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THE LARVAL BEHAVIOUR OF THE NEW ZEALAND GLOW-WORM *ARACHNOCAMPA LUMINOSA*

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INTRODUCTION

The New Zealand glow-worm, *Arachnocampa luminosa* (Skuse 1890), is a member of an Australasian species or closely related group of species placed in the sub-family Ceroplatinae (Diptera, Mycetophilidae). Although variations in size and wing venation of the adult exist between different populations these differences are considered to be intraspecific, so that *Arachnocampa luminosa* is the only known representative from New Zealand. It is widespread throughout the country, occurring in caves, tunnels, and in the bush.

MATERIALS AND METHODS

A preliminary study of *A. luminosa* was carried out on bush specimens from the Waitakere Ranges but the area of study was later changed to the headwaters of the Kauri Park stream at Birkdale (Devonport) following the discovery of a small but accessible population there. Three trips were also made to Waipu Cave, situated 83 miles north of Auckland, in order to study cave specimens.

Cave and bush forms were also studied in captivity where they were kept separately in two plaster-of-paris 'caves' constructed in a completely dark compartment of an underhouse. The plaster caves were sealed with sheet plastic to prevent loss of moisture and each contained a small pool. In front of each cave was a hinged observation window, and in one side a plastic stoppered tube for the introduction of live food consisting of *Drosophila* and psychodids. Condensation on the observation windows was almost eliminated by using double sheets of clear plastic and 'Anti-Mist'.

Working with glow-worms presented difficulties as they are nocturnal and easily disturbed; however, it was found that a dim red light usually allowed up to five minutes observation, during which the larvae seemed to be little affected.

HABITAT

Glow-worms are found in damp caves, in the bush and in tunnels where each constructs itself a nest under an overhanging surface.

Richards (1960) described the cave environment of Waitomo. The caves and tunnels where they occur are always wet, and in them the larvae

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build nests on both wet and dry surfaces. "The relative humidity ranges from 94% to 100%, but is usually 97%..." (Richards 1956).

Bush glow-worms are usually found under banks, but they also build under large roots, fern fronds, or log bridges. The localities where they are found are sheltered and protected from the wind which would tangle their 'fishing-lines'. Shade provided by the bush maintains the necessary high humidity. In flat country they occur near streams because of the available moisture, but in hilly or mountainous districts they are found in suitable places which remain damp throughout the year. Sometimes they are to be found on roadside cuttings, although they avoid places illuminated by road lights.

STRUCTURE OF THE NEST

The larva lives in a nest made from its own clear secretions (Fig. 1). Each nest consists of a long tubular gallery suspended from the substrate by an irregular web of fine branching threads. Vertical threads with evenly spaced sticky droplets hang from the web to form the snare. The name *Arachnocampa* was propounded by Edwards (1924) because of the "Spider-like habits of the larva, forming webs and using them for the capture of insect prey".

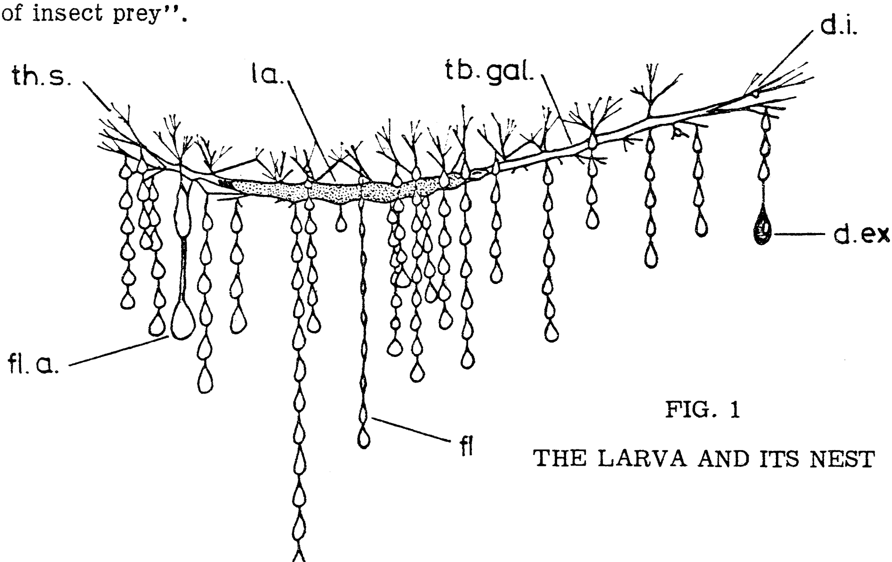

FIG. 1

THE LARVA AND ITS NEST

Legend:

