TRANSACTIONS

OF THE

ROYAL SOCIETY OF NEW ZEALAND

ZOOLOGY

VOL. 1 No. 29 FEBRUARY 10, 1962

[Continued from *Transactions of the Royal Society of N.Z.*, Volume 88, Part 4.]

Aspects of the Biology of the Immature Stages of *Pison spinolae* Shuckard (Hymenoptera: Sphecidae)

By D. R. COWLEY,

Department of Zoology, University of Auckland

[*Communicated to Auckland Institute by Dr. J. G. Pendergrast, June 21, 1961; received by the Editor, June 27, 1961.*]

Abstract

AN account of the duration of life and other aspects of the immature stages of *Pison spinolae* is given. Included is a method of determining the number of larval instars by measurement of the diameters of the first thoracic spiracles. This method proved highly satisfactory, as it could be used while the larvae were still actively engaged in feeding. It was found that *P. spinolae* has a bivoltine life cycle, every second generation being interrupted by a period of arrested growth or diapause, which occurs at the onset of the prepupal period. It is by this means that the wasp tides itself over the cold winter period. Measurements of cocoon lengths indicated that male and female differences in size may be present as early as the late larval period.

INTRODUCTION

ALTHOUGH well established when first discovered in New Zealand by Kirby (1883) *Pison spinolae* Shuckard was first described from E. Australia (Shuckard, 1837). The food of the younger actively feeding stages is torpid spiders of the family Argiopidae, which are placed in the cells by the female during nest construction. These spiders are stung and paralysed by the female when they are captured.

Notwithstanding its wide distribution and great abundance during warmer periods of the year, the biology of the wasp has been almost entirely neglected.

THE EGG

Plate 1, fig. 5. The eggs of *Pison spinolae* are laid singly on the opisthosoma of species of the Argiopidae (orb spiders). Although many hundreds of spiders were inspected only 8 species were represented: *Argiope protensa, Arachnura feredayi, Araneus viriditas, Cyclosa trilobata, Leucage dromedaria, Araneus crassus, Araneus laevigatus, Cyclosa* sp. (undescribed).

Each egg is approximately 2.5 mm in length, sub-cylindrical and tapers slightly toward one of its rounded ends. At its greatest diameter it is no more than 0.5 mm. The whole egg is a delicate opaque white and is slightly incurved and flattened on the surface that is attached to the spider's opisthosoma.

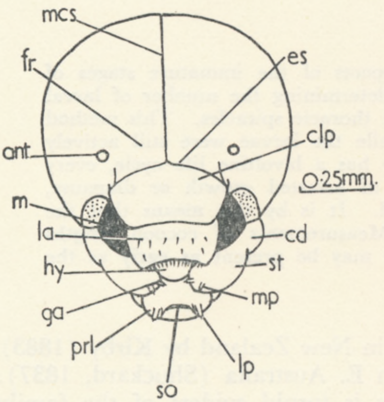
Published by the Royal Society of New Zealand, c/o Victoria University of Wellington, P.O. Box 196, Wellington.

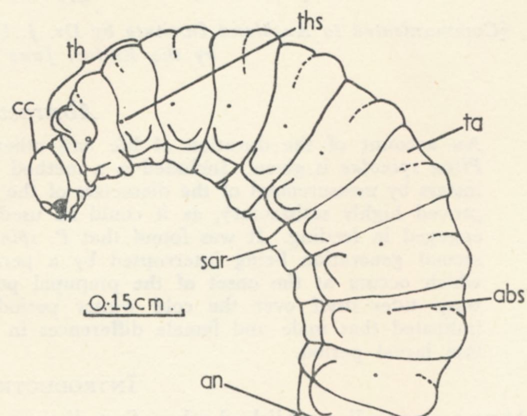
Incubation Period

The average period of incubation in *Pison spinolae* is from 5–7 days. As is typical, the larva, 3–6 hours before hatching rotates inside the flexible chorion of the egg until its ventral surface faces directly toward the spider instead of away from it. High humidity is a prime factor in the development of the eggs and appears to be maintained by the evaporation of water from the freshly finished clay partitions. Many eggs subjected to room conditions collapsed if not supplied with sufficient moisture.

