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The Life History of Some Species of Rhaphidophoridae (Orthoptera)

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Abstract

THE complete life cycle of *Pachyrhamma waitomoensis* takes a little over two years: about seven months being required for the development of the egg; 15 to 16 months for the nymphal instars; and between five and ten months for the adults. Most nymphs hatch in November and December, and adults mature in January. *Pallidoplectron turneri*, unlike *P. waitomoensis*, continues to breed and mature throughout the year. About eight months are required between laying and hatching of the eggs; but the length of nymphal and adult life is very difficult to assess. Indications are that the life cycle was once clearly demarcated, but with adaptation to cave life this has gradually been lost. The adult sex ratio for both species is unequal, more females being present in the population than males. Mating may occur throughout 24 hours of the day. It has been observed throughout the year with *P. turneri*, but with *P. waitomoensis* only between January and September. After the final ecdysis of female *P. waitomoensis* in January and early February, several weeks are required for maturation of the gonads, and mating does not reach its peak until April. Throughout the whole period males and females alike mate with various members of the opposite sex, and there is no regular period between each mating. Although two insects may stay together in the preliminary mating attitude for several hours, copulation is of short duration, and only one spermatophore is produced. Females of *P. waitomoensis* and *P. turneri* oviposit in the soft mud on the walls inside the caves, but the actual process has been observed only for *P. turneri*. Palps and ovipositor are used to find a suitable spot, as the correct texture and depth of mud are a prerequisite for egg-laying, and many areas are tested before one is selected. Only one egg is deposited at each insertion, and usually only one or two eggs at the most are laid in any particular spot. All freshly made ovipositor holes are surrounded with a little ring of mud. The same area of mud is often used over and over again by different females, as examination of mud usually reveals eggs in different stages of development. In both species oviposition reaches its peak between April and June,

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with hatching reaching its peak in December for *P. waitomoensis*, and in January for *P. turneri*. The process of ecdysis is similar to that observed in other Orthopterous insects, but the colour pigment is always present in the exuvia. The number of instars represented in *P. waitomoensis* and *P. turneri* have not so far been determined. In *P. fascifer* seven pre-adult instars are passed through by females and nine by males. By comparison of these results with the instars examined in *P. waitomoensis*, the two species seem to conform to a fairly similar pattern. In *P. fascifer* the period of greatest activity extends between October and April, there being no growth over the winter months, and two generations are nearly always present in a population. By applying Dyar's Law, it has been proved that no instars have been overlooked. In general, however, it appears from these and Hubbell's (1936) observations that in the Rhaphidophoridae the number of instars is variable both inter- and intraspecifically.

INTRODUCTION

RHAPHIDOPHORIDS, or cave-wetas, are a family of Orthoptera. Up till 1955 the life history and behaviour of these insects in New Zealand had not been studied. They are particularly well represented in New Zealand, where they occur throughout the whole country, especially in limestone regions and greywacke tunnels. Many species occur in native bush, where they live in rotten logs and under bark and stones; while others inhabit the old, damp, deserted burrows of petrels and tuataras on a number of islands off the coast of New Zealand. They require environmental conditions of almost complete darkness, cool temperature and high humidity, and are commonly found fairly near the entrances of caves, often hidden in groups behind projecting rocks, or in crevices. Usually the nymphs congregate nearer the mouth of the cave than the adults. Because of their nocturnal habits, these insects are very difficult to observe under natural conditions. The two principal species discussed in this paper, *Pachyrhamma waitomoensis* Richards and *Pallidoplectron turneri* Richards, occur in the limestone caves at Waitomo (Richards, 1958); *Pachyrhamma fascifer* (Walker) occurs in greywacke tunnels and limestone caves in Hawke's Bay, Wairarapa, Wellington, Marlborough and Nelson (Richards, 1954). Similar findings to those recorded in this paper were observed in 1958 by the author with two other species of Rhaphidophoridae, *Pachyrhamma fusca* Richards and *P. uncata* Richards, in the gold mines at Thames. No information is available so far about the life history of bush-dwelling Rhaphidophoridae.

POPULATION ANALYSIS

Nymphs form the largest portion of any rhaphidophorid population. In Aranui Cave the number of adults and half-grown nymphs of *Pachyrhamma waitomoensis* observed from February to October, 1955, is given in Table I. From November to the end of February, 1956, the population could be divided into three groups: newly hatched and small nymphs, large and penultimate instar nymphs, and adult insects. For November, the average ratio of small nymphs to large nymphs to adults was 1.3% to 96.1% to 2.6%. For January, the ratio was 12.7% to 78.6% to 8.7%. The January results show that both small nymphs and adults were increasing in numbers in the cave. By the end of February, no newly-hatched or large nymphs were observed and the pattern reverted to two groups: adults and half-grown nymphs.

In Waitomo Cave, in April and May, 1955, the number of adults and nymphs of *Pallidoplectron turneri* is given in Table II. Floods throughout the greater part of the rest of 1955 prevented further results being obtained.

DEVELOPMENTAL PERIOD AND LIFE SPAN

In early November, 1954, the *Pachyrhamma waitomoensis* population in Aranui Cave consisted of nymphs in the second and penultimate instars. Adult *P. waitomoensis* were observed from January to November, 1955. From the middle of February onwards, no penultimate instar nymphs were seen, from which it is assumed that

TABLE I.—POPULATION ANALYSIS OF *PACHYRHAMMA WAITOMOENSIS* IN ARANUI CAVE, FEBRUARY TO OCTOBER, 1955.

Date	Time	Total Population	Adults as % of Total Population	Nymphs as % of Total Population
8 Feb.	11.30 p.m.	97	20.6	79.4
10 Feb.	2.30 p.m.	82	14.6	85.4
23 Feb.	2.30 p.m.	97	18.6	81.4
27 May	10.0 p.m.	104	19.6	80.4
15 June	2.30 p.m.	129	12.4	87.6
29 June	3.0 p.m.	76	3.9	96.1
11 Aug.	2.30 p.m.	58	13.8	86.2
15 Sept.	9.30 a.m.	160	2.5	97.5
7 Oct.	3.0 p.m.	132	1.5	98.5
16 Oct.	9.30 a.m.	129	0.8	99.2

TABLE II.—POPULATION ANALYSIS OF *PALLIDOPLECTRON TURNERI* IN GROTTO OF WAITOMO CAVE, APRIL TO MAY, 1955.

Date	Time	Total Population	Adults as % of Total Population	Nymphs as % of Total Population
8 Apr.	10.0 p.m.	190	28.1	71.9
11 Apr.	9.0 p.m.	294	30.3	69.7
13 Apr.	9.0 p.m.	227	36.1	63.9
15 Apr.	9.30 p.m.	290	24.2	75.8
17 Apr.	10.0 p.m.	123	29.3	70.7
20 Apr.	10.0 p.m.	130	31.5	68.5
22 Apr.	10.30 p.m.	185	22.2	77.8
26 Apr.	10.30 p.m.	221	21.1	78.9
28 May	11.0 p.m.	131	11.4	88.6

the adult population was relatively stable over the whole of this period. In May, 34 adults were marked with coloured paint, and one of these was still recognizable in early October. From January to the end of May, the adult population averaged 20 insects at any one time; but from June onwards the numbers gradually decreased and dead wetas were often seen. By January, 1956, the penultimate instar nymphs were changing into adults to repeat the cycle. From this it is estimated that the average adult life span of *P. waitomoensis* is five or six months and the maximum span nine months.

