博士学位申請論文

Studies on the biology and population dynamics of tiger beetle, *Cicindela japonica* (Thunberg)

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論文内容の要旨

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（論文題目）

Studies on the Biology and Population Dynamics of Tiger Beetle, *Cicindela japonica* (Thunberg)

（ナミハンミョウの生態と個体群動態）

（論文内容の要旨）

申請者の主論文は、幼虫期・成虫期ともに多食性捕食者であるナミハンミョウについて、京都大学上賀茂演習林に生息する1地域個体群を8年間追跡し、またその間餌条件を変化させて室内実験を続け、それらをあわせてこの甲虫の生活史、成長と発育、繁殖様式、個体群の構造、その動態などを明らかにしたものである。

成虫については数多くの個体を識別して、個体群の諸特性値を季節別・年別に調べ、また幼虫については全巣穴を標識し、各個体の発育・死亡を1つずつ追跡した。その結果まず第1に、本種が極めて変異に富んだ生活環を持っていることを明白にしている。すなわち、成虫は夏に羽化し越冬して翌夏に死亡し尽すが、その間ごく一部のみが秋に産卵を開始すること、幼虫の発育速度には著しい個性差が存在し、最もはやいものは殆ど2年で羽化するが、3年・4年あるいはそれ以上を要するものも存在すること、

どの令においても越冬可能であること、従って、ある年に羽化するものは6群以上の産卵群からなること、などがそれである。

次に申請者は、この著しい発育の変異が専ら期間中に獲得する餌生物量によって決定していることを、実証的に明らかにした。すなわち、幼虫の加令や蛹化は、それらがほぼ一定の体重に達することによって、しかもその場合に限って行なわれ、生存率もまた餌獲得の状況によって殆んど一義的に決定すること、また秋の産卵や越冬が成立するかどうかも、サイズによって定まった特定の体重に達するか否かによって決まること、などを明白にしている。

さらに、この個体群が成虫・幼虫ともに数のうえで安定していることを見つけ、その原因を究明しようとした。その結果、成虫間の干渉とそれに伴なう劣悪な生息場所への個体群の一部の移動が、個体数変化に対して補償的に働くこと、また先に挙げた幼虫の発育の著しい変異性と、一定の体重に達することによって産卵・越冬が開始されることとが、これまた同じく補償的に働くこと、などがこれに寄与しているのだと結論している。

なお、参考論文のうち1篇は、ハンミョウ類2種の生息分布に関するものであり、他の1篇はゲンジボタルの集団産卵の発見報告である。

主論文

STUDIES ON THE BIOLOGY AND POPULATION DYNAMICS OF TIGER BEETLE, *CICINDELA JAPONICA* (THUNBERG)

Michio HORI

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Introduction

Purpose

In the population ecology of insect, the progress made to date is much indebted to the studies on the herbivors such as pest of agricultural crops or forest. There are few basic researches which concern the populations of polyphagous predators, and it has not yet ascertained whether the concepts derived from the herbivors can be also applied to them or cannot.

The present paper concerns with field and some supplemental laboratory investigations of a tiger beetle, *Cicindela japonica* (Thunberg), for 8 years, 1972-'79. The adult and larva are both polyphagous predators; the former is a prowling type and the latter is an ambushing type in its own burrow. The purpose of these studies is to describe the ecological characteristics of the beetle and to analyze the structure and dynamics of the natural population.

In a predacious insect, it is anticipated that a large amount of variation among individuals in developmental speed and nutritive condition may arise depending on the amount of preys they took. In this point of view, individual discrimination should be adopted as far as possible in the field investigations, and special attention was paid to the process during which the variation arose and the manner haw the variation took part in population dynamics.

Material

Japanese common tiger beetle, *C. japonica* is the largest cicindelid in Japan, having body length of about 20 mm. The upper surface of body and elytra are coppery red with metalic luster and dark blue with velvety luster respectively, and a coppery red transverse band and some white spots (see Fig. 68).

This species had been regarded as a variety of *C. chinensis* Degeer which is distributed widely in the Far East. Nakane (1955) treated them as separate species based on differences in male genitalia and elytral markings. This species is found in Honsyu, Shikoku Kyusyu, Tsushima and Yakushima Island (Nakane *et at.*, 1963).

C. japonica is usually seen on paths and roads from the level land to the mountain region (Nakane *et al.* 1963). According to my observations, the beetles also inhabit the precincts of shrines and temples, cemeteries, dry riverbed and so on. Generally speaking, the habitat of this species is the bare ground which has some hardness and moderate moisture.

In spite of the commonness in Japan, there are few reseaches on the life history of this species. Only fragmental knowledges of habits, such as hibernation (Usami, 1950) and an enemy (Sibuya, 1948), and some observations on life cycle in rearing (Kurosa, 1965) were reported. The knowledges on mode of life clarified about European and North American species of this genus are regarded as being applicable to Japanese species (Miwa, 1936).

Study areas

The investigation on a natural population of the beetle was carried out at Kamigamo Experimental Forest Station, Faculty of Agriculture, Kyoto University. This station is situated in the northern slope and skirt of a long stretch of hills which lie from east to west in the northern part of Kyoto City, and its location is 35°04′N. and 135°45′E. (Fig. 1). The area is about 51 ha., most of which is plantation of pines (Pinus spp.) and natural forest of white cedar (Chamaecyparis obtusa Endl.).

In the station there are two sets of bare grounds which are separated from each other by a small hill (Fig. 2). The south side set surrounded by buildings, greenhouses, ponds and seedbeds, and linked together by narrow paths is called as Field-I (Plate 1, Fig. 67). The north side set around and between seedbeds is Field-II (Plate 2). These bare grounds constitute the main habitat of the beetle. The two fields are situated at altitude of about 140 m and at a distance of 50 m from each other connected with a road. The investigation was carried out mainly in Field-I and supplementarily in Field-II.

The meteorological data were recorded in Field-I everyday. Fig. 3 shows an outline of climate in this location during the study. The annual mean temperature, total precipitation in a year and normal value of total snow coverage is about 15°C, 1,300-2300 mm and 10 cm respectively.

Besides the survey at the station, the adult sampling was carried out in various places within Kyoto City (Fig. 1). The laboratory and an adjoining experimental field of Faculty of Science, Kyoto University, were also used for rearings of adults and larvae and for some experiments. In this location the meteorological data were recorded everyday in a screen apart 300 m from the laboratory.

Chapter I Life cycle

The life history of tiger beetles had been reported by Enock (1903), Criddle (1907), Shelford (1908) , Willis (1967) and others, and were reviewed by Balduf (1935). According to Balduf, in genus *Cicindela*, the eggs are laid separately in the soil. The larvae inhabit cylindric burrows prepared by their own effors at the just sites where they hatched, and catch small animals which pass by their burrows. There are three instars during the larval stage. The larva shuts the entrance of burrow with soil when to molt or hibernate. After each molt the larva reopens and enlarges the burrow to meet its larger body. When to pupate, the burrow is closed again, and the pupal cell is made in the soil. The newly emerged adult removes the soil at the entrance and comes out on earth. These statements also fit about the life cycle of *C. japonica* clarified by this studies.

Asanuma (1941) noticed that each instar has a defined width of burrow in any species of tiger beetles. Some preliminary surveys at Kamigamo Station revealed that it can be also applied in *C. japonica* (Fig. 4). The surveys also showed that the larvae seldom changed the sites of their burrows, and any other species of tiger beetle did not inhabit virtually in Field-I and -II. These informations indicate that by means of continual observations on the width and the opening or closing of each burrow, the development of each individual can be traced.

Methods

To trace the individual development of larvae, 7 working stations (St. A to St. G) were set up in Field-I. Table 1 shows the condition and period of survey on each station. Though all the stations were surveyed up to October 1978, few data was virtually obtained at Sts. B, E and F since September 1976, because of disappearance of larva.

Every larval burrow in these stations was labelled with plastic tape on which the numbers were carved (Plate 3), and the site of every burrow was mapped. After then, at a proper interval of time (usually either weekly or biweekly, and more frequently such as every day or every two days if necessary), the development and death of each individual were checked.

During this routine work, newly found larva was also labelled and recorded on a map. Of these larvae the 1st instar was regarded as a newly hatched larva, and the 2nd or 3rd instar was as the immigrant. The occurrence of the latters were, howerer, negligible at all. The larva whose burrow was closed and never reopened was regarded to be dead at the time when the burrow was found to be closed. Therefore the individual which died in the closed burrow was treated as the dead before the molt, regardless of the death happened before or after the molt. By the same reason, the death of pupa or adult which did not come out on earth after all was included in the death of the 3rd instar. The larva which closed its burrow in autumn and reopened in the following spring was judged as to enter hibernation at the time when the burrow was closed.

When the 3rd instar closed its burrow, the emergence trap, which have a shape like a sieve with 4 cm inside diamter and 2 cm height (Fig. 25, a), was set on the burrow to catch the emerging adult.

For adult, the investigation was done by the marking and recapture method. The details of the method will be described in Chapter X.

Larval stage

The 1st instars appeared twice every year, i.e., from May to July and in Septermber. These two groups are called here as an early summer and autumn cohort respectively. The number of individuals of the former was much larger than that of the latter.

Life cycle of the early summer cohort

Fig. 5 shows the seasonal change in number of larvae of each instar appeared in early summer 1975 in St. A. The 1st instars begin to appear in late May, and reach their maximum number in mid-June. By mid-September they disappear, as they die or grow into the 2nd instars, which appear from late June, and their peak is in early August.

Some individuals grow into the 3rd instars in August and September, and enter hibernation in October. But an appreciable amount of individuals do not attain the 3rd instar within the year.

They enter hibernation as the 2nd instars. Both groups reopen the burrows and begin their activities in the following mid-April.

Most of the 3rd instars close their burrows for pupation from mid-June to early August. The new adults emerge from mid-July to mid-September. The remainder of the 3rd instars hibernate again, and pupate at the same season of the 3rd year.

After the hibernation, the 2nd instars grow into the 3rd instars from mid-May to late June. A small portion of these 3rd instars pupate at mid-September, a little later than that of the group which wintered as the 3rd instar. But most of these 3rd instars do not pupate within the year but hibernate again, and pupate at the same season of the following year. And further, a small portion of these 3rd instars do not pupate but enter the 3rd hibernation, and emerge at the same season of the 4th year.

Thus, the larval growth of the early summer cohort is not monotonous but has great variations. The larval and pupal period inclusive is about 14, 26 or 38 months.