The Larva

Plate 1, figs. 1–3; Text-figs. 1 and 2. The newly hatched larva has an ill-defined head region with a pair of acutely pointed, pincer-like mandibles which have slightly incurved, finely dentate internal borders. It is with these mandibles that the larva pierces the elastic cuticle of the spider's opisthosoma soon after eclosion. The larva remains anchored in this position throughout the earlier instars of its life and ingests the body fluids of the spider by the sucking movements of its hypopharynx.





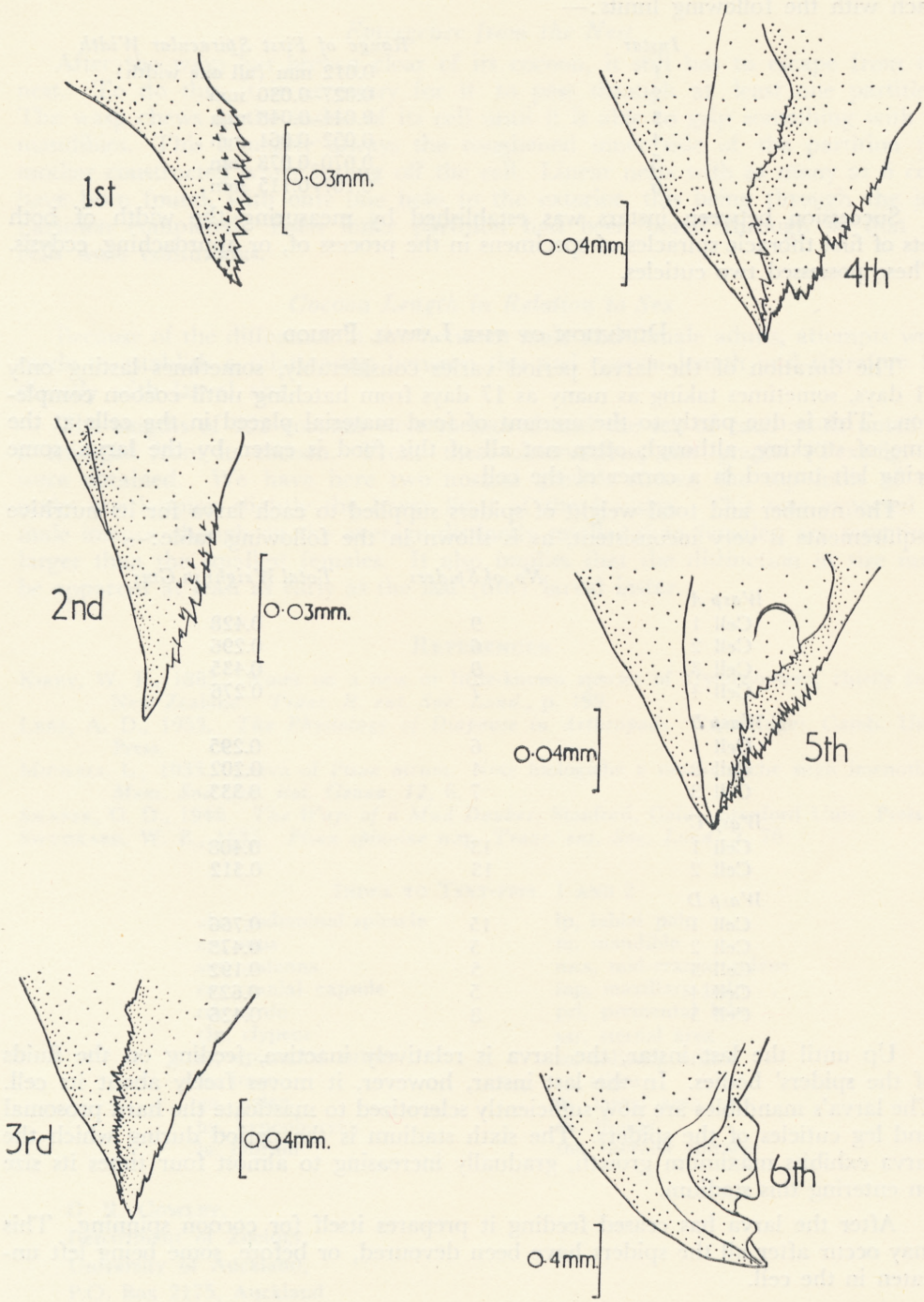
Text-fig. 1.—Head of sixth instar larva, frontal view.