Observations have shown that the period from egg-laying to hatching extends over six to seven months; the duration of time spent in nymphal instars covers from 15 to 16 months; and the length of time as adults varies from five or six to nine or ten months. Thus the complete life cycle from oviposition to death takes a little over two years, or nearly two years from hatching to death.

Pallidoplectron turneri does not have a seasonal life cycle, but continues to breed and mature throughout the whole year, so that all instars can always be seen in the cave. This has so far made the assessment of length of nymphal and adult life very difficult.

Sex Ratio of Adults

From 17th May to 29th November, 1955, a record was kept of the total adult *Pachyrhamma waitomoensis* population seen in Aranui Cave. Over this period 63 marked individuals were observed, 36 (57%) being males and 27 (43%) females. In January, 1956, the observed population consisted of 93 (61%) females and 60 (39%) males. These were based on single sightings, since individuals were not marked. These observations indicate that the sex ratio is unequal, more females being present in the population than males. Owing to the egg-laying habits of the females from April to July, and their constant frequenting of inaccessible cracks and crannies in the limestone, it is to be expected that the proportion of males visible during that period might slightly exceed that of females.

Similar observations on *Pallidoplectron turneri* in the Grotto of Waitomo Cave could not be made because of the Waitomo Stream flooding the cave during the greater part of this period.

Courtship

Courtship follows the same pattern as that most often observed among the Orthoptera. It consists of the two insects facing each other and fencing with their antennae.

Mating Behaviour

Observations were made to ascertain:

(1) If Rhaphidophoridae have a marked diurnal rhythm.
(2) If mating times could be related to a particular time of day.

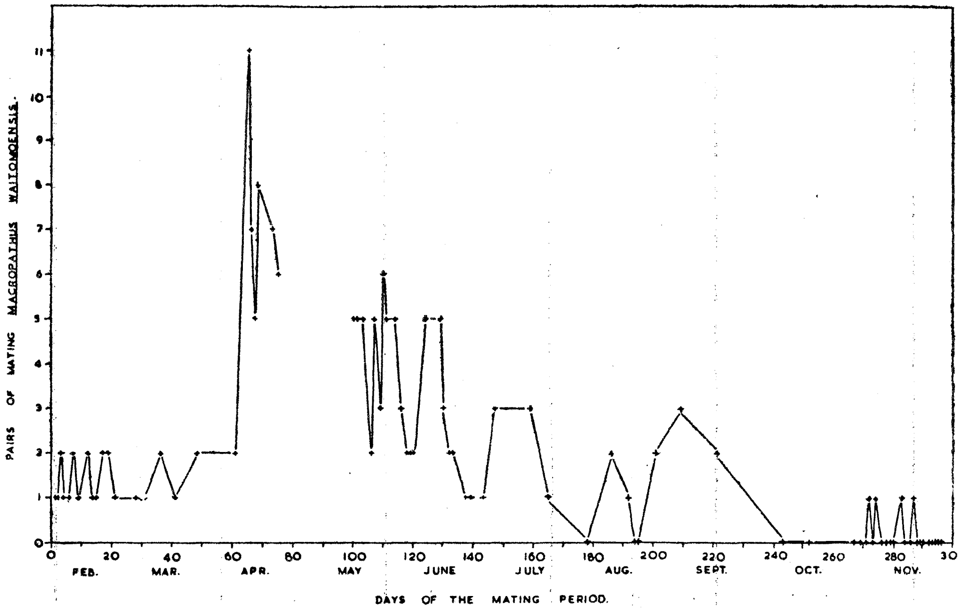
As Rhaphidophorids are nocturnal in their habits, it was expected that mating would take place at night only. However, results showed that mating could not be related to any particular time, and that there was no diurnal rhythm. No matter when the caves were visited, one or two pairs were always seen, nor did there tend to be any increase in the number of mating pairs at a particular time of day.

With *Pallidoplectron turneri,* in the constant conditions met with in the Grotto of Waitomo Cave, the mating period extends over the whole year, six or more mating pairs usually being observed. There was no evidence of an increase in this number during certain months of the year, although from November to January the numbers did drop sometimes to one or two pairs.

Pachyrhamma waitomoensis does not penetrate as far into the caves as *P. turneri,* and so is more subject to the effects of seasonal periodicity. Adults occurred in Aranui Cave from January to November, 1955. In January, 1956, a constant check was kept on the number of *P. waitomoensis* reaching maturity. Very few adults were observed at the beginning of the month; but they increased in number during the latter half of the month. Mating was recorded on 18th, 20th, 22nd and 23rd. Mating does not take place immediately the final ecdysis is completed. A maturation period of several weeks has to elapse before the gonads fully mature. In several cases females observed mating were collected, and when their gonads were examined no eggs had developed. In February and March, 1955, one or two pairs of mating *P. waitomoensis* could usually be observed. In the middle of April mating reached its peak, when up to 11 pairs could be observed. During May and the first half of June five or six pairs were common. From then on mating decreased to two or three pairs seen at irregular intervals until September, when it stopped completely (Text-fig. 1). In November, a pair of wetas was observed to mate on four occasions. This, however, was irregular, and cannot be included in the normal pattern.

Thus mating extends over eight months of the year, the period of greatest activity being reached during the third and fourth months from commencement.

In 1931, Remy concluded that the reproductive period of European troglophile Rhaphidophorids living in the midst of very constant conditions extends over the greater part of the year; but no regular observations were made to confirm this. Thus these results are the first conclusive evidence in support of this statement, which it seems may apply to cave-dwelling members of the family in different parts of the world.



TEXT-FIG. 1.—Frequency of mating of *Pachyrhamma waitomoensis* in Aranui Cave between February 7 and November 30, 1955.

In May, 1955, 34 *P. waitomoensis,* 19 males and 15 females, were individually marked with coloured paint. The movements and behaviour of these wetas were recorded over a seven weeks' period till the end of June (Table III). During the whole of this period *P. waitomoensis* mated haphazardly. There was no permanent pairing off among them nor a single mating, but males and females alike mated several times with various members of the opposite sex. Mating several

TABLE III.—*PACHYRHAMMA WAITOMOENSIS* MATING IN ARANUI CAVE, MAY AND JUNE, 1955.