d.i.	Droplet caught on intersecting threads
d.ex.	excretory droplet
fl.	fishing-line
fl.a.	accumulation of hauled up fishing-line
la.	larva
tb.gal.	tubular gallery
th.s.	suspendory threads

The nest is about two or three times as long as the larva. In the bush one end is generally bent into a crevice (where the larva hides during the day), but in caves or tunnels where it is always dark the nest remains fully exposed. The gallery, which is usually unbranched, consists of an elastic tube of silk filled with mucus, through which the larva 'glides'. Unoccupied parts of this gallery contract slightly because of their elastic nature.

The fishing-lines usually hang from points of intersection on the web. The droplets are about 0.5 mm in diameter and about 0.5 mm apart, but there can be considerable variation. Droplets dried on glass are not very hygroscopic and take about two days to reform in saturated air (100% humidity).

In cave forms "a larva lets down up to 70 strings of sticky droplets. Depending on the size of the larva, the fishing-lines ... vary in length from under 1 cm to 50 cm" (Richards 1960), but in the bush the fishing-lines seldom exceed 10 cm in length because of the wind, vegetation, and other obstacles. These conditions also limit the number of fishing-lines which are seldom as dense as in caves.

CONSTRUCTION OF THE GALLERY AND WEB

The gallery and web can be considered as an elaboration of the larva's method of travelling.

A glow-worm is seldom found out of its gallery in which it lives (on its back) but it frequently adjusts the position of its nest by forming new parts and leaving others. More rarely, a larva will move to a new site altogether. If a larva is removed from its nest its reaction is to suspend itself as soon as possible by threads. These threads are attached to an enveloping tube of silk which the larva continuously secretes from its mouth, whether it is moving on the ground or suspended. There is no apparent process by which this tube of silk is formed. It appears as the larva moves forward within it, and is left behind rather like a snail's trail.

The method of progression is shown diagramatically in Fig. 2a. When the larva is advancing, the front part of the worm is arched forwards and moved around until the head touches the ground, where it rests momentarily. The head is then withdrawn leaving the thread of silk. When the thread is of sufficient length, two or three peristaltic waves are passed forward over the anterior two segments, ending each time in the partial withdrawal of the head into the body. During this process the thread is passed back on to the tube. The larva then makes a thread on the opposite side and moves forward. When it is on the ground it progresses in the same way. The larva