Text-fig. 2.—Sixth instar larva, lateral view.

Number of Larval Instars

Because of the transparency of the cuticle it is very difficult to observe a larval ecdysis, and it is not uncommon for a larva to have more than one cuticle still partially covering it. The use of characters associated with the head for instar determination was avoided because these could not be examined without interrupting a larva engaged in feeding. The mandibles do, however, have distinct dentition which varies from instar to instar, and illustrations of these (Text-fig. 3) have been included to be used in conjunction with the following more satisfactory method.

The only features that could be clearly seen throughout the whole of the larval period were those of the spiracles. The number of larval instars was therefore determined by measurements of the diameters of the first thoracic spiracles (the largest). Because of the circular nature of the spiracles, an accurate measurement can be taken from any angle, as long as the maximum diameter of the apparent elliptical outline is considered.



TEXT-FIG. 3.—Mandicular Dentition of larval instars.

Using this method, six clearly defined instars were determined (Text-fig. 4), each with the following limits:—

Instar	*Range of First Spiracular Width*
1	0.012 mm (all one width)
2	0.027–0.030 mm
3	0.041–0.048 mm
4	0.052–0.061 mm
5	0.070–0.078 mm
6	0.107–0.115 mm

Succession between instars was established by measuring the width of both sets of first thoracic spiracles of specimens in the process of, or approaching, ecdysis. These possessed two cuticles.

Duration of the Larval Period

The duration of the larval period varies considerably, sometimes lasting only 11 days, sometimes taking as many as 17 days from hatching until cocoon completion. This is due partly to the amount of food material placed in the cells at the time of stocking, although often not all of this food is eaten by the larva, some being left unused in a corner of the cell.

The number and total weight of spiders supplied to each larva for its nutritive requirements is very inconsistent, as is shown in the following table:—

	No. of Spiders	*Total Weight in Gms*
Wasp A		
Cell 1	9	0.428
Cell 2	6	0.296
Cell 3	9	0.435
Cell 4	7	0.276
Wasp B		
Cell 1	6	0.295
Cell 2	4	0.202
Cell 3	7	0.333
Wasp C		
Cell 1	13	0.408
Cell 2	13	0.312
Wasp D		
Cell 1	15	0.766
Cell 2	5	0.473
Cell 3	5	0.192
Cell 4	5	0.623
Cell 5	8	0.426

Up until the last instar, the larva is relatively inactive, feeding on the fluids of the spiders' bodies. In the last instar, however, it moves freely about its cell. The larva's mandibles are now sufficiently sclerotized to masticate the hard prosomal and leg cuticles of the spiders. The sixth stadium is the period during which the larva exhibits maximum growth, gradually increasing to almost four times its size on entering this stadium.

After the larva has ceased feeding it prepares itself for cocoon spinning. This may occur after all the spiders have been devoured, or before, some being left uneaten in the cell.

Cocoon Construction

Soon after the larva stops feeding, it starts to ingest small pieces of clay which it removes from the inner walls of its cell. It is this clay and the silk that the larva exudes which is used to form a hard, shell-like cocoon.

