Gatenby 1959; Stringer 1967). This suggests that some spiders may be attracted to the bioluminescence, make webs in front of the light, and exploit the insects that fly towards the glowworms' bioluminescence. At least 1 other orb-web spider is known to actively choose artificially lit sites for constructing its webs and exploiting the attraction of insects to the light (Heiling 1999).

Any reduction in food availability probably adversely affects the glowworms but they can apparently live long periods without food, as shown by the survival of glowworms enclosed by our adhesive traps. These must have prevented the glowworms within from capturing almost any of the available prey during the 60 to 78 days that the traps were in place. The only access was through the small opening at the lower end and it seems unlikely that many insects would fly through these unless they were attracted by an odour from the glowworms. We never observed any feces or other discarded material inside the traps that could have originated from the glowworm and this suggested they had not fed.

Significant attraction to glowworm bioluminescence could be demonstrated only for taxa caught in large numbers but it is likely that many others, such as Sciaridae, Trichoceridae, Mycetophilidae, Heleomyzidae, and Tipulidae, may be attracted to glowworm light. Meyer-Rochow & Eguchi (1984) pointed out that almost all insects have a photoreceptor containing photopigment with peak sensitivity to green light, so they can presumably detect glowworm bioluminescence, with a maximum spectral emission in the blue-green at 487 ± 5 nm (Shimomura et al. 1966). Meyer-Rochow & Eguchi (1984) also argued that this light is likely to attract many insects, especially the adults of those aquatic ones that enter caves accidentally as larvae. The adults of many aquatic insects have been reported from glowworm snares in the Waitomo area (Richards 1960; Pugsley 1980, 1984; Broadley 1998), but these were rarely caught in our traps either inside or outside Reserve Cave. However, there is no stream at the entrance to this cave and only a very small one at the trapping site inside the cave.

Adults of *A. luminosa* are a relatively rare component of the flying fauna and so it is not surprising that they were not caught on any of our adhesive traps. They can detect glowworm bioluminescence (Meyer-Rochow & Waldvogel 1979) and have occasionally been observed caught in fishing lines in other studies (Gatenby 1959; Pugsley 1984) although most manage to break free (Richards 1960). It is not known, however, whether they are attracted to the light, or whether they simply blunder into the fishing lines. Sivinski (1982) found 3 adult males of *O. fultoni* caught on traps over larvae of *O. fultoni* and 1 female was caught on a control trap. In contrast, no imagines of the non-luminescent keroplatine *Neoditomya farri* COHER were attracted to light of any wavelength in a Jamaican cave; again, adults may have been too rare to detect (Stringer & Meyer-Rochow 1994). The larvae of *N. farri* make webs with fishing lines similar to those of *A. luminosa* and obtain enough prey, despite lacking bioluminescence, because of the large numbers of flying insects in the caves they inhabit (Stringer & Meyer-Rochow 1993, 1996).

What is the function of bioluminescence in the pupa and adult of *A. luminosa*? Meyer-Rochow & Eguchi (1984) suggested that it could keep the cannibalistic larvae away from the pupae by maintaining larval spacing. The adults have small mouthparts unsuited to predation and apparently do not eat (Richards 1960; Harrison 1961). Because mature female pupae often glow before adult males alight on them, some authors have speculated that their bioluminescence aids sexual attraction (Richards 1960; Meyer-Rochow & Waldvogel 1979; Meyer-Rochow & Eguchi 1984; Meyer-Rochow 1990). However, we have seen males alight on female pupae that were not glowing and immature male and female pupae also produce light intermittently (Richards 1960) so it seems likely that other cues are involved in mate attraction. Furthermore, as Gatenby (1959) suggested, if bioluminescence alone attracts males to females, then males could be confused by the lights of larvae, which are usually much more numerous than pupae. The Malpighian tubules of Diptera are not affected by metamorphosis (Locke 1985) so it is not surprising that the distal tips in glowworms, which are the light producing organs, differ little between larvae, pupae, and adults (Ganguly 1960; Green 1979). It may be that bioluminescence serves no function in the pupae and adults of *A. luminosa* but is simply inherited, together with the Malpighian tubules, from the larvae.

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