Life cycle of the autumn cohort

Fig. 6 shows the seasonal change of abundance of each instar larva appeared in St. A in 1975. The 1st instars appear from the end of August to the end of September having their maximum number in mid-September. A part of the early appearing individuals grow into the 2nd instar from mid-September to early October, and enter hibernation. The rest hibernate as the 1st instar. The two groups reopen their burrows toward mid-April in the following year, and develop into the 3rd instar sooner or later. They never pupate in that year, but hibernate again. Most of them pupate from July to August in the following year, but a small portion of this 3rd instars do not pupate, which enter the 3rd hibernation and emerge at the same season of the 4th year.

In this cohort, the larval and pupal period inclusive is about 24 or 36 months.

Adult stage

Emergence period

In 1973 the emergence traps were left for a year. But newly emerged adults were obtained only from mid-August to the end of

September (Fig. 7). Though the period varied yearly from the end of July to the end of October, the maximum number of the emergence is always observed in early September.

Adult life cycle

Fig. 7 also shows the seasonal change of the number of adults estimated by the marking and recapture method. The number of eggs laid within St. A was also shown, which was estimated by the method described later (p. 21).
The adults appear from August, attain to its maximum number in mid-September, then decrease in number gradually, and enter hibernation by mid-October. In the following year the adults begin their activities from Mid-April. From this time the adults decreased in number rather rapidly and die out by mid-July. Though the adults appeared again in the following month, there was no marked individual among them, i.e., they are newly emerged ones.

Thus the adult period is about a year at most, and the adults reproduce twice in a generation, i.e., in autumn immediately after the emergence and in early summer in the following year after the hibernation.

Life cycle of C. japonica

As mentioned above, the two cohorts derive from an adult generation. According to the observations under rearing condition, which will be shown later (p. 21), the egg period is 10 to 19 days and has no diapause or quiescence. Though the developmental speed of individual in both cohorts is much variable, most of them emerge as adults in the same period after two years from their parents did.

These facts mean that any two adult generations which appear consectively in the same place are not in the same strain or the parent-offspring relation.

A small portion of larvae, 0 to 14 % of the newly appeared 1st instars, never emerges at the emergence period after two years from their parent did, but hibernates again. The survivors of these larvae emerge as adults after three, or four years in very rare cases from their parents did. Thus, a small portion of larvae leaves their own strain and join with the other one at the period of adult emergence.

As a conclusion, Fig. 8 shows the life cycle of this species schematically.

Chapter II Foods

It is well known that both larva and adult of tiger beetles are polyphagous predators. For example, Shelford (1909) said that the food of the larvae consisted of land crustacea, centipedes, spiders, dragonflies, butterflies, flies, beetles and larvae of many sorts. As food of adult, Bulduf (1935) gave ants, flies, small beetles, aphids, spiders and a variety of nymphs or larvae. And they both considered that the *Cicindela* fed on any small animals which could be caught.

However, any detailed and quantitative reports on this subject have apparently not been published to date.

Methods

Foods of larva

Observation under the rearing conditions shows that the larva eats the soft parts of the prey caught, and the hard parts such as exoskeletons or appendages are thrown away in one lot around the entrance of burrow, though the minute pieces are often pressed tightly against the bottom of burrow. It is also observed that most of the leftovers are abandoned within a day since the prey was caught.

The leftovers around each burrow of all the 3rd instars were collected regularly from September 1975 to July 1977. This research was done in Sts. A, D and G, and three new stations (Sts. H, I and J) were settled. In St. J the work came to an end at October 1976, because of the extinction of larva. Collecting was done every day except on rainy days in September 1975, but after then at the intervals of 2 to 6 days.

For the 1st and 2nd instars, collection was only done at Sts. A and G from May to September 1976 on the same days as the 3rd instar.

The collecting was done with the naked eye in creeping posture. In the laboratory these leftovers were identified to the species if possible. The widest part of each material, such as the head or abdomen for ants and flies and the forewings for beeltes and Orthoptera, was measured by the micrometer set on the binocular microscope. The materials which lacked these parts were excluded from the analysis of the size of prey.

Foods of adult

When the adult which was eating a prey was found during the work of marking and recapture, it was caught, and the prey was brought to the laboratory to identify. Collecting were limited to the solid materials, and the liquid form mixed with saliva was abandoned. The width of the widest part of each material was measured.

Foods of larva

Validity of the materials

During the field survey, it was never observed that the leftover abandoned by larvae were carried away or eaten up by other scavengers, such as ants or silphid beetles. So, the disappearance of the leftovers may be caused, if any, only by some physical incidents.

There are some leftovers which can be identified in the field without any intricate procedures in the laboratory. To test the speed of disappearance, some leftovers, such as the heads of some ants, thoracic segments of some millipedes and the wings which belong to some sort of insects, were left on the ground and checked everyday in September 1975. These materials were never disappeard as far as there was no rain. When it was a heavy rainy day, almost all of them disappeared. For example, the heavy rain such as 66.2 mm in 11 hours or 6.3 mm in 2 hours was sufficient to remove them, while the light one as 7.2 mm in 9 hours or 6.0 mm in 4 hours had no effect. Thus, only the leftovers which were abandoned during the period between a heavy rain and the latest working day must be missed from collection. It means that as far as there was ro heavy rain, the frequency of survey has no effect on the efficiency of collecting at all.

As the collecting was done carefully around every burrow, and as almost all the leftovers which had been left on the ground were recorded every time, the efficiency of discovery on the leftovers of the 3rd instars must be high as close to unity. As the burrows and leftovers of the 1st and 2nd instars are small, there are possibilities that the efficiency for them is low and variable between stations or seasons. Thus, the materials of the 3rd instar are mainly analyzed, and comparative analysis between stations or seasons are refrained from for the 1st and 2nd instars.

Composition of preys of the 3rd instar

The leftovers obtained for the 3rd instars at all stations totaled more than 3,000. Appendix 1 tabulates the preys identified which cover almost all the orders of terrestrial insects.

Fig. 9 summarizes the food-composition and its seasonal change. In spite of the variety, some features are seen. Firstly, the preys mainly consists of ants, other kinds of Hymenoptera, flies, Orthoptera, beetles, Diplopoda and spiders, which are account for more than 80 % of the whole. Secondly, some seasonal trends are revealed in both years. For example, the ants increase in early summer and the Orthoptera do in autumn, Thirdly, the insects which move not only on foot but also by wing usually, such as flies and wasps, are caught appreciably. Lastly, not only the diurnal animals but also the crepuscular or nocturnal ones, such as Diplopoda, crickets and ground beetles, are caught in fair amount. These features indicate that the larvae ambush in all day and feed on any pray which can be caught.

Fig. 10 shows food compositions among the different stations from September 1975 to August 1976. There are some differences among them. From the indication mentioned above, the composition in each station must be the reflection of the fauna which are available to the larvae at each station.

Amount of preys eaten by a larva of the 3rd instar

As mentioned above, the leftover must be missed from the collection during the days between a heavy rainy day inclusive and the latest working day. Checking up the meteorological data, these days are excluded from each month. Here, a rainfall more than 2 mm per hour is defined as heavy rain. The number of the 3rd instars on residual days in the month are added up. Then an index is obtained as

$$\frac{\text{total number of leftover collected}}{\text{total number of 3rd instar larvae in the effective days}}$$

It means the relative value for the number of preys eaten per day by an individual in non-rainy days in the month. But, because the amount of preys in rainy day seems to be not so much and the efficiency of discovery on leftovers is considered to be high, the value may be not so much different from absolute one.

Fig. 11 shows these results. The amount of preys caught by a larva is very small; one prey per five days at most. In every station the amount of preys decreases in August, and rises again in September. The minimum value lies before and after the hibernation period. There is large difference in the amount of preys among stations, i.e., the value of St. D, the highest, is about three to four times as much as that of St. H, the lowest.

These results show that the seasonal change is the most prominent and the difference among places is more than that among years. The variability of food among places and among seasons may be a cause of the vaiability in the larval development, which was shown in the preceding chapter.

Difference in preys among instars

The compositions of preys of the larvae are compared among three instars with the materials collected from Sts. A and G (Fig. 12). Because each instar does not appear in the same season, the difference would not mean the change of larval preference for food. But this results and Appendix 1 show that the more the instar advances, the more diverse the preys are.

Size of prey

Fig. 13 shows the size of prey for each instar of larvae with the diameter of their burrow. Each instar eats most the preys whose sizes are approximately one half of the diameter of the burrow. The 3rd instar can eat also larger preys than the diameter of own burrow. The more the instar advances, the more the larva can utilizes broad range of prey, and the range covers that of the younger instar. This phenomenon may contribute the low mortality of the advanced instars (See Figs. 5, 6 and also Chapter VIII).

Foods of adult

Appendix 2 and Fig. 12 show the preys of adult and its composition respectively. The composition of preys has a variety, but not so wide as the extent of the larva. Ants, earthworms and the larvae of Lepidoptera are popularly eaten, and the adult should be called as polyphagous predator on ground. But it has some characteristic of scavenger, as some dead animals and even fruit which are going spoiled are eaten. In contrast with the larva, the adult shows a preference or selection for food, as soft and juicy animals such as earthworms and larvae of Lepidoptera are much eaten, and hard ones such as beetles, Diplopoda and land Crustacea are never recorded.

Fig. 14 shows what size of food the adult eats. They attack live animals of 0.5 to 3.8 mm in width, but eat larger organisms which are dying or decaying. The range of live animals is covered entirely by that of the larva.

Besides these collected materials, it was often observed that the adult picked up some minute materials on the ground and mumbled. Observing with the field glasses, some cases of them could be identified as small ants. And another ones seemed to be aphids, as the adults were earnestly picking up something on the ground where pterous aphids were abundant.

Chapter III Behavior and other habits

Methods

Adults

The general informations about adult behavior and habits were obtained by the survey at Kamigamo Station and the other sampling localities.

To obtain quantitative data, the adult locomotion was traced for one to three hours in every fine day from September 13 to 28, 1972, mainly in St. D. A range (3.5 x 3.5 m^2) of even bare ground in St. D was divided into 49 quadrats of 0.5 x 0.5 m^2 and each point of intersection was marked. All the loci of adults which appeared into this area were recorded on map as to be able to know the position of each individual at every 5 minutes. The observation was made from a shelter.

To know the habit of hibernation, the adults were searched and obtained from earth at three periods, i.e., at the beginning of, the middle of and the ending of hibernation from 1972 to 1978 and in 1981 at Kamigamo Station and the sampling localities. And some records on the hibernacula were made, such as depth from the surface and so on.