Sex and Colour of Weta.	Number of Times Seen	Number of Times Seen Mating.	Number of Different ♂s or ♀s Mated with.	Number of Times Same ♂ or ♀ Mated with.
♂ R	6	4	3	2
♀ R	6	5	4	2
♂ B	2	1	1	1
♀ B	2	2	2	1
♂ Y	6	2	2	1
♂ W	13	10	6	2, 4
♂ WW	13	10	7	4
♀ WW	1	1	1	1
♂ P	7	4	4	1
♀ P	8	8	7	2
♂ RR	21	6	5	2
♀ RR	4	3	2	2
♂ G	5	1	1	1
♀ G	2	2	2	1
♂ BB	7	1	1	1
♀ W	4	2	2	1
♂ GG	5	4	4	1
♀ GG	3	2	2	1
♂ YY	2	0	0	0
♀ Y	12	8	4	4, 2
♂ WWW	5	1	1	1
♂ BBB	2	0	0	0
♂ PP	6	3	2	2
♀ YY	8	6	3	4
♂ YYY	8	7	6	2
♀ YYY	2	1	1	1
♀ PPP	3	3	2	2
♂ PPP	5	2	2	1
♂ GGG	2	1	1	1
♀ BB	7	1	1	1
♂ SY	7	3	3	1
♀ SY	7	3	3	1
♀ PP	1	0	0	0

B, BB, BBB—Blue.
P, PP, PPP—Pink.
SY—Silver and Yellow.
Y, YY, YYY—Yellow.
G, GG, GGG—Green.
R, RR—Red.
W, WW, WWW—White.

times with the same weta was due to chance, as the wetas continually moved about on the walls of the cave in search of a mate. There was no regular period between each mating, it varying from a few hours to up to a fortnight or longer. The period of copulation was short, being only two or three minutes in duration, but the same wetas sometimes copulated several times in one day. It is improbable that females always laid their eggs between each mating. In the laboratory, although mating occurred very frequently, eggs were seldom laid. The female would lay eggs only when the right conditions were available. The protracted mating period is probably due to the long life of the adults, and this may govern the egg-laying behaviour of females, very few eggs being laid on any particular occasion. According to Chopard (1938), in the majority of cases matings are repeated among Orthoptera; Gryllids, Mantids, Phasmids and Acridids all copulate numerous times, but Gryllacrids are not mentioned. This behaviour may not have been observed before among members of that group. The mating of penultimate instar males of *P. waitomoensis* with adult females is recorded for the first time among the Gryllacridoidea.

Most Rhaphidophorids which have been studied in other parts of the world possess abdominal glands known as " alluring glands " or " Glands of Hancock ". These glands are found only in the males, and play an important role in bringing together the sexes in the darkness. The glands each consist of a small exertile organ, which can be made to project from the membrane uniting two abdominal tergites. These glands have not been observed in any species of New Zealand Rhaphidophoridae studied by the author. Copulation and the preliminary mating stage have been observed on numerous occasions, both in the field and in the laboratory, but females have never shown any interest in, or desire to lick the abdominal terga of males.

The characteristic preliminary mating attitude in New Zealand Rhaphidophorids is for the female to sit between the hind legs of the male, with the fore and middle legs of both insects interwoven. The two insects may stay together in this position for several hours without copulation taking place. When it does the male slides its body back under that of the female. The end of the male's abdomen is turned dorsally, and the female's abdomen bends ventrally. The subgenital plate of the female is grasped and reflected by the parameres so that the penis can enter the copulatory chamber. This process is very different from that of *Ceuthophilus* Scudder as described by C. L. Turner (1916). He described the two insects as facing in opposite directions, while the end of the abdomen of the male is inverted and grasps that of the female by the subgenital plate. This he considered was the typical position for the Locustidae. It appears, therefore, that there are two distinctive mating processes at least among the Rhaphidophoridae, and information on the behaviour of other members of the family would be of great interest.

While in coitus a spermatophore is produced and deposited by the male at the entrance to the copulatory chamber of the female. Only one spermatophore has been observed on each occasion. As in the Dolichopodini, it is relatively small, and is not accompanied by the sticky substance produced by the accessory glands of the male in members of the Rhaphidophorini. After copulation the insects sometimes separate, but more often the female returns to her preliminary mating attitude. The female has never been observed to eat the spermatophore, but leaves it in place to dry and fall off.

Because of the semi-darkness of their environment, sight probably plays no part in the sexual behaviour of cave Rhaphidophoridae. They rely entirely on their senses of touch and smell. Thus the antennae and palps appear to be of chief importance in the recognition of the sexes, and although the " Glands of

Hancock" may be of added assistance in the finding of a mate, they are not indispensable. Seliskar (1923) regarded the glands as a character peculiar to cave dwellers, but Chopard (1938) considered them to be a morphological characteristic of most Rhaphidophorids, without any relation to the adaptive characters of cave dwellers. Chopard's opinion appears to be correct, as the glands are absent from all New Zealand members of the family so far examined.

OVIPOSITION

Very little is known about the egg-laying habits of the Gryllacridoidea; but they are believed to be similar to those observed among the majority of Gryllids and Tettigoniids, the eggs being deposited in the earth. Until this study the only information on egg-laying in the Rhaphidophoridae was by Hubbell (1936), who discovered that the majority of species of *Ceuthophilus* oviposit in the ground at a depth determined by the length of the ovipositor. He also found eggs in rotten wood, and in loose materials composing beaver and musk-rat houses. Many of the more strictly hypogenic species he considered probably oviposit in their burrows. In the limestone caves at Waitomo *Pachyrhamma waitomoensis* and *Pallidoplectron turneri* oviposit in the soft mud on the walls inside the caves.

Females of *P. turneri* were observed ovipositing on the walls of the Grotto in Waitomo Cave in January, March, April, June, July and November at times ranging from 10.30 a.m. to 10.30 p.m. This differs from what has been observed with *Ceuthophilus latibuli* where, according to Hubbell (1936), the eggs are laid at night. The female *P. turneri* begins by selecting a suitable spot. This it does by making a number of short, jerky, running movements with its maxillary palps directed straight out anteriorly to explore the surface of the ground. The antennae are not used, or are of secondary importance. When a site has been chosen, the insect raises itself upon the tips of its legs, and arches its abdomen until the ovipositor can be brought forward to a position slightly in front of vertical. The legs are well spaced apart. Then the ovipositor is thrust into the mud to a depth of about 7 mm to test its thickness and texture. If the mud is not suitable, the ovipositor is immediately withdrawn and several more probing movements are made in the same area. If still unsuitable, the maxillary palps are again directed anteriorly and the short, running movements are recommenced. Only when thick, soft mud is encountered does the ovipositor remain embedded in it for three or four minutes, or even longer. The body is lowered to a slightly arched position, and remains motionless, except for a peculiar twisting of the abdomen from side to side. At the end of this period, the ovipositor is withdrawn with a sudden, sharp movement, the insect arching its body to do so. Then, with another abrupt movement, the ovipositor is returned to its normal position. The female immediately moves away from the spot and, if oviposition is continued, it recommences probing the mud for another suitable spot. Only one egg is deposited at each insertion. A female which has been ovipositing can always be detected by the coating of mud adhering to its ovipositor. On two occasions marked wetas travelled 12.4 m and 43 m respectively from the area where last recorded to the particular spot selected for oviposition.

The walls of the Grotto tunnel contained several thousand ovipositor holes, ranging from 1.3 m to less than 30 cm above the water level. Consequently the areas were usually covered by water a number of times, depending on how many floods there were in a season, and often large areas of mud were washed away. Usually about 50 ovipositor holes occurred together over an area 2.5 cm square. Most of the holes were preliminary probes, usually only one or two eggs at the most being laid in any particular spot.

Light intensity and temperature fluctuations had very little influence on oviposition. Egg-laying was observed in temperatures ranging from 12.1° C. to 16.1° C.

inside the cave, and as low as 8.8° C. at the river entrance. The temperature of the mud into which the eggs were deposited was about half a degree or one degree higher than the air temperature. The relative humidity remained almost constant at about 97% throughout the year.