Larvae deprived of clay still constructed cocoons, but these were soft and flexible and not sealed off from the exterior. After gnawing at the inner wall of the cell for some time, the larva starts to place a silken network about itself. Shafer (1948) states that the mud-dauber *Sceliphron cementarium* cannot spin unless it can repeatedly rub its labium against a surface, thereby initiating secretion of silk. *Pison spinolae* can secrete silk without this stimulus.

Extending the labio-maxillary complex well forward, the larva attaches the end of a thread to one side of the cell, then turning its head to the other side, attaches the thread again. A repetition of this gradually builds up a loose network around the upper half of the body. Occasionally, however, about once every hour in those observed, the larva turns completely over on itself by bending its head towards its tail and rhythmically contorting its body. It therefore eventually forms a complete network of silken thread around itself, a process which may take up to 8 hours. At this stage, the larva may again spend time nibbling mud from the cell walls. The network acts as a scaffolding for the building of the cocoon proper.

Starting at the mid-region of its body, the larva then constructs a close network about itself, first on the ventral side, then by rotating, forms a ring of closely woven thread. Into this it incorporates small particles of regurgitated mud and large quantities of liquid. Parts of masticated spiders may also be included in the structure of the cocoon. The ring is gradually enlarged until the anterior half of the body is completely enclosed. At this stage the larva turns on itself so as to face in the reverse direction, and then builds the other end of the cocoon, completely obscuring itself. At this stage the walls of the cocoon are still very thin and flexible and the larva continues adding silk, mud and liquid until the whole structure is quite rigid and of a capsular shape.

The completion of the cocoon after the network has been formed takes 1–2 days, and when finished the moisture evaporates to leave a strong, inflexible shell.

Oxygen Deficiency and Its Effects on Larvae

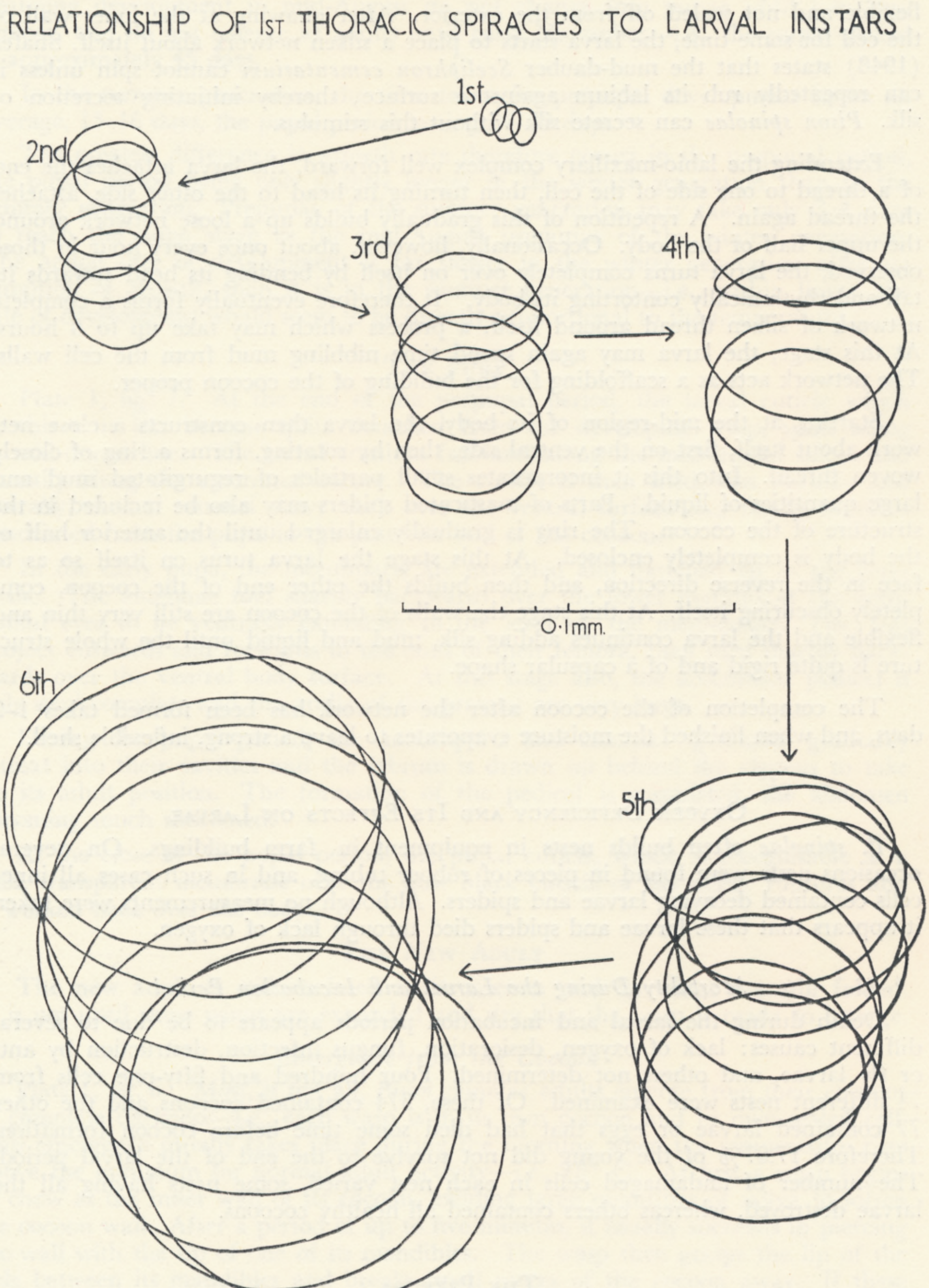
P. spinolae often builds nests in equipment in farm buildings. On several occasions nests were found in pieces of rubber tubing, and in such cases all inner cells contained decaying larvae and spiders. Although no measurements were taken it appears that these larvae and spiders died through lack of oxygen.