Oviposition and egg

To obtain the knowledge of ovipositing behavior and of egg, several females were reared in the experimental field from late April to mid-July 1973.

A pair of plastic baskets (22 x 27 x 6 cm^3) with large meshes (4 x 5 mm^2) were used as the rearing cage. One of these was backed with nylon cloth and filled with soil which was passed through a sieve of fine meshes size (1 x 1 mm^2). The basket was buried in the field as the upper end was at the same level to the surface of ground, and another basket was coverd on it (Plate 4). As a shelter, a cylinder (4 cm in diameter and 5 cm in height) was cut half vertically, and set at the center of the cage.

Each 8 females and males were collected from a sampling locality on April 26, and a pair was put in each cage. After the copulation was observed, which happened within the day or the following day, the male was removed from the cage.

In every morning the surface of soil in the cage was soaked enough with a watering can, and 2 fully grown and freshly killed maggots of blowfly (Lucilia illustris) were thrown into each cage as the prey, though small insects might come into it through the mesh. Each female was moved into a newly settled cage every two days, and the laid eggs were sorted out. The rearing was continued to the death of each female.

Cutting off the soil little by little with a surgical knife, the depth from the surface to the bottom of each egg and the number of eggs in each cage were recorded. The eggs were gently moved into Petri dishes, which were filled with fine soil sterilized by heating and were wet moderately. The dishes were settled in the laboratory, and the hatchability and the number of days till hatching were recorded.

Efficiency of the sorting was examined as follows. The same rearing cage and the beads whose size, shape and color were similar to the egg were prepared. My colleague buried a known number of the beads into the soil at the same depth to the actual oviposition. After soaked with water, I sorted out the beads with the same manner to the actual sorting. This simulation was repeated 6 times. The efficiency was always high, and its average was 95.9 %. As the egg is laid in a cavity, the actual efficiency should be higher than this. So, it may be regarded safely that almost all the eggs were discovered.

Larvae

To see the larval behavior of ambushing and jumping at prey, two obsevations and an experiment were done as follows.

i) The diel change of ambushing behavior was observed in the laboratory. As larvae retire quickly into the burrow as soon as to feel someone approaching, the automatic photographing device was used. Fourteen of the 3rd and eight of the 2nd instar larvae were offered to the observation. As described later (Chapter V), the larvae had been reared individually in a cylinder filled with soil, in which each larva dug his burrow and settled.

Arranging these cylinders by the window, the entrances of burrows were shot by 35 mm camera from overlooking angle every 10 minutes for 36 hours on June 6 and 7, 1975. This observation was carried out in the labotatatory closed completely not to disturb them, and no food was provided during the observation.

The developed films were examined to judge whether the individual was ambushing or not at each moment.

ii) The behavior of jumping at prey was observed in the field. As the hehavior is too swift to observe with the naked eye, the high speed movie films were used. Making a prey walk toward the burrow of the 3rd instar larva, the scene that the larva jumped at and pulled it into the burrow was shot. The millepeds, which were popularly eaten and walk slowly, were mainly used as the prey. Some injured ants, beetles and dummies of prey, which will be referred just below, were also used.
400 frames per sec., which is about 16 times as fast as the ordinary speed. This was done in the fine daytime during August and September 1974, 1976 and 1978 in co-oparation with Japan Broadcasting Corporation (NHK), and 33 scenes were obtained in total.

The developed films were examined to measure the time taken to catch and pull into, and the distance between the burrow and the site captured the prey.

iii) The relation between the size of prey and the jumping-at behavior was examined in Field-I on fine days in September 1978. As the dummy of prey, black balls of lead were prepared. With a rod and line, each ball was brought slowly toward an ambushing 3rd instar larva in the manner of angling fishes. Changing the diameter of ball from 2.3 to 14.5 mm, whether the larva jumped at it or not was observed. The trial was repeated about 10 times with each diameter of ball for different individuals.

Behavior and activity of adult

Diurnal change of activity

In general, the adult appeared in the bare ground at about 9 a.m. and disappeared from there at about 6 p.m. at latest in both autumn and early summer. But they were often delayed to appear in cloudy and cool days, and did not appear on rainy day.

The diurnal change of activity on the bare ground were studied based on the data of tracing, which cover the time from 10 a.m. to to 6 p.m.. As a criterion of activity, the walked distance for 5 minutes was measured from the locus on map with curvimeter, and the average values of every hour were compared (Fig. 15). The activity was high at 1 to 2 p.m., but low in the morning and evening. This change of activity agrees apparently with that of temperature. Dreisig (1980) reported a similar result for C. hybrida. The walked distance averaged for overall period was about 4.8 m for 5 minutes.

Roosting at night

The adults began to leave the bare ground about 5 p.m.. Seventeen events which ended in roosting were observed. In 7 cases of these, adults moved on food to the stones, concrete blocks and fallen logs, and concealed themselves under these. The remainder slipped away on wing into the foliages of cherry, abele, oak and so on. They perched on a leaf and lied there on their stomach with their legs stretched. Some of them were observed there again after sunset as it had been. Some of the roosts were examined again at 9 or 10 a.m. in the following morning, but all of them had left there already.

In the midnight of June 1974, two adults were collected by sweeping with net from the foliages of shrub at a height of 3 or 4 m, and three individuals were also taken from under the stones. They seemed to spend all-night at rest there.

Thus, there are two types of roosting sites, and which site is used seems to be not so important for adult. But, an impression was given that during the cool periods before and after winter they preferred to roost under stones rather than into bushes. There was no appreciable difference between both sexes in usage of the two kinds.

Adults are attracted to light at night. For example, 4 males and 2 females flew to a light in Field-II during 8 to 10 p.m. on July 18, 1973. And when I visited Kamigamo Station at night during the seasons of adult activities, I always found some adults at light. It seems a conflicting habit to that described above. But many authors reported this habit of Cicindela, and Larochelle (1977) reviewed them and totaled up to 111 species and subspecies. The observation under the light proved that these adults were never foraging there during night.

Behavior on bare ground in daytime

Fig. 16 shows an example of loci obtained by tracing adults. The adults were keeping the way out of grass, and were prowling about on the sunlit bare ground. So it resulted that they changed their prowling ranges gradually as the shade moved. They hardly flew up on their own accord, but did so when driven to the wall in a blind alley or when attacked suddenly by other individual of the same species or other insects.

Though the adults walked apparently around the same range of an area in Fig. 16, they left gradually from the beginning points as time passed, and showed no tendency to return there. In the more open area a locus of an individual was rarely entangled in itself, and often stretched in one direction straightly.

The adults showed neither any adherence to nor driving the other individuals away from a specific area. Thus, the adult is likely to have no territory as "any defended area" (Noble, 1939) or no restricted home range. The same result was reported for two species, Cicindela sachalinensis Morawitz and C. japana Motschulsky, in Japan (Hori, 1976).

Interaction between individuals

Even though the adult has no territory, the behaviors of running after or repulsing each other were often obseved. According to the tracing and other obsevations, when an individual encounters with another, the sequence of events is as follows in general.

At first, the adult orientates himself toward anything moving. At this time the adult stands still with his fore-legs stretched. This posture seems as if the beetle is watching for the situation.

Next, the adult starts to run toward the object. If the object is the adult of this species, it also starts to run toward the approaching one. Usually, they stop and face each other for a moment at a distance of 40 to 50 cm. At this time they often take a posture of stooping down, i.e., getting their bodies down and keeping their legs close to bodies. This posture seems as if they glare at each other to assess the identity and ability of the other.

Immediately after then, one of the three events happens; they run away each other to the opposite directions, they run against and grapple with each other, or one runs after the other. In the third case the chase results furthermore in one of the three events; the chaser stops chasing and runs away in the opposite direction, the escapee flies up and the chasing is ended, or the chaser catches up with the other and they grapple with each other. The grappling is violent but momentary, and results in running away each other to the opposite directions.

In the rare cases the grappling results in the copulation. In this case the chaser is the male. In other cases the possible combinations of both sexes are seen in any event.

The sequence can be summarized as that the encounter of two may cause the approaching each other. Except for the copulation, it necessarily ends in repulsing each other to the different directions, whether the grappling may happen or not.

Quantitative analysis of the interactions

Fig. 17 shows the distances between every two adults at every 5 minutes within a definit range (3.5×3.5 m^2) in St. D. The solid line is the theoretical values which are calculated with the formulae of spacing method proposed by Morisita (1950), and it means the frequency distribution of distances between any two individuals, if they are scattered at random. The observed values agree well with the theoretical ones in the range where the distance is much more than 2 m. So, they seems to have no relation with each other beyond this distance, because of being out of perception. Within the range where the distance is shorter than 2 m, the two values do not agree. When the distance is shorter than 0.4 m, no instance is observed. It must be caused by that whenever a collision happens, they repulse each other on the moment. The peak which lies in the range of 0.4 to 1.2 m may agree with the distance at which they stand and face each other, and the peak of 1.6 to 2.0 m must be the distance at which they can percept each other and orientate themselves to watch for the situation.

Fig. 18 shows the frequency of angles at which every two adults face each other in each grade of distance between the two. As the angle was determined between the directions of adult loci, the acute angle near 0° means that one approaches from behind of or runs after the other, and the obtuse angle near 180° means the approaching each other or the staying face to face.

The result shows that as the distance between two adults becomes shorter, the intensity of interference between the two increases, and that a sort of interference, i.e., orientation, occurs already at the distance from 1.2 to 1.6 m.

Fig. 19 shows the effect of the distance between two adults upon their activities after then. As the distance becomes shorter, the activities increase, i.e., the chasing or repulsing is apt to occur. The activities increases already at the distance of 1.2 to 1.6 m.

The adults seem to be settling down when they are apart from each other, as they walk at the relatively low speed. The encounter of two adults necessarily results in the separation from each other within a short period of time. So, in a long period of time each individual may be prowling about in a manner so as to maintain a relatively constant distance from the others. This behavior of adult may be called as "spacing" with a broad sense, containing in it a set of elements, i.e., approaching and repulsing

The approaching seems to have some meaning for hunting the prey and meeting with the opposite sex, and the repulsing may be efficient for dispersion of individuals and share the possible amount of preys. It will be partly discussed again in Chapter IX.

Hibernation of adult

It has been known that in many species of *Cicindela*, the adult digs a burrow in the soil for hibernation (Balduf, 1935). Shelford (1908) reported that *C. repanda* and some other species often hibernate in a group under the ground. For *C. japonica*, only one instance was reported (Usami, 1950) that 4 individuals were hibernating in a burrow.