According to Hubbell (1936), in the Ceuthophilinae the surface of the ground is explored by the tip of the ovipositor for a suitable place to lay an egg. In the New Zealand Macropathinae the ovipositor is thrust right into the mud with short, jerky movements, and then quickly withdrawn until the right spot is selected. In *Ceuthophilus,* after egg-laying the ovipositor is held poised above the hole and is then used to rake small particles of earth over the opening of the hole. The raking movements are never omitted, and are usually performed eight or ten times. At their conclusion the ovipositor is returned to its normal position. In the Macropathinae mud is never raked from round the edges of the ovipositor holes after the ovipositor has been withdrawn. When mud on the tunnel walls was examined between floods in May and June, 1955, it became possible to distinguish between old and new ovipositor holes by the little ring of mud surrounding the holes. This ring was always present in freshly made holes, but had been either smoothed over or washed away by the river in the old ones. Mud rings occurred round the test holes as well as those containing eggs.

In *Pachyrhamma waitomoensis* the process of oviposition has not been observed, although a number of females have been seen with lumps of mud adhering to their ovipositors. Ovipositor holes, however, were discovered in the Side Branch of Ruakuri Cave, in Aranui Cave, and in Waitomo Cave. In most cases these holes were up to 2.5 cm in depth.

In May, 1955, 75 holes were discovered on a ledge inside the Side Branch of Ruakuri Cave, many of them going into the soft mud at 75° angles. Each hole was surrounded by a little ridge of mud, and most holes appeared very old. Higher up the wall on another ledge a number of very old holes were discovered almost completely filled with dust and mud. Wherever the mud was deepest the greatest number of holes occurred. Most of the holes were laterally elongated, one dorso-ventrally, and a few were round. The elongated holes were just over 6 mm long by about 3 mm wide, and the round ones 4.5 mm in diameter.

On the right wall of Aranui Cave, 23.25 metres inside the entrance, a large area of thick, rather dry mud was discovered riddled with thousands of ovipositor holes similar to those observed in Ruakuri Cave. (Plate 1.) When a portion of the mud was broken off and examined it was found to contain the impressions of dozens of ovipositors. The imprints of both dorsal and ventral valves were clearly visible (Plate 2, Fig. 2). The ovipositors of female *P. waitomoensis* were found to fit these imprints exactly. No eggs were discovered, although the impressions of a few were found in the mud. The ovipositor thrust marks penetrated the mud at all angles, and were so thick that in numerous cases they crossed and recrossed each other. It seems probable that these ovipositor impressions were not recent ones, but may have gradually accumulated over the years, the same area being used by generation after generation of female *P. waitomoensis.* A number of larger round holes to the left of these holes may have been made by emerging nymphs. The main area of mud was one metre wide by 61 cm high, and consisted of 64 large indentations 4 cm high by 2.5 cm wide (Plate 1). Each indentation contained at least 120 ovipositor thrust marks. A conservative estimate of the total number of ovipositor holes was about 10,000. In the same area similar holes were discovered higher up the wall. This was the only area in the first 34 metres of the cave in which mud occurred in any sizeable quantity, and it must have gradually accumulated there over the years by constant seepage through the limestone.

A number of areas were discovered on the left wall where mud had seeped through and accumulated in little pockets in the limestone to a depth of 1–5 cm. They were honeycombed with ovipositor holes, but no eggs were found. The chitinous chorion had decomposed in all cases leaving the impression of the egg behind it. These areas may have been abandoned by females because they had become so riddled; or perhaps the mud, due to so much use, may have dried out a little and lost its required consistency. With *Pallidoplectron turneri* the correct texture of the mud is a pre-requisite for egg-laying, and the same probably applies to *P. waitomoensis.*

These observations indicate that the eggs of *P. waitomoensis* are laid inside the cave, where constant humidity and temperature create remarkably uniform conditions. A large number of female wetas were observed to have muddy ovipositors to a depth of 13 mm or more from the tip. Oviposition, however, was not observed. It appears that female *P. waitomoensis* go high up the walls through tiny cracks and fissures in the limestone to inassessible parts of the cave to lay their eggs in fresher supplies of mud. The tendency of small nymphs to inhabit large cracks in the limestone 4.5–6 metres above the duckboards on the left wall supports this.

Ovipositor holes and ovipositor thrust marks from *P. waitomoensis* were found a short distance inside the main entrance to Waitomo Cave in thick mud, but no eggs nor impressions of them were found. Large areas in Aranui Cave and Waitomo Cave covered with thick mud were passed over by female *P. waitomoensis.* Only those parts where the mud was of a fairly moist, firm and uniform texture were selected, and these areas when discovered were always riddled with ovipositor holes.

THE EGG, EMBRYO AND HATCHING

Pallidoplectron turneri

In the Grotto of Waitomo Cave, the eggs of *Pallidoplectron turneri* are deposited in the deep mud which accumulates low down on the walls, and are usually covered by water a number of times before they hatch. The mud surrounds the eggs and adheres to them, while the water ensures a high humidity and an even temperature. The eggs are a pale cream colour, oval in shape, each being 3.5 mm long and 1.5 mm wide. Most eggs were discovered at the base of a clearly defined ovipositor thrust 6.5 mm long. Thus the depth penetrated into the mud by the egg was 10 mm. The ovipositor thrust was at a slight angle, but the egg was always vertical in position. Where the empty chorion was found it was sometimes at an angle, or even horizontal. The imprints from the ovipositor valves of the females were always visible in the mud. On all occasions when samples of mud were examined newly laid eggs, eggs containing partly developed embryos with eye spots, eggs with well developed embryos inside brown chorions and empty chorions were collected. It is probable that a large number of eggs are washed away each year by the floods. When the nymph emerges from the egg it crawls up the hole made by the ovipositor thrust to the surface of the mud. Thus where an egg has hatched, the marks of the ovipositor thrust are obliterated by the action of the nymph crawling up to the surface.

A number of old, dark chorions showed different patterns of dehiscence. Some had split at the animal pole of the egg, others along the whole length of the egg, while some had a round hole at the anterior end where the nymph had emerged. The chorions were all thin, some being very soft, while others were hard and brittle. A few were perfect, showing clearly the little cap area which surrounds the abdomen of the embryo.

As each *P. turneri* lays only one egg at a time, and as the same area of mud is used by different females, it is quite possible that where two eggs are found close together, they belong to different parents. This habit of laying one egg at a time

FIG. 1.—Part of area of mud on right wall inside Aranui Cave riddled with ovipositor holes made by *Pachyrhamma waitomoensis* females.

Photo: A. M. Richards.