Mortality During the Larval and Incubation Period

Death during the larval and incubation periods appears to be due to several different causes: lack of oxygen, desiccation, fungus infection, destruction by ants or fly larvae, and others not determined. Four hundred and fifty-one cells from 74 different nests were examined. Of these, 374 contained cocoons and the other 77 contained larvae or eggs that had died some time before cocoon formation. Therefore 17.07% of the young did not survive to the end of the larval period. The number of undamaged cells in each nest varied, some nests having all the larvae destroyed, whereas others contained all healthy cocoons.

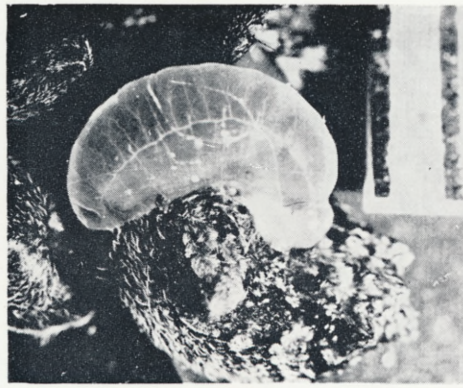
The Prepupa

Plate 1, fig. 4. Three to seven days after the larva has finished spinning its cocoon, the faecal material which has accumulated in its midgut throughout the larval period, is cast into the posterior end of the cocoon enclosed in the larval peritrophic membrane. This faecal material hardens into a solid plug in the end of the cocoon.

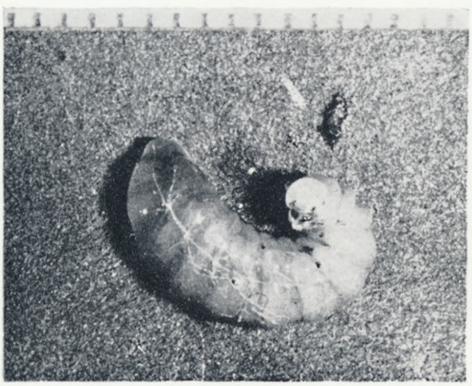


Text-fig. 4.—Relationship of 1st Thoracic Spiracles to larval instars.