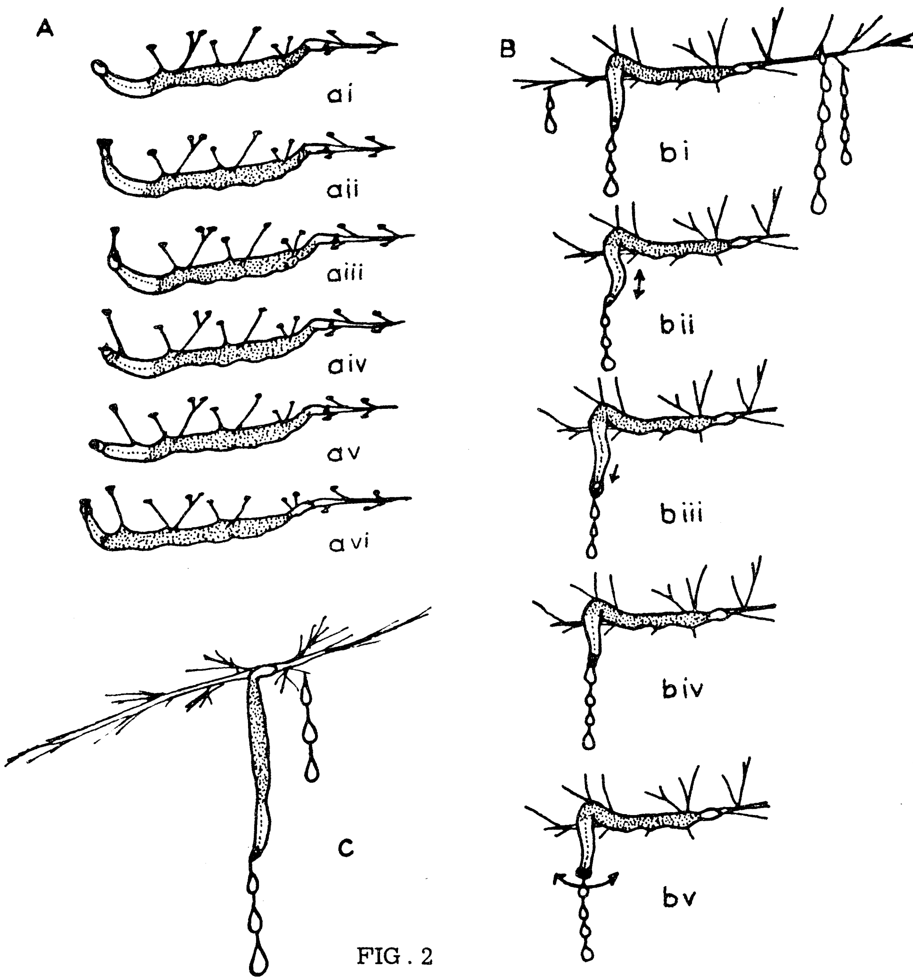

FIG. 2

A. METHOD OF PROGRESSION

a i Larva arches front forward and searches for the substrate
a ii Larva touches head to substrate and rests momentarily
a iii Larva withdraws its head forming the thread
a iv During peristalsis the thread is passed back onto the tube.
a v Corresponding to a i, but making thread on opposite side.
a vi Corresponding to a ii, on opposite side.

B. FORMATION OF THE FISHING - LINE

b i Larva hangs anterior third of body down.
b ii Three peristaltic waves are passed over the part of the body between the head and the junction of the hepatic caecae.
b iii Mucus can be seen accumulating around the head during peristalsis.
b iv On the last peristalsis the head is slightly withdrawn and the droplet forms.
b v The head is then moved up and down during which the droplet is hung from the thread.

C. SMALL LARVA HANGING

arrives beneath an overhanging surface and the threads then suspend the insect as it proceeds, leaving behind the suspended tube. If one of the suspending threads breaks, the animal reacts by applying the anterior portion of its body on to the substrate, to which it sticks, and then suspending itself again.

When the glow-worm has found a suitable position for its nest it goes up and down that portion of the tube (now the gallery) adding to the suspending threads to form the web. It can break through the tube at any point with a quick biting movement to make these additional supports.

FORMATION OF THE SNARE

A larva usually makes its fishing-line after the web is completed, but they are also made on rare occasions when the larva is still searching for the nest site or even while the web is being strengthened. A bush larva will rest up to two days before beginning the snare, and, once made, the wind is constantly entangling the lines causing the larva to repair them.

Fishing-lines are hung from the web by the larva's moving a short distance outside the gallery but a few are hung from the gallery. When constructing a fishing-line the larva hangs the anterior third of its body vertically downwards (Fig. 2b). Small larvae lower more of their body; sometimes all but the last segment (Fig. 2c). A large peristaltic wave (in the region between the head and the junction of the hepatic caecae of the gut) moves back and forward three times, during which mucus can be seen to accumulate around the head. With the last peristalsis the head is slightly withdrawn into the body and the droplet appears. The head is then rocked up and down five times while the jaws are opened and shut, during which the droplet is lowered on its thread. The average larva rhythmically produces a droplet every 15 to 18 seconds, but in lowered humidity (about 80%) a glow-worm takes longer (up to six peristaltic cycles).