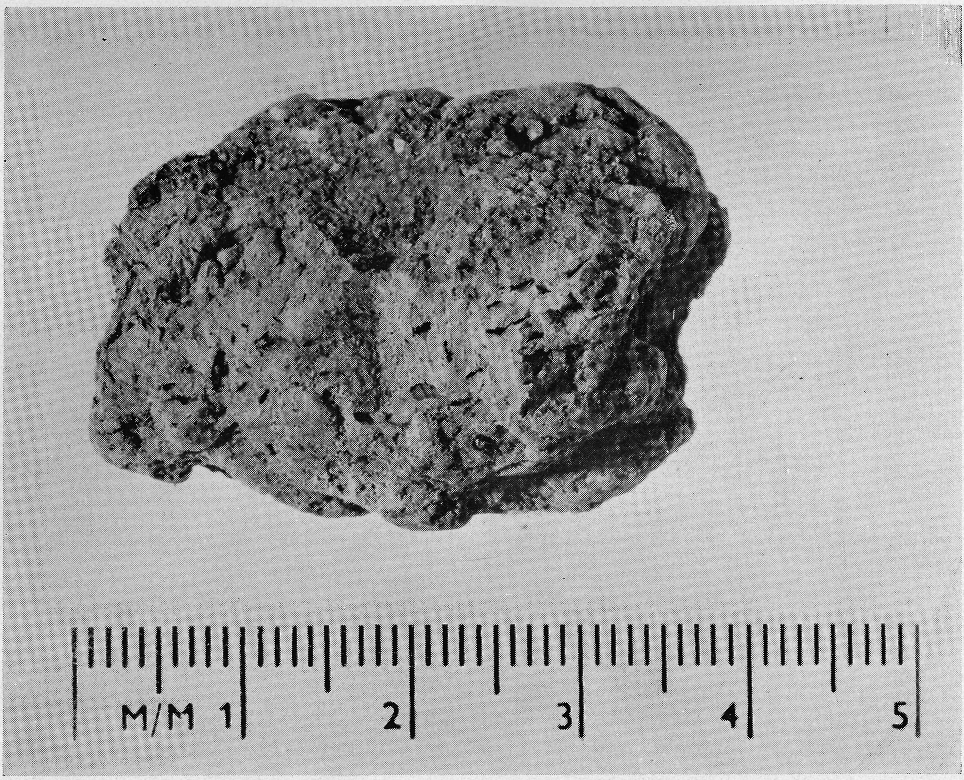


FIG. 1.—Portion of mud broken off from area of mud inside Aranui Cave, showing elongate ovipositor holes made by *Pachyrhamma waitomoensis* females.

Photo: J. W. Endt.

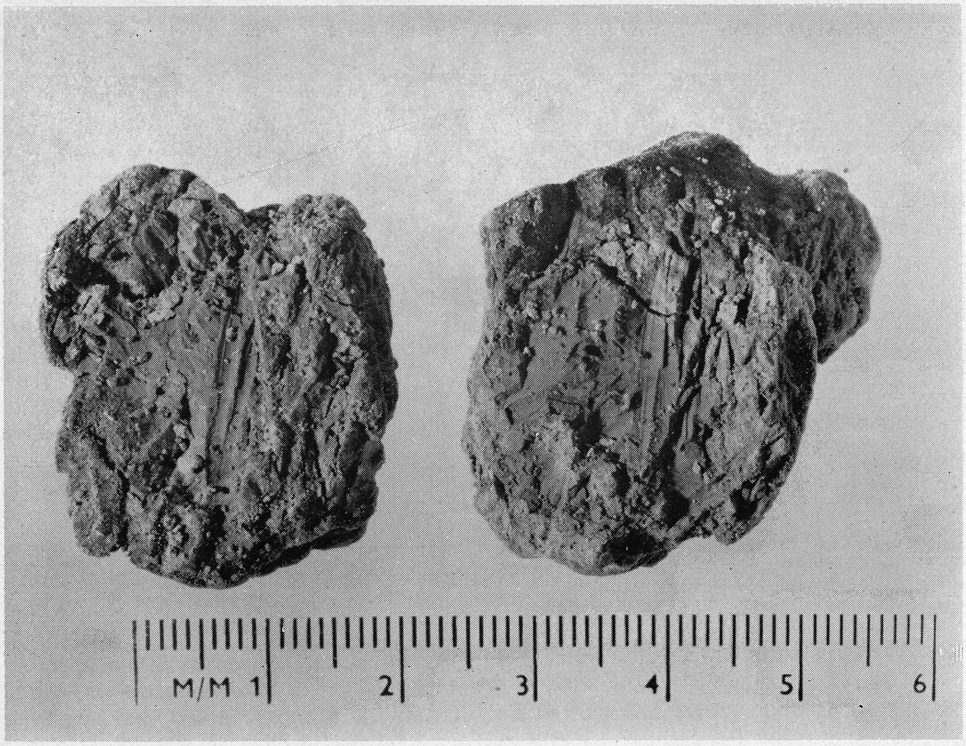
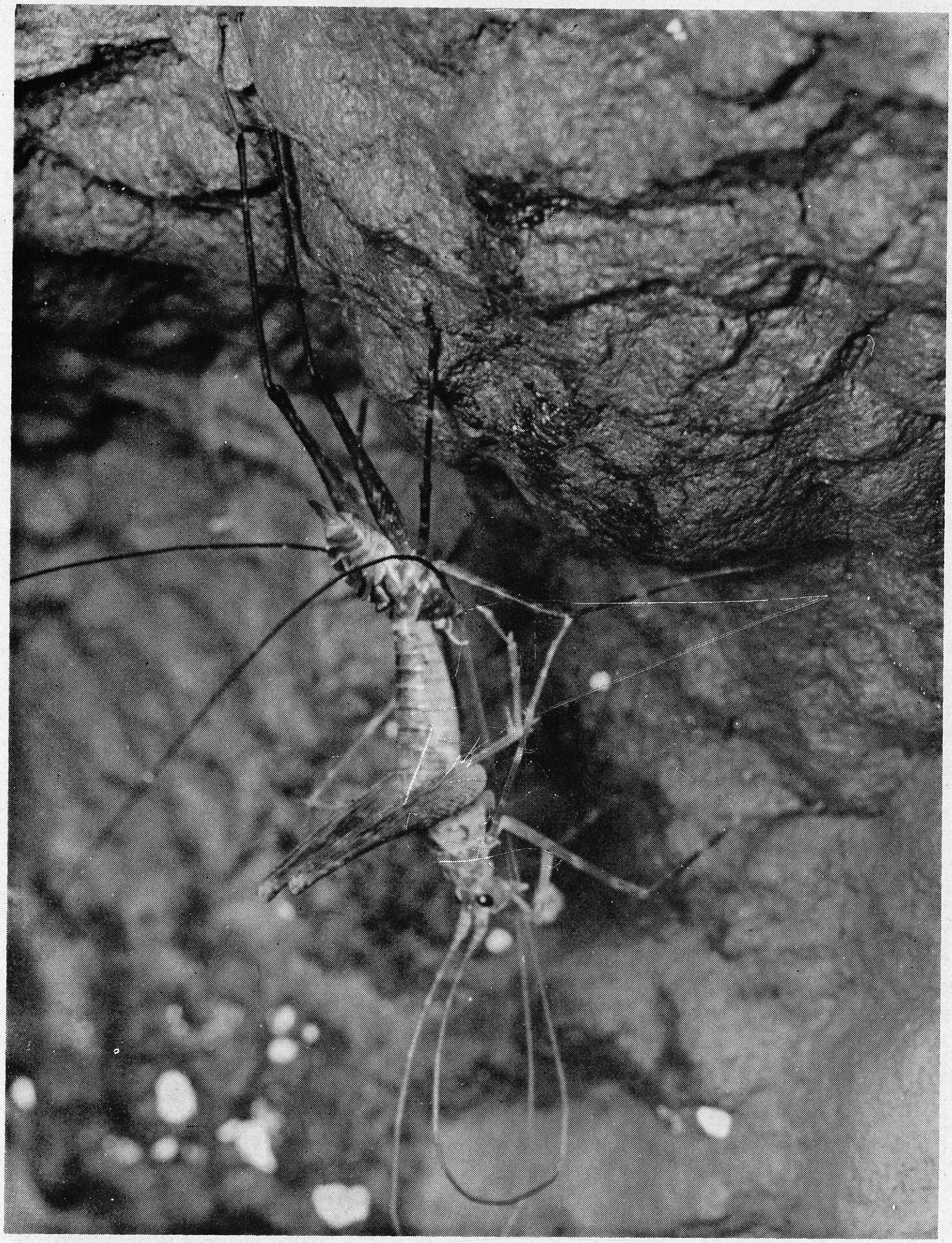


FIG. 2.—Lump of mud from Aranui Cave split open to show imprints of ovipositors of *Pachyrhamma waitomoensis* females. Note the different angles at which they have penetrated the mud.