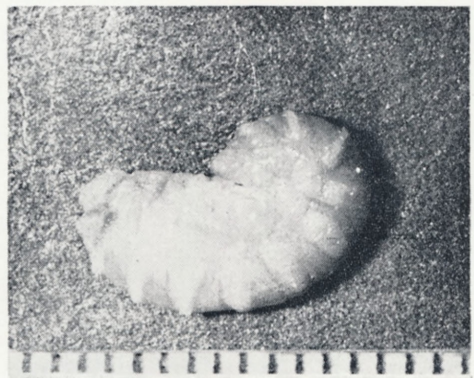
1.



2.



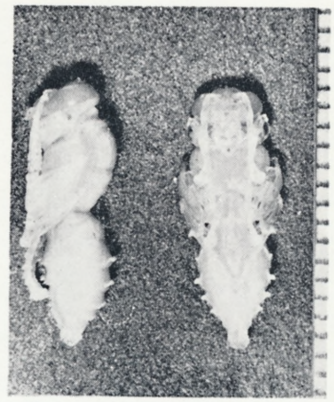
3.



4.

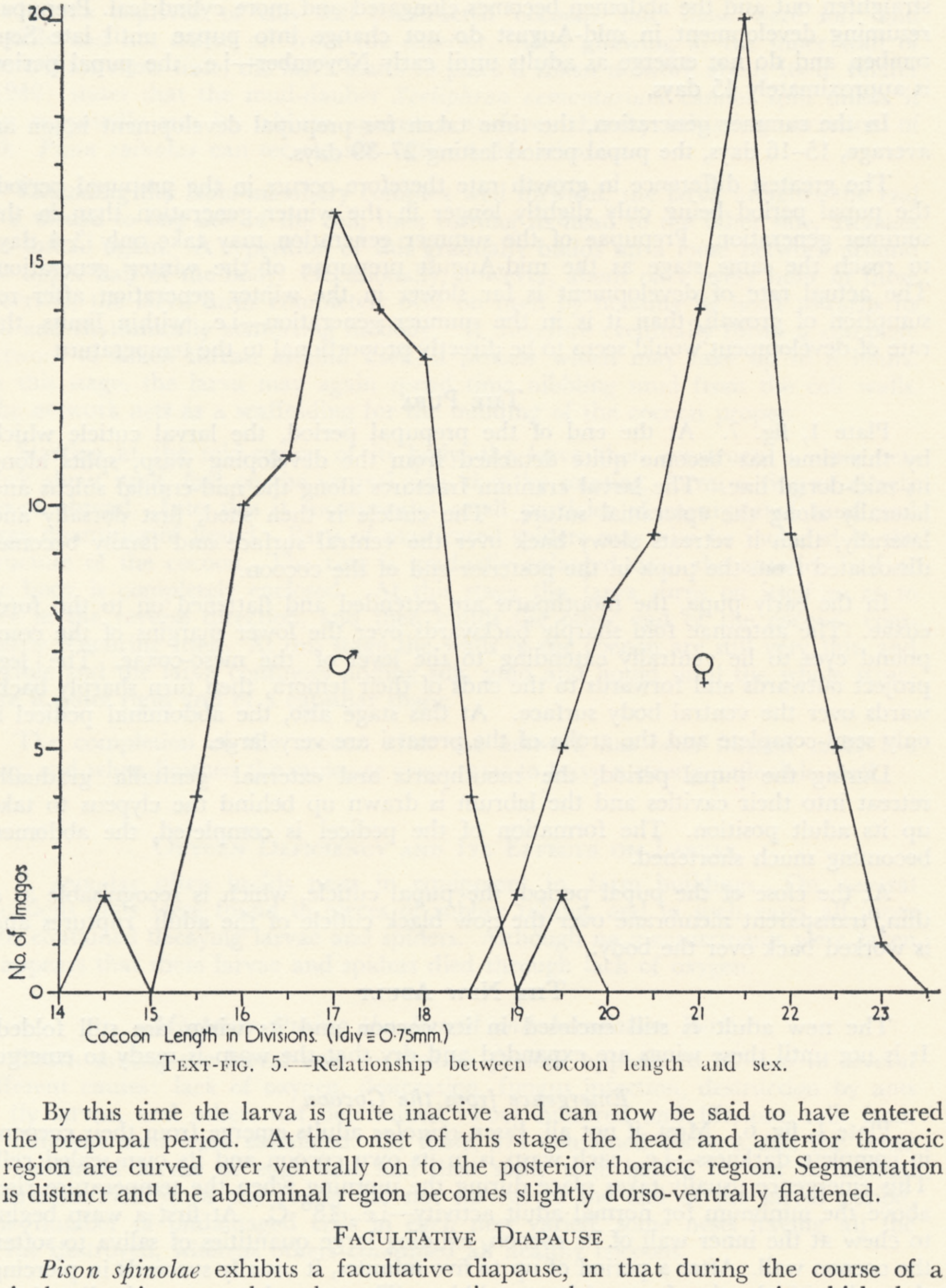
5.