The first droplet on the end of the line is always the largest; it needs the greatest effort to produce, taking up to 10 peristalses, which suggests the weight of the hanging line adds in the formation of the following droplets by pulling them from the larva.

"Formation of fishing-lines is a continuous process in which the larva moves along the nest gradually increasing the length of each fishing-line." (Richards 1960). Bush forms restrict their activities to dusk and night time, and they usually form complete fishing-lines (as they are usually restricted in length) although they can add to them later or move them to other positions.

USE OF THE NEST

Bush worms are nocturnal and during the day they are usually found in that part of the nest built into a crevice or hole. Even a very small hole (in which only the head of the larva is hidden) is sufficient.

Sometimes nests are found in open places without crevices to build into, and here a larva either lies extended and still in the gallery throughout the day, or more often bends the front of its body up and out of the gallery, where the head hangs from the substrate by a short thread. While the larva is resting in one of these positions, the jaws move every few minutes and a drop of mucus is exuded which slips back down the larva to the gallery, but sometimes these drops are retained on the web (Fig. 1).

In late afternoon the glow-worms come out and lie in their galleries to await dusk when they begin the night's activities of rebuilding nests and snares, and capturing prey.

LOCOMOTION

Since the larva is always within its tube, it moves in the same way whether suspended or on the ground.

During forward movement,successive waves of linear contraction move anteriorly in the body wall. These waves are not accompanied by any constriction and usually only one is present at a time, although the following wave may start as the preceeding wave is finishing. Ventral bands of minute bristles arranged intersegmentally down the length of the body give it purchase on the enveloping tube, while haemocoelic pressure re-extends it as the wave passes on.

If alarmed the larva can move backwards for a short distance by reversing the waves of contraction, but it normally turns around within its tube (Fig. 3b) by folding back upon itself.

CAPTURE OF PREY

The carnivorous glow-worm attracts its prey (consisting mainly of insects) by its light. When the prey becomes entangled in the snare it is pulled up and eaten.

A bush glow-worm glows brighter as soon as anything is caught in the snare and proceeds, hesitantly, to the fishing-line concerned. It seldom goes to the wrong line, but if it does it quickly corrects itself. When it has the right fishing-line it rapidly crawls down until only its posterior half is left on the web (Fig. 3c). Then it hauls up the line by vigorous

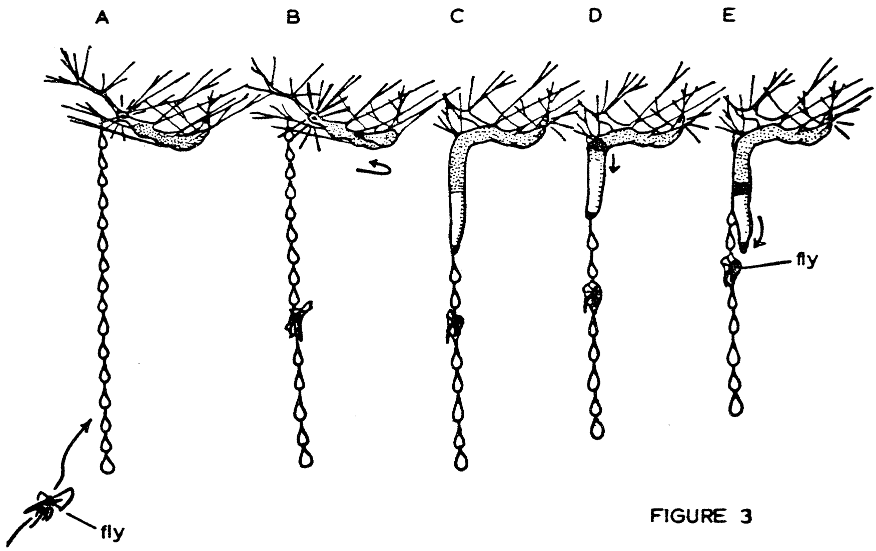

FIGURE 3

A. Fly is attracted to the fishing-line by glowing larva
B. Fly becomes entangled and glow-worm turns around to find the snare
C. Glow-worm crawls down the fishing-line
D. Initial contraction lifts the rest of the body and line, then it continues forward until
E. The larva arches the front of its body over the next 2 or 3 droplets: then the process is repeated until it reaches the fly
(Contractive wave shown as band)