Photo: J. W. Endt.



Male nymph of *Pallidoplectron turneri* hanging from wall of tunnel in Waitomo Cave as it undergoes its final ecdysis into an adult weta.

Photo: S. A. Rumsey.

over a large area is quite different from the behaviour observed in most members of the Orthoptera.

The length of time required for development of the embryo has not been determined. The first visible signs of the developing embryo are the appearance of the compound eyes as two dark red spots through the chorion. The egg gradually swells and the chorion becomes a light or mid-brown colour. A short time before hatching a dark brown cap becomes apparent at the vegetal pole of the egg. In some cases the chorion becomes transparent, and the embryo can be seen quite clearly through it. This differs from Hubbell's (1936) observations on *Ceuthophilus* sp. where the eggs are soft and translucent when first laid, with the chorion gradually becoming a chalky white, rather hard, brittle shell.

One light brown egg with eye spots was opened up. The embryo was unpigmented, except for its light brown compound eyes. It was divided into head, thorax and segmented abdomen, with anus and limb buds clearly recognisable. The thorax and head were covered with a white spongy material from which a viscous fluid was secreted, and to which both embryo and chorion adhered.

Another egg, containing an embryo in a more advanced stage of development was examined. The chorion was very swollen, with a dark-brown cap area at the vegetal pole. Apart from brown compound eyes, the embryo was unpigmented. It was divided into head, thorax and abdomen, with segmentation well developed. The legs were divided into femur, tibia and tarsus. The antennae passed posteriorly along the sides of the body and curved back anteriorly under the abdominal sterna to the thorax. Very little of the white, spongy material remained in the egg, what was left being round the head.

The transparent chorion was brown in colour and very brittle. The embryo inside was fully developed and pigmented; the compound eyes were black.

As in *Pachyrhamma waitomoensis*, nymphs and adults are usually segregated, the small nymphs at the entrance and the large nymphs and adults further inside the cave. Although ovipositing females and first instar nymphs were observed throughout the year, oviposition reached its peak between April and June, while most first instar nymphs were seen from January to March. This indicates that the length of time required for development of the embryo is about eight months.

First instar nymphs of *P. turneri* are always very strongly pigmented, being dark-brown mottled with a few paler markings. As the nymphs pass through their instars the amount of pigmentation decreases, till as adults they acquire a rather uniform colouration of ochreous mottled with light brown. According to Chopard (1938), this characteristic is frequent among certain species which live in the open and in caves, the young individuals of cave species having a much more marked pigment than that of the adults. He considers that depigmentation is a character acquired inside caves. It is very unstable and could easily be modified if the insects were kept out of their normal habitat for a certain length of time. *P. turneri* were removed from the cave several times but the insects never survived long enough for any appreciable changes in colouration to be noticed. With *Pachyrhamma waitomoensis* there is no difference in the degree of pigmentation of nymphs and adults; all stages are quite heavily pigmented.

Pachyrhamma waitomoensis

Although large quantities of mud were examined, no eggs of *Pachyrhamma waitomoensis* were ever found. Thus no information has been obtained on the embryology of this species.

On numerous occasions in May and June, 1955, female *P. waitomoensis* were observed in Aranui Cave with muddy ovipositors. In November several first instar nymphs were seen, and hatching reached its peak in December, indicating an incubation period of about seven months. The small nymphs were all confined to the left wall of the cave in areas where the greatest numbers of females with muddy ovipositors had been observed. In Waitomo Cave similar conclusions were reached over the incubation period of *P. waitomoensis*.

ECDYSIS

The process of ecdysis has been observed with nymphs of *Pachyrhamma waitomoensis, P. fascifer* and *Pallidoplectron turneri*. It is identical in all cases so probably is characteristic for the Macropathinae (Plate 3).

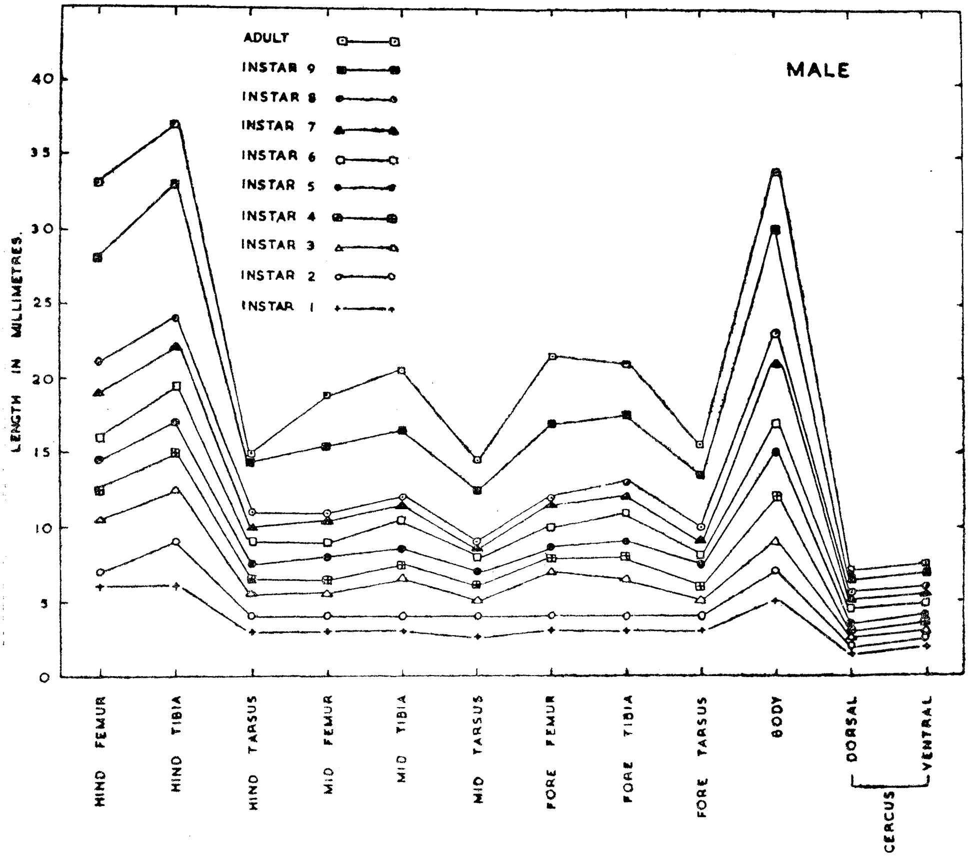
The nymph hangs head downwards, with its legs well spaced out so as to get a firm grip of the wall or other supporting structure. Then the abdomen is contracted, driving the body fluid into the head and thorax. The ampulla, situated in the cervical membrane, swells out and the thorax becomes distended. Next the abdomen and cerci are partly withdrawn from the old cuticle. The ecdysial line extends from the fastigium on the head capsule to the metanotum, and pressure now exerted splits the cuticle down this line, allowing the thorax and part of the abdomen to protrude. The insect then slowly draws itself out, aided by gravity. Movement is started in the legs, and these are gradually withdrawn from the exuvia, while at the same time head capsule, tentorium and mouth parts become free, along with the more proximal part of the antennae. The mouth parts are not turned inside out, although the head capsule is, and their apodemes can easily be distinguished. Two large colourless areas show where the compound eyes have been. By the time the abdomen is almost completely free, the fore and middle femora have emerged. Next the middle tibiae and tarsi are drawn out, followed by the fore tibiae and tarsi, while the hind legs remain passive, clinging to the substratum. The hind femora are then withdrawn, followed by the hind tibiae and tarsi. With the complete freeing of the legs, the abdomen is drawn clear of the exuvia. Finally the antennae become free. If undisturbed, the time required for a complete ecdysis is about 20 minutes. The newly emerged insect is a pale grey colour, with the colour pattern clearly, though faintly visible. A day at least is required for the exoskeleton to harden properly, and the colour to intensify to the characteristic shade. On several occasions while being observed, legs have been bent or twisted and antennae broken because of the softness of the new exoskeleton. In one case the insect became completely crippled.