6.



7.

FIG. 1.—First instar larva. FIG. 2.—Third instar larva. FIG. 3.—Sixth instar larva. FIG. 4.—Early prepupa of winter generation. Fig. 5.—Egg on *Araneus crassus*. FIG. 6.—Adult breaking out of its cocoon. FIG. 7.—Early pupae. All measurements in millimetres.



TEXT-FIG. 5.—Relationship between cocoon length and sex.

By this time the larva is quite inactive and can now be said to have entered the prepupal period. At the onset of this stage the head and anterior thoracic region are curved over ventrally on to the posterior thoracic region. Segmentation is distinct and the abdominal region becomes slightly dorso-ventrally flattened.

FACULTATIVE DIAPAUSE

Pison spinolae exhibits a facultative diapause, in that during the course of a single year, it passes through two generations, a short summer one in which there is no arrest of growth (no diapause), and a long winter generation in which growth is suspended (diapause) for 6 or 7 months. This period of arrested growth is spent in the prepupal state.

Prepupae of the winter generation may pass into a state of diapause from as early as the beginning of February till late March and show no visible external change until mid-August, when the head and anterior thoracic region begin to straighten out and the abdomen becomes elongated and more cylindrical. Prepupae resuming development in mid-August do not change into pupae until late September, and do not emerge as adults until early November—i.e., the pupal period is approximately 45 days.

In the summer generation, the time taken for prepupal development is, on an average, 15–16 days, the pupal period lasting 27–39 days.

The greatest difference in growth rate therefore occurs in the prepupal period, the pupal period being only slightly longer in the winter generation than in the summer generation. Prepupae of the summer generation may take only 3–4 days to reach the same stage as the mid-August prepupae of the winter generation. The actual rate of development is far slower in the winter generation after resumption of growth, than it is in the summer generation—i.e., within limits, the rate of development would seem to be directly proportional to the temperature.

The Pupa

Plate 1, fig. 7. At the end of the prepupal period, the larval cuticle which by this time has become quite detached from the developing wasp, splits along its mid-dorsal line. The larval cranium fractures along the mid-cranial sulcus and laterally along the epicranial suture. The cuticle is then shed, first dorsally and laterally, then it retreats slowy back over the ventral surface and finally becomes dissociated from the pupa in the posterior end of the cocoon.

In the early pupa, the mouthparts are extended and flattened on to the fore-coxae. The antennae fold sharply backwards over the lower margins of the compound eyes to lie ventrally extending to the level of the meso-coxae. The legs project outwards and forwards to the ends of their femora, then turn sharply backwards over the ventral body surface. At this stage also, the abdominal pedicel is only semi-complete and the arolia of the pretarsi are very large.