Group hibernation

This study made sure that the adults commonly hibernate in groups. The habit may be called as group hibernation.

During the hibernation period 81 burrows were dug open. The number of individuals in each burrow varied from 1 to 28, and the average was 4.6 (Fig. 20). The sex ratio was about 0.5 when the number of individuals were much more than 10, but fluctuated in other cases.

Hibernation site and period

The sites of hibernating burrows are on vertical or inclined plane of precipice on the side of roads, the banks of streams or pond and heaps of soil. In general the burrow is dug horizontally. The depth of the burrow varies 3 to 20 cm and the average is 10.3 cm (Fig. 20, C). There is no appreciable relationship between the depth of burrow and the number of individuals in it. The inner part of burrow is somewhat broad and a narrow passage leads to this from the entrance, though the forward half of the passage is closed with soil during winter. It looked to be done by own effort of the adult.

These burrows are found in the state of their entrances opened at late September in early cases, but usually in early and mid-October. The entrance is left open usually for a week or ten days, but for three weeks in a longest case. It is reopened in mid-April, and the adults emerge. The time of opening is fairly constant year to year from April 13 to 18 inclusive in Kyoto City in so far as 1974 to '78. Once the entrance was opened, all the adults emerge within one or two days.

Behavior at entering hibernation

At noon of October 3, 1978, I happened to see a male digging a burrow on a precipice in Field-II. In the evening of the day day, the burrow had been dug so deep that the adult almost disappeared from the surface. According to the observations done every three days after then, the amount of soil thrown away by the entrance was increasing by degrees every time, and the entrance was closed 15 days after the finding. Digging out the burrow, 11 individuals were obtained.

In the afternoon of September 24, 1976, my colleague, who was observing the adult behavior in Field-I, happened to see that one individual just entered a burrow which was already there with its entrance opened. During two days after the day, he had observed at the same place for 5 and 2 hours respectively in the afternoon but no adult entered the burrow. During 4 hours in the afternoon of October 1, another adult entered the burrow (Nishimura, personal communication).

These obsevations indicate the process of group formation as follows. A burrow is dug completely by an individual, and its entrance is left open. During one or two weeks after then, the others looking for a hibernation site enter it one by one. They enlarge the inner part of burrow according to demand, and the surplus soil is brought to the outside.

The hibernating burrow whose entrance is open is easier to be found than one whose entrance is close. The open burrows, in turn, have the possibility that some individuals will be added after then in October or were lost already in April. Therefore the number of collected adults from each burrow mentioned above must be smaller than that of the actual.

There are 11 instances that an individual was collected from the burrow whose entrance was obviously closed. Thus the group hibernation may be the common habit for this species, though they can hibernate solitarily.

Sruvivorship during hibernation

No dead adult was found from these hibernacula. Taking account of the considerable number of collected adults, which must be smaller than that of the actual as mentioned above, there may be no death at all during the hibernation, apart from the possible destruction of burrow itself by the accident.

Oviposition and egg

The ovipositing behavior observed in field and under rearing condition was almost the same to those of _C. campestris_ and _C. purpurea_, which were summarized by Balduf (1935). The female first feels the ground with the protruded ovipositors as if to find soil of a texture suitable for digging. After then, she digs a hole with the ovipositors and lays an egg in it. During the work the female raises herself on her front legs till her body almost stood. Finally, she takes out the ovipositors, fills up the hole and rakes up the surface with the ovipositors.

C. compestris takes from 15 to 25 minutes during the whole operation of preparing a hole, laying the egg, and filling and scraping (cited by Balduf, 1935). In our species, the time varied from 1.4 to 23.5 minutes and its average was 8.8 from 11 times of observations in field. Under the rearing condition provided with the sieved and soft soil, the time was only 1 to 3 minutes. So, the preparing hole must take most period of the whole operation.

The sorting of egg revealed that an egg was laid in a cavity about 11 mm in depth from the surface of soil. The egg was an yellow elipsoid about 2.2 mm in length and 1.5 mm in width, and the cavity had about double size both in length and width. Sometimes, two cavities, or three ones in rare cases, containing an egg in each were made adjoining. The careful tracing of the soil texture revealed that the female made the cavities from the same point on the surface of soil. The ratio of these couple of cavities was about 22 % to the total diggings.

Fig. 21 shows the number of eggs laid by each female every 2 days. Every female oviposited continually till her death. Though the activity looked to have a cycle with an interval of several days. The eggs were apt to be laid on the day when it had rained just before and became warmer. As the result, the cycle of each individual was often synchronized with each other. The tendency was much clear in May.

Most females could survive till July, but died out in the month. There was a tendency that the death happened just after the oviposition which had been refrained for a long time.

The total number of laid eggs was also much varied among females. As this rearing had been started before the oviposition was observed in field, the fecundity in this species was regarded about 310, if we left the ovipositon in autumn out of consideration.

The hatchability of egg was 0.829 averaged for all females, and no difference among females could be detected. The period of egg stage was about 19 days in early May, and 10 days in early July.

To see the seasonal change of oviposition in field, the rule of total effective temperature was applied to the development of egg. Under a fixed temperature (T), the thermal constant (K) is expressed as

$$K = N\ (T - T_o)$$

where N is the number of days which is necessary to hatch, and T_o is the threshold of development. If the temperature fluctuate day by day (T_i), the formula may be rewritten as

$$K = \Sigma T_i - T_o N$$

$$\therefore\ \Sigma T_i = T_o N + K$$

Fig. 22 shows the relation between the observed number of days till hatching of each egg and the total mean temperature in the laboratory during the egg period, and a significant regression line appears.

Adding the dayly effective temperature in Kamigamo Station retroactively one by one from the day of hatching till the sum is over 110.3 °C, the day of oviposition could be estimated (Fig. 7). In every year the eggs were laid from late August to mid-September in autumn and from following early May to mid-July with its peak in late May.

Behavior and activity of larva

Diel change of ambushing

Fig. 23 shows whether the each larva was ambushing or not at the moment of every 10 minutes under rearing condition. They were ambushing during the night as well as the daytime, as suggested by the analysis of the leftovers. They were not nessesarily ambushing without a break for a long period of time, but often got down to the bottom. They looked to have some diel rhythm in ambushing behavior, though the obsevation was continued only for one and a half days. From midnight to noon of the following day, the rate of ambushing was high, but it decreased and the repairing the entrance of burrow was often observed in the afternoon.

The reason why the rate of ambushing on the first day was lower than that on the second is not clear. There is some possibility that they ambushed more intensely on the second day because of hunger. But there is no appreciable relationship between the intensity of ambushing and the amount of foods eaten or live weight just before the observation. It is also hard to consider that they were in caution at first, as they had been reared under the same condition except for flashing. The large variation of the ambushing behavior among individuals also can not be explained clearly.

This photograph proves that the larva always ambushes facing to the same direction.

Jumping-at behavior

Fig. 24 shows the sites of catching the preys and its range expected which were proved by shooting of high speed movie. The range shapes up a flat hemisphere around the burrow elongated backward but narrowed sidewards. It was also proved that the larva threw back the upper half of his body when catching a prey backward, as had been reported on C. hybrida by Faasch (1968), but he jumped at forward without any change from the ambushing posture, and twisted his body sidewards.

The period of time which was spent from starting to jump at to catch prey with his mandibles is 0.01 to 0.02 seconds in the 3rd instars. No agile animal seemes to elude this attack.

Jumping-at behavior and size of prey

The larvae of all instars easily reacted to the lead balls presented just above their burrow (Table 2). But they did not react to the freshly killed insects which were placed by the burrows during they got down to the bottom. They did not also react with jumping-at behavior to the sound and vibration caused by various sized tuning forks. When the tuning fork was touched on ground near the burrow (less than about 30 cm), all of them got down to the bottom quickly.

Table 2 shows that they jumped at most of the dummies whose diameters were less than 3.0, 6.4 and 7.2 mm inclusive for 1st, 2nd and 3rd instar larvae respectively, but got down to the bottom when the diameter was greater than each of those. Thus, there is a limit of prey size for each instar whether the jumping-at behavior is elicited or not, as suggested by the analysis of leftover (Fig. 13). But the value of the limit in this experiment was a little greater than that of the leftovers. Though size of leftover was measured at its widest part, the width of any appendages such as legs was excluded. And all the possible preys does not necessarily approach showing their front view. Therefore the value of limit in this experiment must be more critical than that of leftovers for the perception of larva. Holling (1966) suggested that the reaction of predator was varied with the own condition such as hunger. Thus, the value mentioned above itself does not necessarily show a definite limit.

As a conclusion, the larva has a particular range around his burrow. He perceives visually the moving object, and if it is preferable in size, he jumps at it when it enters within the range.

Chapter IV Enemies of adult and larva

It has been known that the adult of *Cicindela* is eaten by various kinds of predators, for example, the badger (Criddle, 1907), various kinds of birds in the world including shrikes (Larochelle, 1957, 1978), asilid fly (Wallis, 1913, Lavigne, 1972) and dragonfly (Graves, 1962). But detail study has not been reported. For *C. japonica*, an instance of asilid fly was reported (Sibuya, 1948).

No predator on larva of *Cicindela* have been known, but a bombyliid fly (Shelford, 1913) and some methocid wasps (Williams, 1913, Burdick & Wasbauer,1959) were reported as the parasites of the larva. Two species of *Methoca* have been known from Japan (Iwata, 1936), but there has been no report for attacking *C. japonica*. This study proved that one of the two, *M. yasumatsui* Iwata attacked the larva.

Methods

When the adult was observed to be caught or eaten by a predator during the routin work of marking and recapture, the predator was collected and brought to the laboratory to identify. When the dead adults were found during the same work, they were picked up to preserve, and their states were classified into three categories (see footnote of Table 4).

The female of *Methoca* has no wing and walks around on the ground. The male could never be found in this study. When the female was found during the routin work of the larva in each station, the site, the time and the size of wasp determined with the nacked eye into three grades were recorded. Tracing some female wasps in Field-I, the attacking the beetle larva was observed.

As the wasp closes the larval burrow with grains of sand after oviposition, the parasitized burrow is easily detected as long as there is no heavy rain. These burrows were recorded when they were found during the routin work of larva.

To see the development of wasp larvae and the number of eggs laid by the emerged female, some female wasps collected from Field-II were reared in the laboratory with the beetle larvae till the wasps of the following generation died out.