peristalsis which travels anteriorly, and is the same as the locomotive waves, except they are confined to the part of the body down the fishing-line. The peristalsis starts with a sudden contractive jerk in the region where the body leaves the web, and this raises the hanging portion of the body along with the fishing-line. The peristalsis continues towards the head, and, as it terminates, the larva arches its head region forward, relowering its body over the next two or three droplets. The complete cycle takes little more than a second, and by this method large larvae haul up the line at an average rate of about 0.2 cm/sec. The hauled up fishing-line accumulates in the region of the initial contraction which does the actual hauling up.

Movement of the mandibles can be seen, and on careful observation it appears that the larva grasps the line with them, often after the initial contraction has raised the line, then opens them to arch the head forward.

The fishing-line thread travels up the ventral surface of the larva where it is held by the anterior bands of bristles, enabling the line to be raised in the initial contraction. Since the bristles are ventral and band the posterior two thirds of the larva's body this accounts for the larva's hanging half of its body down. Close attention was paid to the possibility of the thread being swallowed, but typically the head region is arched over the droplets while the thread accumulates as a ventral mass, as already described. Glow-worms do not crawl down to their prey (as suggested by Gatenby 1960), although small worms can crawl up fishing-lines if placed on them, but the weight of a large worm breaks the line.

When the larva reaches its prey it becomes cautious and often withdraws a few times before finally hooking its head under it, and biting. The animal usually ceases struggling soon after it is caught on the line, although it is not dead. It often recommences struggling when it is bitten and dies fairly quickly. Often before biting the prey the larva drags it up by by a series of jerks back into the mass of accumulated fishing-line, which serves to dampen the prey's activity if it is large, making biting easier.

If there is abundant prey, the larva sucks out the juices. If more than one insect is caught at a time, the larva lowers them by short threads from the web for storage. When prey is less plentiful (usual case), the larva sucks it then chews it up and swallows it, but if the prey is large it eats it by instalments, keeping the uneaten portion lowered as before, between feeds.

The fate of the fishing-line after it has been hauled up is not known, although it is often left as a large irregular drop (Fig. 1) for up to two days before it "disappears".

In the laboratory the glow-worms were fed on *Drosophila* and psychodids for convenience, although they could handle most insects collected around a light bulb, as the larger insects became entangled with several threads.

In glow-worms' nests at Kauri Park about half the food found were red ants, while the next most plentiful were large tipulids and amphipods. Other prey included small nemotoceran flies, millipedes and (small) land snails. However, it was quite common to find nothing in these snares at all, and most prey found was dead and hanging from short threads.

The capture of non-flying prey becomes important when spiders, by building their webs in front of the glow-worms' snare (as they often do), shield it from flying insects. A partial explanation of how this sort of prey is trapped could come from the following observations. When something crawling towards the light touches a supporting thread of the web, the larva glows brilliantly, and this has been observed to cause some forms to jump, fly, or drop and get caught. This is particularly effective in the case of day-flying insects which, at night, often crawl towards the light. Millipedes, snails and ants probably crawl above the nest and fall on to the gallery (which effectively snares any ants placed on it).

In Waipu Cave the troglophytic chironomids *Chironomus zelandicus*, *Polypedilum opinus* and *Anatopynia languidus*, and trogloxenes including tipulids, moths and adults of aquatic insects have been found snared in the fishing-lines.

The larva is cannibalistic on both pupae and other larvae. During this study no fighting or predation on other larvae was observed, but Richards (1960) describes this.