During the pupal period, the mouthparts and external genitalia gradually retreat into their cavities and the labrum is drawn up behind the clypeus to take up its adult position. The formation of the pedicel is completed, the abdomen becoming much shortened.

At the close of the pupal period, the pupal cuticle, which is recognisable as a thin, transparent membrane over the now black cuticle of the adult, ruptures and is worked back over the body.

The New Adult

The new adult is still enclosed in its cocoon and its wings are still folded. It is not until these wings are expanded and dry that the wasp is ready to emerge.

Emergence from the Cocoon

Plate 1, fig. 6. Most, if not all, *Pison spinolae* adults emerge from their cocoons in complete darkness—i.e., each wasp is in its own cocoon and its own sealed cell. This emergence usually takes place during the morning when the temperature rises above the minimum for normal adult activity—i.e., 18° C. At first a wasp begins to chew at the inner wall of its cocoon, exuding large quantities of saliva to soften the cocoon wall. After a period of up to five minutes, it usually succeeds in piercing the wall with the tip of one of its mandibles. The wasp then grasps the lip of the hole between its mandibles and breaks small pieces of the cocoon away. If these pieces fall into the cocoon they are pushed aside by the mouthparts and legs. As soon as the hole in the cocoon is large enough, the wasp thrusts its head and fore-legs out and pulls itself free.

A wasp may take 10–15 minutes from the time it starts chewing at the inside of the cocoon, until it emerges. On many occasions, when a wasp was not successful in breaking out of its cocoon it would cease activity until the following morning.

Emergence from the Nest

After the wasp has broken clear of its cocoon, it still has to escape from the nest. To do this, it is necessary for it to pass through at least one partition. The wasp chews at the inside of its cell until it is able to grip something with its mandibles. This is nearly always the roughened inner side of the partition the mother constructed when sealing off the cell. Linear nests with as many as 6 cells have been found, with only one hole to the exterior, this being through the last partition completed. Each inner partition had been bored through so that all cells were continuous.

Cocoon Length in Relation to Sex

Because of the difference in size between male and female adults, attempts were made to establish a relationship between this and cocoon length and therefore indirectly with larval size.

The lengths of 152 cocoons were measured and the sex of each adult noted as it emerged from its cocoon. From these observations, the graphs (Text-fig. 5) were obtained. We have here two normal growth curves, the top limit of the males overlapping slightly the lower limit of the females. This was expected as male imagos, though on the average distinctly smaller than females, are sometimes larger than the smallest females. It also implies that the distinction in size must be apparent at least as early as the last (6th) larval instar.

REFERENCES

KIRBY, W. F., 1883. Notes on a new or little-known species of Hymenoptera, chiefly from New Zealand. *Trans. R. ent. Soc. Lond.*, p. 199.

LEES, A. D., 1955. *The Physiology of Diapause in Arthropods.* Cambridge: Camb. Univ. Press.

MICHELI, L., 1933. Larva of *Pison atrum.* Note biologiche e morfologiche sugli imenotheri *Mem. Soc. ent. ital. Genoa. 12,* 6.

SHAFER, G. D., 1948. *The Ways of a Mud Dauber,* Stanford, Calif., Stanford Univ. Press.

SHUCKARD, W. E., 1837. *Pison spinolae* n.sp. *Trans. ent. Soc. Lond. 2,* 76.

INDEX TO TEXT-FIGS. 1 AND 2

abs, abdominal spiracle
an, anus
ant, antenna
cc, cranial capsule
cd, cardo
clp, clypeus
es, epistomal suture
fr, frons
ga, galea
hy, hypopharynx
la, labrum
lp, labial palp
m, mandible
mcs, mid-cranial sulcus
mp, maxillary palp . .
prl, premental lobe
sar, sternal area
so, salivary orifice
st, stipes
ta, tergal area
th, thorax
ths, thoracic spiracle

D. R. COWLEY,
Department of Zoology,
University of Auckland,
P.O. Box 2175, Auckland