Enemies of adult

Table 3 shows the predators on the adult which were observed and identified. The largest number of records is of the weasel. In their droppings the elytra and other parts of the beetle were often found with the parts of carabid beetles. All of the listed predators are the polyphagous ones, and belong to the taxons which have been reported as the enemies of adult Cicindela except for the mantis. It seems that these predators are always present during the seasons of adult activities, but that non of them has a particular preference to the beetle. It also seems that the adults were all caught during the flight or roosting by these predators except for the shrike and the mantis, which were observed to attack the beetle on the ground in the daytime. So the adult may be relatively safe from the predation during the walking on the bare ground.

The dead adults were often discovered in Field-I. Table 4 shows the monthly number of collected carcases, classified into three categories according to their states. Those of category I was never caused by the predation. Most of category II had no sign of predation. Therefore an appreciable amount of death was caused by some reason besides the predation.

Most of category I was recorded in October. Considering the small number of working times in that month, the fact was more clear. It suggests that a considerable number of adults did not hibernate, but died. In the early summer the adult population is going to extinction, and as mentioned later (p. 73), the mortality is relatively high. The number of carcases was larger in May and June than in autumn. It suggests that the high mortality is caused by some reason besides the predation.

These results indicate that there is no predator which attacks the adult with paticular choice and that the death caused by the polyphagous predators is not so important for the adult.

Enemies of larva

Any predator on the larva was never found during this study. Only once the body parts of the 1st instar larva were found in a leftover of the same instar, but it may be an exceptional accident.

The attacking of M. yasumatsui on the larva was observed 37 times. The wasp parasitized only the 2nd instar larva. Though they attacked the 1st instar larvae twice and the 3rd instar once, they all stopped the attacking halfway and left the burrow.

The habits of the wasp observed in the field and laboratory agree well with that reported by Iwata (1936). The mature female usually oviposited once but exceptionally twice in one day. An egg was deposited on the ventral surface of the 3rd to 5th abdominal segment of the paralyzed larva. The period from egg to female emergence inclusive was 26.5 days averaged for 5 individuals in June and July, and their adult period was 21.0 days. One female ovipossited 8.3 times in average during the life time.

Table 5 shows the number of wasps observed in Field-I for 6 years. As the wasp was found to attack the larva of this species in the middle of 1972, the data of this year is excluded. Taking account of the number of working times, the wasps appeared in similar number from June to August. The 2nd instar larvae are always present during this period (Figs. 5, 6), though the abundance varies. Thus, the wasp can find their host in every season.

The result of rearing suggests that the wasp has at least three generations in one year. The small wasps appearing in midsummer must have emerged from the 2nd instar larvae which had been born in the year. The body length of the largest wasp and the smallest one are 7.0 mm in mid-August and 3.5 mm in late June respectively on the specimens collected from Field-II. The mortality of the larva caused by the wasp will be analyzed in Chapter VIII.

Any parasitic fly, and any other parasite could not be found. As the large amount of time were spent in the work on larva and a lot of the emergence traps were settled, which can catch the possible parasite of the 3rd instar larva, no parasite on the larva besides Methoca must be present at least in this field.

Chater V Growth and development of larva

As shown in Chapters I and II, the speed of larval development is much variable among individuals, and the food condition seems to be most responsible for this. To ascertain the problem and to obtain the other knowledges of the growth and development, the larvae were reared under various food conditions in the laboratory. The larvae were also reared outdoors, and some experiments were carried out, which yielded some supplemental knowledges.

It has been known that the larva of Cicindela closes its burrow above and constructs a special cell in which it pupates (Shelford, 1909, Criddle, 1910). Though the pupa was not investigated in field, some informations about this stage could be taken from the rearings and the experiments, which are also analyzed in this chapter.

Methods for rearing in laboratory

Rearing apparatus and foods

To rear the larva, a special cylinder and an equipment were devised (Fig. 25). Each individual was left to make its burrow within the cylinder. The equipment was set by a window which was left open except for winter.

As the preys, the adults of the flour beetle, Tribolium confusum, and the fruit fly, Drosophila melanogaster were used, both of which had been reared for long years in the laboratory. The latter is used only for the 1st instars in one rearing. Some fixed number of them (1 to 24 insects) were thrown twice every week in each cylinder, and the preys uneaten which had been provided at the latest time were removed from. At the same time the developmental stage of each larva was recorded judging from the diameter of or the state of the entrance of burrow.

Tracing the growth of individuals

The live weight of each individual was measured at the times as follows; the starting of rearing, when the entrance of burrow was reopened after the molt and after hibernation, when the fully grown 3rd instar larva closed its burrow, and when emerged adult appeared above ground. Besides these measurements, the weights of all the larvae whose burrows were open were measured simultaneously once or twice every month.

The times of rearing and the treatment

The rearing was done twice for the larvae which hatched in early summer and once for those hatched in autumn in different years. These are called as Summer-I, Summer-II, and Autumn rearing respectively.

Summer-I rearing consists of three series of larvae (A, B and C), and all the larvae derived from the experiment of oviposition in early summer of 1973. Among these larvae, a number of hatched ones were treated in Series A. The other larvae were left in the experimental field and collected again in August of the year and in April of the following year for Series B and Series C respectively. These three series of rearings were done abreast with the simultaneous food supply and measurement of live weight. Table 6 summarizes the other details in each rearing.

Growth and development in rearings

Results of Summer-I rearing

Fig. 26 shows the changes of live weight and the times when the instar advanced for the individuals which survived till summer of the following year. No individual survived to the pupal stage in Division e, f and i. As the variation of live weight was much small among hatched larvae (the mean and S.D. were 2.6 and 0.3 mg respectively), they were regarded to start from the same level of nutritive condition. The 2nd instars appeared from mid-July to the end of September, and the live weights at that times were also diversified from 17 to 23 mg.

The fastest individuals grew into the 3rd instar in early August, but those which had hatched late and were supplied with a smll amount of foods could attain this stage in July of the following year. The latest individual could not grow into this stage by August. The live weights of the new 3rd instars varied from 58 to 95 mg.

The increases of the live weight were S-shaped in general, and they were repressed before hibernation. The decreases during hibernation were a little. The reason why some individuals look to increase their live weights during winter is that they continue to feed from the last measurement for a while.

Among those which were supplied with a large amount of foods, only three individuals could survived and closed the entrance of burrow to pupate within the following year, and their live weights at the time was about 225 mg. The times of closing were from mid-June. The smaller the amount of foods supply was, the later the time was. Among the other divisions, any survived larva could not pupate, but hibernated again. In early August of the second year the survived larvae were heavier in an order based on what amount of foods they were supplied with. Among the same division the larvae were heavier in an order based on how earlier they had hatched. Thus, the speed of larval growth and development was changed conspicuously according to the amount of food supply. All the modes of development observed in this rearing were also seen in field.

The 1st and 2nd instar larvae grow into the following stage regardless of season except for the period before and after hibernation. A certain level of body weight is necessary to grow into the following instar, and the individual which cannot attain this threshold stay in the same instar. The shreshold descends as season progresses. This problem will be refered again in Chapter XI.

The 2nd and 3rd instar larvae can hibernate regardless of their body weights. Though the mortality during winter was rather high, there was apparently no relationship between their body weights and the survival.

Fig. 27 shows the growth and development averaged for the survivors of each division in the rearing of Series B and C. In Series B, the similar results were shown as those in Series A, and the former was supplementary over the range of food conditions which could not be covered by the latter.

The results of Series C can be regarded as if the food conditions were reset after hibernation for the individuals of Series A whose growth was delayed under poor condition. Among the 3rd instars in this series (Divisions t to w), the individuals under good condition of foods grew rapidly and pupated. Under poor condition, especially in Division t, the individuals hardly showed any growth, but hibernated again. All the individuals of the 2nd instar (Divisions n to s) grew into the 3rd instar, and individuals under good conditions pupated later than those which had hibernated as the 3rd instar.

In Divisions q and u, some individuals could pupate, but the others could not. The former was those which showed the better growth than the rest in each division.

These results prove that the larvae which winterd as the 2nd instar can also pupate within the second year, if their food condition is improved. In field some individuals grew in the same manner in every generation.

It seems to be necessary to get over a threshold of body weight when they pupate, as seen in the occasion when the instar advances. The threshold looks to descend as season progresses, and at least about 180 mg of live weight is required at mid-August. However a larva may attain to this level of live weight after the end of August inclusively, they never pupate within the year.

Results of Summer-II rearing

In this rearing the larvae which had hatched at the same day were treated and the amount of food supply was changed when the instar advanced (Fig. 28). The obtained results were almost the same as those of Summer-I rearing. The variation of the growth and development among individuals in the same division was fairly small.

Among the individuals which were supplied with a relatively large amount of preys during the preceding instars and the same amount in the 3rd instar, such as Divisions b'' and c' or Divisions b'and c, the difference was small and the effect in preceding instars was extinguished at all. The individuals which were supplied with a relatively poor amount of foods during the preceding instars but with a good condition in the 3rd instar, such as Division a'' compared with Division b, could catch up with the other which in turn get a poor amount of foods, within a short period. These results indicate that the food condition during the 3rd instar is more influential than those during the preceding instars in the growth and development of the 3rd instar larva.

Results of Autumn rearing

Fig. 29 shows the growth and development of larvae which hatched in autumn. The mortality during winter was fairly high, and in Divisions d and a, all the individuals which grew into the 2nd instar within autumn died out. Only several individuals of the other divisions grew into the 3rd instar.

The 1st instar larva could hibernate and the period of hibernation was long compared with those of the other instars. When the larvae grow into the 2nd instar within autumn, their body weight was much larger than those which had hatched in early summer. Especially among the former, the body weights of those which survived during winter was 25 to 35 mg, which was never observed in the latter. It is probable that the individuals of Division a which grew into the 2nd instar within autumn but died out in winter had an insufficient body weight to hibernate.

As this rearing was put an end at August of the second year, it is not clear whether the 3rd instar larvae which grew fast can emerge within summer of the second year or cannot. Considering the body weight only, it seems apparently not so hard to attain the level of 180 mg, if the food condition is good. But in field there was not an individual which emerged within the second year during the survey for 8 years. So, I am inclined to consider that these individuals hibernate again and emerge in the third year, no matter how large their body weight is. Based on the field obsevation, I also consider that the individuals which hatched in early summer never emerge within the year.

Purpose and methods for outdoor rearings

To see the exhaustion during winter, which could not be assessed accurately in laboratory, the outdoor rearing were done twice at the experimental field in the Faculty of Sience, Kyoto University, which are called as Outdoor rearing-I and -II.