In females the last portion of the body to be withdrawn from the exuvia is the ovipositor. In the penultimate instar this remains a deep grey colour. In the adult insect it is translucent on emergence, except for the tip, which is a pale reddish-brown, but gradually the whole ovipositor deepens to a deep reddish-brown. The colour and opacity of the ovipositor is a good method for recognising an adult female Rhaphidophorid.

Unlike the Henicidae, the colour pigment of the Rhaphidophoridae is always present in the exuviae. As the newly emerged insect always hangs below its exuvia, it is possible to mistake a weta which has just ecdysed into an adult for a pair of mating insects. Apart from the split along the ecdysial line, and a slight split at the proximal end of the hind femora, the fresh exuvia is an exact replica of a nymph with the linings of the trachea attached. However, it soon collapses and dries up. The exuvia is usually eaten almost immediately after an ecdysis, but old exuviae may sometimes be found on the floors of caves.

NUMBER OF INSTARS AND GROWTH RATE

The number of instars represented in *Pachyrhamma waitomoensis* and *Pallidoplectron turneri* have not so far been determined. However, from observations in the field and in the laboratory, the number of instars in *Pachyrhamma fascifer*, the



TEXT-FIG. 2.—Growth rate and number of instars in male *Pachyrhamma fascifer*.

common Wellington cave-weta, has been ascertained. By comparison of these results with the instars examined in *P. waitomoensis*, the two species conform to a fairly similar pattern, with eight to ten instars.

In *P. fascifer* no insects were reared under observation from egg to adult, although some nymphs passed through up to five instars in captivity. The insects were kept in the laboratory during 1953 and 1954, and frequent trips were made to their natural habitats for comparative purposes. By comparing the measurements of numerous examples, it was found that nine pre-adult instars were passed through by males and seven by females (Text-figs. 2, 3). These results are similar to the conclusions reached by Hubbell (1936) with *Ceuthophilus gracilipes*. He also was unable to rear the insects, but concluded that there were possibly eight pre-adult stadia in the females, and eight or even ten pre-adult stadia in males.

The attempt to determine the number of instars in *P. fascifer* was made difficult by the size variation in each stadium. Because of this, instead of falling into sharply separated groups, the nymphs could be arranged in an evenly graded series from smallest to largest. The degree of development of the ovipositor in females was a useful character in determining the number of instars, but even this was subject to variation. The attempt to separate males was even less satisfactory. These observations corroborated Hubbell's (1936) assumption that in the Rhaphidophoridae the number of instars is variable both inter- and intraspecifically. This would help to explain the regular gradation found in any large series of nymphs.

The length of the developmental period varies considerably. In some nymphs an instar may extend over four weeks, while in others it may last up to eight weeks or longer. Adult insects appear between October and May, but most penultimate instar nymphs mature between the end of December and the end of January.

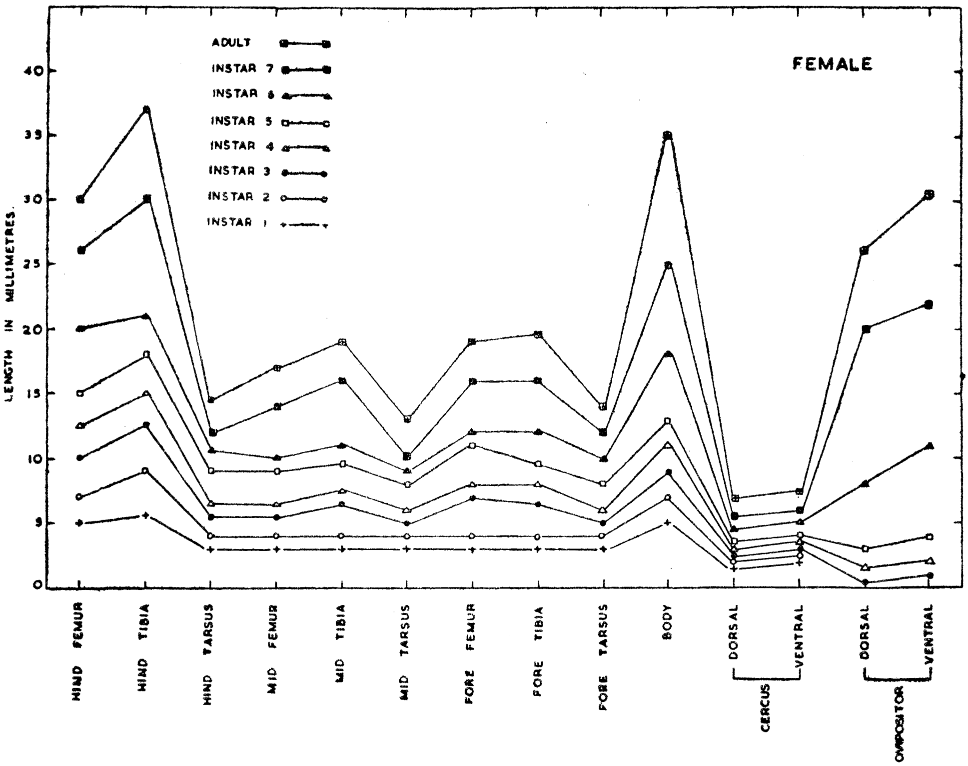
TABLE IV.—NUMBER AND DURATION OF INSTARS IN *PACHYRHAMMA FASCIFER*.

Instar	Number of Days Males	Month	Number of Days Females	Month
1	24–30	Sept.-Oct.	24–30	Sept.-Oct.
2	28–32	Oct.-Nov.	27–32	Oct.-Nov.
3	44–50	Nov.-Jan.	44–52	Nov.-Jan.
4	21–44	Dec.-Jan.	46–50	Dec.-Feb.
5	26–28	Jan.-Feb.	64–70	Feb.-Apr.
6	63–65	Feb.-Apr.	200–220	Apr.-Nov.
7	190–200	Apr.-Oct.	55–65	Nov.-Jan.
8	28–30	Oct.-Nov.	170–190	Jan.-July
9	45–55	Nov.-Jan.		
10	170–190	Jan.-July		

From Table IV it can be seen that the period of greatest growth extends between October and April. From then till the following October there is no growth, the nymphs remaining in the same instar over the winter months, the males in the seventh instar and the females in the sixth. Between April and June eggs are laid, and shortly afterwards the adults die. In September the first instar nymphs hatch out. Thus two generations are nearly always present in a population.