When eating a pupa, the larva extends its nest up to it and then climbs down the suspended pupa. The preying larva appears to suck out portions of its victim, returning to its gallery for long rests between feeds. The pupa, which may last the larva several days, glows as it is eaten. Richards (1960) states that "Occasionally the adult fly is caught in larval fishing-lines, drawn up and eaten by the larva, but most of the flies caught manage to break free."

SANITATION OF THE NEST

"After eating, the larva removes the remains of its meal from the nest, so that the fishing-lines are kept clean and in good repair for catching further prey," (Richards 1960). The remains are contained in a droplet and lowered on a thread until it either breaks or is dropped.

The larva defaecates by lowering the posterior half of its body down a thread or fishing-line and making a large 'excretory' droplet. It then crawls back into the gallery, turns around and lowers the thread with the excretory droplet before dropping it. Occasionally, while lowering an 'excretory' droplet or the remains of its food, the larva "forgets itself" and starts making a fishing-line. This accounts for "rejected" droplets occasionally found incorporated into fishing-lines.

The larvae are extremely sensitive and are easily disturbed during defaecation and detailed observation of it has so far been impossible.

LUMINESCENCE

The light from the glow-worm is emitted from the posterior segment, which "is a gelatinous and semi-transparent structure, capable of a great diversity of form" (Hudson 1890), and it was established by Wheeler and Williams in 1915 that the light organ consisted of the swollen ends of the four malphighian tubules.

When both bush and cave larvae are disturbed they fade off their lights for one or two minutes, although they can be dimmed quickly by the withdrawal of the photogenic organ from the terminal segment into the adjacent region containing fat body which partially shields the light. Bush specimens often give the appearance of suddenly dousing their lights when they retire quickly into their retreats.

Dr A.M. Richards, who daily observed the Waitomo Cave glow-worms for most of 1955, stated that "the larvae are capable of glowing 24 hours of the day when in the dark, but usually they do not glow in daylight." She also noted that "(in) the tunnel area of the Grotto very few glow-worms turn their lights on in the daytime, the few observed to do so being restricted to the areas with a light intensity of 0.5 f.c. or less". At dusk in Kauri Park the glow-worms wait until the reflected light intensity reaches about one foot candle when the first larvae begin to glow. They continue to glow erratically until the reflected light intensity goes down to 0.1 to 0.05 foot candle when the number of glow-worms glowing begins to increase rapidly. Dense cloud lowers the light intensity sooner at dusk, and this causes the glow-worms to start glowing earlier. At dawn the glow-worms start dousing their lights when the reflected light intensity reaches 0.1 to 0.3 f.c. They all stop glowing when the intensity rises to about 1 f.c.

The intensity of the light emitted from a glow-worm does depend upon the size of the specimen, although there is variation.

A closely related species of fly to the glow-worm, *Platyura fultoni* (sub-family Ceroplatinae), from North Carolina shows a diurnal rhythm of luminescence when placed in continual darkness, however *A. luminosa* does not appear to show a diurnal rhythm.

While the larva lies in its gallery it changes its position from time to time. Sometimes a larva will stop glowing for a period but why they do this is not clear since they have been observed glowing while forming fishing-lines, eating, defaecating, and while repairing their nests.

SUMMARY

1. Bush and cave glow-worms show similar behaviour when constructing nests and snares, hauling up prey, and removing waste from their nests.
2. The larva always moves within a secreted tube anchored by threads and the nest is made by elaborating this.
3. The production of fishing-lines involves the formation of the thread and the rhythmical ejection of mucus droplets onto the thread as it is lowered from the mouth of the larva. During this process the anterior half of the larva hangs vertically from its nest.
4. In the bush, food consists mainly of small crawling Arthropoda and when

prey is caught the fishing-line is hauled up by muscular body movements; the prey is then eaten.

5. Faecal material and food remains are dropped from the nest to keep it clean. Each globule of waste is first lowered on a short thread produced from the mouth of the larva. These threads are identical to those in the fishing-lines.
6. Glow-worms are nocturnal, and in the bush the level of light intensity appears to be the factor determining whether they luminesce or not.
7. Bush glow-worms do not retain any diurnal rhythm when kept in darkness.

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