In field it can be expected that the amount of food is variable with time and space in a dissimilar manner to the laboratory condition, in which the same amount was supplied regularly. To see the effect of the variability of food supply on the growth and development of larvae, two outdoor experiments were carried out in the same field, which are called as Outdoor experiment-I and -II.

To rear the larvae outdoors, a special cylinder was devised (Plate 5). The cylinders were buried as their upper end were at the same level to the surface of ground, and each larva was driven to make its burrow within a cylinder. They were supplied no food artificially but left to catch the natural preys with their own efforts. At proper intervals, the cylinders were dug out simultaneously to measure the live weights of larvae or pupae, and were put back to their former places. After they pupated, the emergence traps (Fig. 25; A-a) were settled to catch the emerging adults.

Outdoor rearing-I

On November 22, 1972, 16 larvae of the 3rd instar and one of the 2nd were collected from field, and driven into the cylinders, which were arranged in a lattice at 20 cm apart from each other. Within several days all of them closed the entrance of burrow to hibernate. The cylinders were dug out to check the survival and to measure the live weight once for every month till April 23 in the following year, when all the survivors reopened the burrows.

Outdoor rearing-II

In October 1973, the rearing was started with 2, 21 and 11 larvae of the 1st, 2nd and 3rd instar respectively all of which derived from one pair of adults in early summer of the year. The arrangement of cylinders was the same as that of Outdoor rearing-I. Any treatment was not done during winter. In late April in the following year, the larvae were dug out and their live weights were measured, and put back to their former places. On July 28 they were dug out again, and the pupae or newly emerged adults were obtained. These pupae were buried again and were traced till the adults emerged.

Outdoor experiment-I

On May 16, 1975, each 24 larvae of the 2nd and the 3rd instar which derived from one pair of adults in early summer of the preceding year, were driven to make their burrows within the cylinders. The arrangement of cylinders was the same to that of Outdoor rearing-I. The larvae of each instars were divided into three groups, Divisions a to c, and treated differently as follows.

Division a; setting a cover (using the emergence trap) on each entrance for 4 days and removing it for the following 4 days for the half number of the larvae in turns, the period of time available to catch preys were restricted half.

Division b; standing a screen (a plate of transparent plastics, 10 cm width x 5 cm hight) just behind each entrance of burrow, the approaching direction of prey was restricted half.

Division c; as control, the larvae were left as they were.

Each 8 individuals of the 3rd and 2nd instar were submitted in each division. The adults emerged from the 3rd instars were caught with the emergence traps. For the 2nd instar, pupae or emerging adults were collected by digging out the cylinders on August 24.

Outdoor experiment-II

Only one nest of the ant, *Formica fusca japonica* Motschulsky, happened to be in an area (160 x 200 cm^2) of the experimental field in May 1975. Around this nest, 8, 8, 8 and 6 cylinders were arranged on the concentric circles whose radii were 20, 40, 60 and 80 cm respectively (Plate 5). On May 14, 36 larvae of the 2nd instar which derived from another pair of adults in early summer of the preceding year were driven to make their burrows within these cylinders. All of them had grown into the 3rd instar by June 14. Then their live weights were measured to see the effect of the distance from the source of food supply on the growth of each larva.

Exhaustion during winter and variability of food amount

Decrement of body weight during winter and survival

Only three individuals of the 3rd instar died in Outdoor rearing-I, whose live weights was not necessarily smaller than the survivors. In Outdoor rearing-II, there were two individuals of the 2nd instar which seemed to be just after the molt judging by their live weights, but they all survived during winter. Thus the larval survival during winter is fairly high, which is also observed in field.

Fig. 23 shows the decrement of body weight during winter in Outdoor rearing-I. After an decrease, the live weight of each survivor increased slightly. As the feeding is impossible within the hibernacle, the increase may be attributed to the water absorption. The mean total decrement of each survivor during the hibernation is 6.4 % of the initial live weight. This light burden seems to make the high survival possible.

All the three individuals which died during winter increased their live weight after a month to more than 10 % of the initial. The phenomena suggests that the digging-out and the measurement during the hibernation might upset their physiological condition. As a circumstantial evidence about it, all the individuals survived during winter in Outdoor rearing-II in which any disturbance was refrained from.

In the laboratory rearings, the live weights were increased little during the month before hibernation in spite of the feeding on preys. It indicates that some preparation to hibernate is made during the period. The outdoor rearings have showed that the preparation is possible whichever the larval stage is and whatever its body weight is, and that it is good enough to stand the exhaustion during winter.

Variability of food amount and larval growth

Table 7 shows the results of Outdoor experiment-I. The increases of live weights from the 2nd and 3rd instar to pupal and adult stage respectively in Divisions a and b was smaller significantly than those in Division c. The days of adult emergence were also delayed in both divisions compared with the control.

The laboratory rearings showed already that the speed of growth and pupal live weight varied according to the difference of food amount. This experiment shows that the reduction of the time available to catch preys or of the approaching direction of prey has the same effect on their growth.

But, the difference among individuals of the same division is often greater than the difference of mean among the divisions. It suggests that there is some other important condition which is responsible for whether each larva can catch the preys much or cannot. It is assumed that the condition is the accessibility of preys to each larval burrow, which is defined by the microtopography such as the subtle unevenness arround each burrow.

Fig. 31 shows the result of Outdoor experiment-II. Between 20 to 60 cm of distance from the nest of ant, the more the distance was, the less the increase of the live weigh was. But the increase at 80 cm was great as much as that at 20 cm. The difference of the increases among individuals of the same division was also great, and the ranges of divisions overlapped widely each other.

These results can be interpreted as follows. The nearer the larval burrow is to a source of food supply, the more the larva can catch preys on an average. But, the other preys may immigrate into this experimental area from the outside, and the larvae nearest to the border may catch them most. The number of ants which pass by each burrow is varied according to not only the distance from the nest but also, as mentioned above, the subtle unevenness around each burrow. The latter might cause the large difference among individuals in the same division.

Thus, the concrete condition such as the definite site at which each burrow is settled seems to be more important to the amount of preys catchable for each larva than the general condition around the burrow. This must be one of the main causes which give rise to the great difference of the larval growth within the same station as seen in Chapter I.

Some notes on pupa and adult emergence

Pupa

Table 8 shows the period of pupal and adjacent stages. The period of time when entrance of burrow closed was about a month, and it was a little shorter in female, though it differed considerably among individuals within each sex.

This period consists of three stages, i.e., the mature larva, the pupa and the newly emerged adult, though these could not be discriminated in the field survey. The period of pupal stage occupied only about a half, and the mature larva, which stays quietly within the pupal cell prepared by itself, took the time a little shorter than that of the pupal stage. The emerged adult also stayed within the pupal cell for several days, during which the elytra grew hard. The length of each stage also differ much among individuals.

The measurment of live weight proved that the decrease of weight in pupa just after molt was about 5 % of the mature larva. After they had developed into the pupal stage, their weight changed little.

During these three stages, the mature larva and the pupa just after molt seem to be the most vulnerable. In the laboratory rearings the larva was dug out when the burrow was closed and its weight was measured. After this treatment, about a half of them did not pupate but died. In the outdoor rearings and experiments the individual which was dug out as the mature larva or pupa just after molt was apt to die after then. It is a conspicuous phenomenon compared with the other period of the 3rd instar, in which they hardly die. Most of the mature pupae and the emerged adults survived till appearing above ground.

Adult emergence

Fig. 32 shows the relation of the live weight of emerged adult, its size and the time of emergence to the live weight of pupa. There is a nearly linear relationship between the pupal and the adult live weight, and any significant difference cannot be detected between both sexes. The plots of adult live weight nearest to the equivalent line indicate that the adults are just after molt. The vertical difference between these plots and the line shows that the decrement of live weight involved at the emergence is about 10 to 15 mg. There is also fairly large decrement from the emergence till the appearance above ground, though it differs much among individuals.

There is a curvilinear relationship between the pupal live weight and the adult size. The variance within each sex is not so much, and the regression lines are separated each other clearly. It means that the female emerges with larger size than the male from the pupae of the same body weight, in spite of having similar body weight.

The live weights of pupae which developed into the adult stage by the end of August are more than 220 mg. The heavier the pupa is, the earlier it emerges, though this tendency is not so clear. The difference between both sexes is illegible. But, the live weights of pupae which developed into the adult stage after early September show the thendcy clearly. The smallest and the latest emergence is about 180 mg of pupal live weight at the end of September.

Fig. 33 shows the relation between the size and the live or dry weight of emerged adult. The both show the curvilinear relationship, though the former has a large variance. So, the large variability among the adult live weights related to the pupal live weight, as seen in Fig. 32, can be attributed not to the exhausion involved at the emergence but to the dehydration and the timing of appearance above ground. Therefore the live weight is inadequate criterion for the nutritive condition of each individual at emergence. The size seems to be suitable one, though there is a troublesome problem as that the both sexes cannot be compared each other directly.

Chapter VI Growth and maturity of adult by analyzing sampled materials

As shown in Chapter I, the adults emerge in August and September, hibernate from early October to mid-April and die out by July. Though they oviposite a little in autumn, the main reproductive season is from early May to their dying out. To see the growth and maturity along this cycle and to clarify what condition enable them to reproduce, the body weight and other characteristics of sampled adults were examined.

Methods

From August 1975 to October 1978, 8 to 25 individuals for each sex were collected with a insect net every one to three weeks during the period of their activities from the sampling localities (Fig. 1).

On the materials, the width of elytra, live weight, the number of eggs contained, and the number of corpora lutea, if any, were measured in the laboratory. Besides these, from August 1975 to June 1977, the measurements of the followings were obtained; the dry weight, crude fat contents, wet and dry weight of gonad, wet weight (Aug. ′75 to June ′77) or size (Sep. ′76 to June ′77) of testis, crude fat contents of gonad. From May to August 1978, the width of ovary, the number of ovarioles and the presence of sperms in the testis and the spermatheca were examined.

Out of these, the crude fat contents were measured by the procedure as follows. Each dried-up material was soaked in 30 ml of pure ethyl ether for more than three days. After the ethyl ether was renewed twice, the material was dried up again, and the difference between its dry weights before and after the extraction was regarded as the total crude fat contents.

The presence of the sperms was examined as follows. Dissecting the fresh materials, the seminal vesicle and ejaculatory duct of male or the spermatheca of female was observed with the smear method under the microscope. Besides this routine work, to obtain the histological informations on gonads of both sexes, the paraffin sections were prepared with the ordinary method.