In *P. waitomoensis* there is much less variability in the length of an instar, so that the wetas fall into more sharply separated groups than in *P. fascifer*. The final ecdysis is almost entirely confined to January and part of February, but in *P. fascifer* it may extend from October to May. In *P. fascifer* it is common to find several different instars in the population at any one time; but with *P. waitomoensis* it is very rare for more than two instars in each generation to be present. Between April and October, there is no fluctuation in the number of instars. Although a representative series of *P. waitomoensis* have not been collected, the size range observed inside the caves seems to agree very closely with that in *P. fascifer*, so it is assumed that the number of instars is probably of the same order. As *P. waitomoensis* is a larger insect than *P. fascifer*, and as Hubbell (1936) considers that the number of pre-adult instars is related to the size of the adult insect, there may be an extra instar present in its life cycle.

As the rate of growth from instar to instar varied slightly from nymph to nymph, the figures used in Text-figs. 2 and 3 were those which, after examination of numerous nymphs, appeared most representative of each instar. In some cases a variation of one or two millimetres was recorded on either side of the figures selected for each instar. These figures were again used in assessing the percentage increase growth rate in Tables V and VI. The figures in the first instar column and in the third instar column with the ovipositor, refer to the initial length of the segment in millimetres. From these results the greatest amount of growth occurs at the second and eighth ecdyses in males, and in the second and sixth ecdyses in females. The appendage undergoing the greatest increase in growth at each ecdysis is the ovipositor. Not appearing until the third instar, by the time the eighth and final instar is reached the ovipositor is subequal in length with the body, having doubled or trebled its length in all but the final ecdysis.



TEXT-FIG. 3.—Growth rate and number of instars in female *Pachyrhamma fascifer*.

The rate of growth in the antennae was not included in the graphs or tables because of the tendency of these appendages to break, thus preventing accuracy of measurement. Several cases of regeneration in the length of the antennae have been recorded. The average increase in length in the final ecdysis is about 20 mm, or 19%. In one male the antennae, which were broken, measured 70 mm in the penultimate instar, but in the adult insect they measured 126 mm, showing an increase in length of 56 mm, or 80%.

It was shown by Dyar (1890) that the head capsule of Lepidopterous larvae grows in geometrical progression, increasing in width at each ecdysis by a ratio, usually about 1.4, which is constant for a given species. This rule applies to many parts of the body, so that when the number of the instar is plotted against the logarithm of some measurement on the insect, a straight line is generally obtained. Although it is now known that the progression is rarely regular, it is usually sufficiently nearly so to discover whether an instar has been overlooked. In *Pachyrhamma fascifer* the logarithm of the linear measurements of the hind femora in both males and females were plotted against the number of instars. Calculated values following Dyar's Law were obtained from fitted regression lines and are given in Table VII.

From Table VII it can be seen that the approximation of the observed to the calculated measurements is sufficiently close to remove the possibility of an instar

TABLE V.—PERCENTAGE INCREASE GROWTH IN LENGTH IN EACH INSTAR IN MALES OF *P. FASCIFER.*

Instar	1	2	3	4	5	6	7	8	9	10
Hind Femur	6 mm	16.6	50.0	19.0	12.0	14.3	18.8	10.5	33.3	17.9
Hind Tibia	6 mm	50.0	38.9	20.0	13.3	14.7	12.8	9.1	37.5	12.1
Hind Tarsus	3 mm	33.3	37.5	18.2	15.4	20.0	11.1	10.0	31.8	3.4
Mid Femur	3 mm	33.3	37.5	18.2	23.1	12.5	16.6	4.8	40.9	22.6
Mid Tibia	3 mm	33.3	62.5	15.4	13.3	23.5	9.5	4.3	37.5	24.2
Mid Tarsus	2.5 mm	60.0	25.0	20.0	16.7	14.3	6.3	5.6	38.9	16.0
Fore Femur	3 mm	33.3	75.0	14.3	6.3	17.6	15.0	4.3	41.7	26.5
Fore Tibia	3 mm	33.3	62.5	23.1	12.5	22.2	9.1	8.3	34.6	20.0
Fore Tarsus	3 mm	33.3	25.0	20.0	25.0	6.7	12.5	11.1	35.0	14.8
Body	5 mm	40.0	28.6	33.3	25.0	13.3	23.5	9.5	30.4	13.3
Cercus, Dorsal	1.5 mm	33.3	25.0	20.0	16.7	28.6	11.1	10.0	18.2	7.7
Cercus, Ventral	2 mm	25.0	20.0	16.7	14.3	25.0	10.0	9.1	16.7	7.1

TABLE VI.—PERCENTAGE INCREASE GROWTH IN LENGTH IN EACH INSTAR IN FEMALES OF *P. FASCIFER*

	1	2	3	4	5	6	7	8
Hind Femur	5 mm	40.0	42.9	25.0	20.0	33.3	30.0	15.4
Hind Tibia	5.5 mm	63.6	38.9	20.0	20.0	16.7	42.9	23.3
Hind Tarsus	3 mm	33.3	37.5	18.2	38.5	16.7	14.3	20.8
Mid Femur	3 mm	33.3	37.5	18.2	38.5	11.1	40.0	21.4
Mid Tibia	3 mm	33.3	62.5	15.4	26.7	15.8	45.5	18.8
Mid Tarsus	3 mm	33.3	25.0	20.0	33.3	12.5	11.1	30.0
Fore Femur	3 mm	33.3	75.0	14.3	37.5	9.1	33.3	18.8
Fore Tibia	3 mm	33.3	62.5	23.1	18.8	26.3	33.3	21.9
Fore Tarsus	3 mm	33.3	25.0	20.0	33.3	25.0	20.0	16.7
Body	5 mm	40.0	28.6	22.2	18.2	38.5	38.9	40.0
Cercus, Dorsal	1.5 mm	33.3	25.0	20.0	16.7	28.6	10.0	27.3
Cercus, Ventral	2 mm	25.0	20.0	16.7	14.3	25.0	9.1	25.0
Ovipositor, Dorsal			0.5 mm	200.0	100.0	166.7	150.0	30.0
Ovipositor, Ventral			1 mm	100.0	100.0	175.0	100.0	38.6

Abbreviations in Tables V and VI.
1, 2, 3, 4, 5, 6, 7, 8, 9, 10 — instars 1, 2, 3, 4, 5, 6, 7, 8, 9, 10.

TABLE VII.—FIT OF DYAR'S LAW TO INSTAR MEASUREMENTS IN *P. FASCIFER*

	Female		Male	
Instar	Observed Length in mm	Calculated Length*	Observed Length in mm	Calculated Length*
1	5	5.5	6	6.5
2	7	7.1	7	7.8
3	10	9.2	10.5	9.4
4	12.5	11.8	12.5	11.2
5	15	15.2	14	13.4
6	20	19.6	16	16.1
7	26	25.3	19	19.3
8	30	32.5	21	23.1
9			28	27.7
10			33	33.1

Proportionality constant: 1.29 for females; 1.20 for males.
* From regression line.

having been overlooked. When applied to other parts of the body and appendages similar results are obtained. It is probable that if other members of the Rhaphidophoridae are reared and studied, they will give similar results to those obtained with *P. fascifer*. Success in keeping them alive in captivity will form one of the major factors in obtaining this information.

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