In May 1976, taking out some fully mature eggs from the ovaries of some females which had various sizes and weight, the wet and dry weight and the crude fat contents of each egg were measured.

Some examinations on suitability of the methods

Comparison between the materials from the various places

The width of elytra, as mentioned in the preceding chapter, is affected largely by the food condition of larval period. The mean values of the width in samples differed from each other considerablly between the localities. So, the mean sizes of adult cannot be treated as if they are from the same population.

About all the other characteristics such as the weight and the state of maturity, it is proved as follows. When the mean values of every sampling time from the same localities were arranged seasonally regardless of the year, they did not show any clear seasonal changes. On the other hand, when the mean values from the same year were arranged seasonally regardless of the localities, they show smooth and some reasonable changes. Thus, it may be safe to comaper the characteristics of samples with each other seasonally without regard for the difference of the localities.

Crude fat contents

To ascertain the accuracy of the crude fat contents determined with the procedure mentioned above, some samples were soaked in ethyl ether four times in the same manner, and the dry weights were measured every time. After then, using a Soxhlet´s extractor with ethyl ether, the residual crude fat contents of these samples were measured in one lot. This test was done three times (Fig. 35). The results proved that almost all the amount of crude fat to be extracted by soaking could be taken by the 3rd time, and that the residual was almost negligible.

Judgement of the female maturity

The histological research proves that the ovary of each side consists of a number of ovarioles, whose mean is about 12.6 with the range of 10 to 16. There is no clear relationship between the number of ovarioles and the adult size. The ovariole is typical adephaga type (Evans, 1975), i.e., the developing egg cells alternate with groups of nutritive cells, and the mature eggs desend into the oviduct. In this type, the number of laid eggs cannot be assessed from the number of eggs contained in the ovary, because the egg cells develope continually and the mature eggs are laid one after another. But, as the degenerating nutritive cells remain behind at the base of ovarioles as corpora lutea, the experience of oviposition and the rough number of laid eggs can be known.

The maturity of each female can be classified by the state of its ovaries into five stages as follows (Fig. 36). Stage I; The ovary is thready and hardly shows any development. The female of this state is called as teneral. Stage II; The ovary swells slightly, but the egg cells hardly show any development. The female is immature. Stage III; The ovary swells fully, and the developing egg cells are present, but mature egg is absent. The female is maturing. Stage IV; The mature eggs are present usually accompanied with some corpora lutea. The female is reproductive. Stage V; The ovary is thready and any mature egg is absent, while many corpora lutea are present. Some degenerating eggs are often present. The female is spent.

Among these features, the width of the ovary which had been judged as Stages I, II and III is proved to change continually (Table 9). So, this classification is somewhat arbitrary near the border. The inseminated female can be detected by the presence of sperms within its spermatheca (Plate 6; 1 and 2).

Judgement of the male maturity

The testis is also a typical adephaga type (Evans, 1975), i.e., a simple coiled tube. The sperms are, if any, present from the base of testis to the ejaculatory duct, mainly between the vas deferense and the seminal vesicle. The maturity of each male can be classified into three stages as follows (Plate 6; 3 to 5). Stage I; The spermatocytes are already present in the testis, but spermatid and sperm is absent anywhere. The male of this stage is called as teneral. Stage II; The spermatids are present, but sperm is absent. The male is immature. Stage III; Sperms are present. The male is reproductive.

Seasonal change of adult characteristics

Fig 37 shows the seasonal change of each characteristic of both sexes. The mean width of elytra showed some temporal change. But the change cannot be analyzed as a seasonal one as mentioned above.

The mean live weight was the smallest at the emergence period, and the difference was slight between both sexes. By the time when they hibernate, the live weight increased to about 230 mg in male and 260 mg in female. The live weight of female increased once in September and then decreased by the end of this month. It decreased largely at the end of hibernation in both sexes. After the reproductive preiod began, it increased a little in male, but conspicuously in female.

The water contents were taken from the difference between the live and the dry weight. It was the largest at emergence period as about 70 %, and decreased after then to about 60 % of the live weight in both sexes.

The crude fat was contained little at the emergence period in both sexes. It had been stored up during autumn, and amounted to the maximum just before hibernation, which was about 20 % of the dry body weight. It decreased consistently during hibernation, and only a little amount was left at the end of this period. After then, the female held it more than the male. All over the adult period the absolute amount in female was a little more than that in male, but the ratio to dry body weight was not different between sexes except for the reproductive period.

The size and the weight of testis increased during hibernation, and did not show any clear correlation with their reproductive activity. But all the males held the sperms within their gonads except for the emergence and hibernation period. So, all of them must retain the ability of fertilization during their activities except for the period just after emergence.

A part of females in autumn and almost all of them in early summer held a number of mature eggs and corpora lutea. Along this seasonal change, the live and the dry weight of female gonad changed. The both weights were also large during hibernation in spite of no egg held, because of fat accumulation within the gonad. As the number of eggs averaged only for the females which held eggs in autumn was as much as those in early summer, a reproductive female holds about same number of eggs regardless of season.

In general, the values of male which indicate the nutritive condition, such as the body weight, crude fat contents and weight of gonad, show a single phase with a peak just before hibernation. These values of female show triple phases with peaks in autumn, just before hiberntion and in early summer.

The rate of the inseminated females was not so high in autumn, but 100 % in early summer. In both seasons only the females which held eggs had copulated.

Relationship between adult size and weight, and its seasonal change

Relative growth and its seasonal change

It has been known that the relation between the body weight and the size of insect, especially of adults, can be well described by "relative growth", which is defined as

$$\log W = b + a \log L$$

Here, W and L denote the weight (live weight in this paper) and the size (width of elytra) respectively; a and b are constants. To estimate the line from the measurements of samples, the method of least squares is used.

Fig. 38 shows the relation between the size and weight of all the sampled adults in each month. Though points were scattered, significant regression line was shown for each sex in every month, and it changed seasonally. Thus, this application looks to be effective.

As the adult size never changes, which was confirmed by records of the rearings and the field observation, each point moves only in vertical direction on the figure of relative growth according to the growth or waste of the individual. So, the vertical change of an regression line between successive months means the growth or waste of overall population during the period, and the change of its slope means that the rate of growth or waste is dependent on the size.

Fig. 39 compares the regression lines with each other again in each sex. The lines of both sexes rise continually from August to October, and fall in April. These rise again in May and fall a little in June. The rising of female in May is much more than in October, but that of male is not so. As these changes consist with the results of mean live weight, these are occurred similarly in every sized adults.

However, examined in detail, the slope of the line in April is smaller than those in the other months for both sexes. As the rate of decrement of weight during winter is about the same among various sized adults as proved below, the phenomenon can be interpreted as that the small-sized individuals grow faster than the large-sized ones after hibernation. The slope of line also decreases from August to September in each sex. The same process mentioned just above might be occurred.

Fig. 38 also shows that the relative growth in August and September is more variable than that in early summer. It is probably attributed to that newly emerged adults join the population continually and thus the age composition is much heterogeneous during the former period. So, it is necessary to examin the relative growth for the individuals of the same stage or maturity.

Growth from emergence to hibernation

Fig. 40 shows the relative growth in two stages for both sexes, i.e., just after emergence and beginning of hiberntion. The former data derived from the emerged adults caught by emergence traps, and the latter ones from those collected by digging out the hibernacles (Chapter III). The estimated regression lines are called as emergence line (E-line) and hibernation-starting line (Hs-line) respectively, which show the average live weight in relation to the size at emergence and beginning of hibernation.

The variability in relative growth at emergence is attributed to the variability of the water contents. The relative growth at the beginning of hibernation is also variable. As mentioned in Chapter III, the time to enter hibernation is different among individuals. This fact indicates that the individuals which have already sufficient nutritive store can enter hibernation soon when the period of hibernation begins. But those which have poor store and not ready to enter must continue to feed in order to attain a sufficient level of store. That is to say, there must be a threshold of body weight whether an individual can enter hibernation or cannot, which is defined by its size.

To estimate the threshold, a regression line was calculated for only those which seemed to be the lightest in each size group. The line, which is called as hibernation-starting threshold line (Hst-line), shows the minimum live weight to be able to enter hibernation in relation to the size.

The vertical distance between E- and Hst-line shows that the largest female (7.2 mm of elytra width) and the smallest one (6.0 mm) must increase their live weights at least 81 and 58 mg respectively from emergence to entering hibernation. The largest male (6.8 mm) and the smallest one (5.4 mm) must increase 66 and 50 mg respectively. Thus, the more the size of individual is, the larger the burden of increasing the body weight is for both sexes, though the rate of increase is a little smaller for the large-sized adult than for small-sized one.

Maturity in autumn

As mentioned above, some females hold eggs and the others do not in autumn. Fig. 41 shows the relative growth of the females collected during the reproductive period in autumn with distinction of the two. There is a clear-cut threshold of live weight whether an female can hold eggs or cannot in relation to her size. The regression line, which is estimated with the same procedure as Hst-line, is called as reproductive threshold line (Rt-line) of autumn female.

As most females which hold eggs have also some corpora lutea, they have already oviposited. As there is no female which has some corpora lutea and no egg in this season, the individuals which hold no egg have never been in reproductive stage.

The materials of autumn 1978 were examined on the maturity of their gonads and classified into five (female) or three (male) stages. Fig. 42 shows the relative growth of females with distinction of the stages and the existence of sperms in the spermatheca. The female in Stage V did not appear in this season, as mentioned above. As those in the other four stages are stratified in order of the maturity, the maturity advances with the increase of body weight. As the points of Stage I scatter around E-line, they can be regarded as ones just after emergence. Though Stages II and III were continuous each other in the width of ovary, they are splitted distinctly in this figure by a threshold line whether a female can hold immature eggs or cannot, which is called as maturing threshhold line (Mt-line). All the individuals in Stage IV have copulated, while those in Stages I to III have not. Thus, the threshold line of copulation in female agrees perfectly with Rt-line of autumn.

Hst-line runs lower and steeper than Rt-line. This line is also steeper than Mt-line, though the positions of both lines are not different so much from each other. Therefore, to mature during autumn, the small-sized females have to increase their live weights more than the level demanded to enter the hibernation. The circumstance is contrary in the large-sized female. The account of this fact will be discussed later in this chapter.

Fig. 43 shows the relative growth of males with distinction of their gonad stages. As the individuals in Stage I are around E-line, they are those just after emergence. As the number of those in Stage II is small, this stage must be passed in a short period of time. Most males are in Stage III, and the lower limit of their body weight is clear-cut. With the same procedure as female, reproductive threshold line (Rt-line) of male can be taken, which shows the limit whether a certain sized male can hold sperms or cannot. The estimated line has a position midway between E- and Hst-line with about the same slope as the two. So, all the males can attain the reproductive stage before hibernation, and the rate of increase in body weight is not different according to their sizes.

Waste during hibernation

At early October 1975 in Field-II, a large number of adults were marked and released. On January 29 (about the middle of hibernation) in the following year, digging out hibernacles, some number of marked adults could be recaptured. In April 1976 and '78, some number of adults which were just emerging from hibernacles were collected from the sampling localities.

Fig. 44 shows the relative growth of these materials with the records of the released and recaptured for each sex. The individuals which are just after hibernation are all, except for two females, between E- and Hst-line, mainly near the former. And a significant regression line can be taken, which is called as hibernation-ending line (He-line).

The vertical distance between Hs- and He-line shows the waste of each sized adult during hibernation. As the distance is similar regardless of size, a simple physiological process can be expected. It is partly proved by the fact that the rate of decrease in live weight at the middle of hibernation period is about half compared to those during whole period; the former and the latter are shown as the longest arrows of each period respectively in Fig. 44. There are some individuals whose live weights decrease a little or, on the contrary, increase. As they are all, except for two males, just above or below Hst-line, they might not enter hibernation just after the release, but might feed for a while and increase their live weights once. The result also means that the absolute decrement of live weight is larger for the large-sized adult than for the small-sized one.

On an average, the nutritive condition at the end of hibernation is better merely a little than that at emergence, which was also shown from the crude fat contents. But, in respect to the level of live weight at which each individual starts to grow, there is large variation between individuals. Some adults have a level which is sufficient already to reproduce judging from Rt of autumn. The variation existed already at the starting of hibernation as shown in Fig. 40, and must have been preserved till the ending.

Growth and maturity in early summer

Figs. 45 and 46 show the relative growth in April when adults restart their activities and in May and June when they reproduce respectively with distinction of their maturity in each sex.

In April the females in three stages are splitted with each other perfectly by Rt- and Mt-line of autumn. The males in Stage III and those in Stages I and II are splitted nearly by Rt-line of autumn. So, to start the reproduction, adults of both sexes must attain Rt regardless of season.

After they start to reproduce in May, the situation changes completely. Almost all individuals in both sexes are in reproductive stage whether they are above or below Rt-line. And the rate of inseminated females was 100 %.

Some notes on egg in respect to the size of female

Fig. 47 shows the relation between the size of female and the weight and fat contents of her eggs in early summer. The depth of laid egg from the surface of soil and hatchability of the egg, which were observed within Petri dishes, were also shown. The latter two data derived from the outdoor rearing of female in early summer of 1973. The weight, fat contents and hatchability of egg never looked to change in respect to the female size. The female weight also never looked to affect these characteristics of egg. Thus, the condition of a female is not succeeded into her eggs.

The depth of egg became deeper according to the female size, though it varied much among individuals. It is natural, because the ovipositors may be long for the large-sized female. Thus, there is a possibility that the hatchability of eggs in the soil may differ according to the female size.

Some consideration on growth and maturity of adult

As shown above, live weight of an adult at emergence is defined by its size. After then the size is never changed, while the live weight changes according to their feeding or waste. Though the gonad has been already completed by the emergence, the production of mature eggs or sperms are also dependent on the feeding after then. They must also feed to store an amount of nutrition to hibernate.

There is a threshold of live weight whether an adult can enter hiberntion or cannot, which is defined by its size. As the threshold line is nearly parallel to the emergence line, the rate of increase in live weight demanded is same for any sized adult in each sex. That is to say, as an absolute amount, the large-sized adults have to increase their weights more than the small-sized ones. On the other hand, it is hardly considered neither that the amount of preys caught by each adult for a limited time is sufficient to grow at its best, which will be proved in the following chapter, nor that the amount varies according to the adult size. Therefore the burden of large-sized adult to store nutrition seems to be larger than that of the small-sized one. The circumstantial evidence is given by the fact that the slopes of the regression lines in September are smaller than that of E-line in both sexes.

However, the larger the adult size is, the earlier its emergence time is. So, the period of time available to feed is longer for the large-sized adult than for the small-sized one. Thus, the situation during this period is not necessarily disadvantageous to the large-sized adult compared with the small-sized one. It can be merely said that whether an individual can hold a sufficient store or cannot is dependent on its emergence time, its size and the concrete food condition after its emergence.

Most of the nutrition stored during autumn is consumed during winter. Though the amount of nutrition left is on an average only a little larger than that at emergence, there is a large variation among individuals. The individuals which store an amount much more than demanded for hibernation can start to reproduce with relatively a little amount of feeding in spring, and females gets a possibility to oviposite within autumn. Therefore it is meaningful for each adult to store nutrition as much as possible during autumn.

As the slopes of Mt- and Rt-line of female are both smaller than that of E-line, the rate of increase in live weight from emergence to these stages is larger for the small-sized female. It must be attributed to the facts as follows. The size, weight and crude fat contents of mature egg and the number of ovarioles are all nearly the same with each other regardless of the female size. So, each female must intake the same amount of nutrition regardless of her size to hold a same number of mature eggs.

It means that the burden of small-sized female is larger than the large-sized one to reproduce in autumn. Moreover, the former emerges late compared with the latter in general. So, the small-sized female must be hard to reproduce in autumn, as shown in Fig. 41. The small-sized female, on the other hand, can attain the condition to hibernate more easily compared with the large-sized one. These mean that the small-sized females reproduce mainly after winter.

To mature and reproduce in early summer, the females must attain to the same levels of nutritive condition which are demanded in autumn. So, the levels must be defined by some kind of physiological switching mechanism. After the females start to reproduce, they continue to oviposit regardless of their nutritive conditions. They must change their physiological channels from the self-preservation to the reproduction. They use their nutrition effectively, because the end of the physiological life span is drawing near at any rate.

In autumn, on the other hand, the nutritive condition of females which had reproduced never descend below Rt. It may be disadvantagious to reproduce in autumn at the sacrifice of their survival during and after winter.

The male can reproduce both in autumn and in early summer. The Rt-line is far below Hst-line, and is nearly parallel with E-line. It may be caused by that the male needs not so much nutrition to reproduce compared with the female, and that there is little difference in the burden among every sized males. The fact that almost all the males can hold sperms in autumn seems to secure 100 % of insemination for a relatively small number of mature females.

Both in autumn and in early summer, all the females which hold mature eggs have been already inseminated. It may be caused not by that the copulation urges the eggs to mature, but by that the female which can hold mature eggs changes her attitude and elicits a copulation behavior of male, because the maturation of a female is dependent on its nutritive condition.

Chapter VII Growth and reproduction of adult in rearing

To see the growth and reproduction continually in respect to the thresholds which were revealed in the preceding chapter, the adults were reared under various food conditions.

Methods

Adults were reared once in autumn 1974 for both sexes and once in early summers 1975 and ´76 for female and male respectively. And females were reared all over their life span twice from autumn 1975 and from autumn 1976 to the following early summer. These rearings were called as Rearing-I, -II, ... and -V respectively. The adults derived from larval rearings and collection from field.

To see the growth and reproduction in respect to the amount of food eaten, a rearing cage was devised (Plate 7). These cages were put on shelfs in a roofed passage, where it gets a good light and well ventilation, but direct sunshine and rain were prevented from. The adults were kept individually in these.

As the prey, the fully grown maggots of blowfly (_Lucilia illustris_ Meigen) were used, which are sold as a bait for fishing with a relatively equal quality. From the live maggots, similar sized ones were selected, and fixed with the pin-and-clips on the bottom of the cage. The beetles were divided into some divisions in every rearing, and a fixed number of preys were provided for each division every 2 or 3 days. At the same time, the preys provided at the latest time were removed, and the leftovers were dried up and weighed. The amount of food eaten was assessed by subtracting the dry weight of leftovers from average dry weight of the same number of maggots.

The number of laid eggs were counted with the same sorting method as the outdoor rearing of female (Chapter III). The other details in each rearing were as follows.

Rearing-I in autumn

The newly emerged males and females were obtained from larval rearing and from emergence traps in Field-II at various time, and some females of unknown emergence time were collected from a sampling locality on August 1 and 31.

To make the chance of copulation, every female was kept with a male in the same cage for half a day, two weeks later from the starting the rearing. This rearing was continued till each adult made the hibernacle in the soil and entered in.

Rearing-II and -III in early summer

Every female was contacted with a male collected from a sampling locality on May 6. The both rearings were continued till all of them died out.

Rearing-IV and -V from autum to the following year

The females were reared twice to see the relation between Hst and the survival during winter, and to ascertain whether the female which had oviposited in autumn could survive and oviposit again in the following year or could not.

Keeping the adults alive during winter within the cages was failed in Rearing-I, probably because of its insufficient volume of soil. In Rearing-IV and -V, an outdoor cage was prepared in the experimental field (Plate 8). When each individual began to make the hibernacle in the rearing cage, it was moved into the outdoor cage. The adults which showed no sign to make the hibernacle were moved into the outdoor cage at mid-October (on 11th in Rearing-IV and 15th in Rearing-V). Every individual was marked with brand, which will be described in Chapter IX. Within the outdoor cage, a fairly large amount of preys were provided every day till the end of the month. At the following mid-April, the appeared adults were collected. The rearing was continued again within the rearing cages under the same food condition as autumn for Rearing-IV, but was terminated at the time for Rearing-V.

The eggs were sorted out only to ascertain the oviposition, but exact number was not counted. In Rearing-IV every female was contacted with a male for half a day at the beginning of both seasons. In Rearing-V any chance of copulation was not made.

Table 10 summarizes the number of individuals in each division and the treatments of these five rearings.

Thresholds and relative condition factor

Thresholds in growth and reproduction

Fig. 48 shows the increase or decrease of body weight of each individual for each sex in Rearing-I in a figure of relative growth. The ovipositing female was almost always heavier than the reproductive threshold (Rt), and even only one exception was the female which was just below Rt. These female were the individuals which had taken a chance of copulation when their body weight had been above Rt. The female whose body weight had been below Rt at the chance of copulation never oviposited, even though the female could get over Rt after then. When the individuals in both sexes entered hiberntion, all of them were heavier than hibernation-starting threshold (Hst).

These results confirm the presence of Rt and Hst in the process of growth and reproduction, and show that Rt of female is also the threshold of effective copulation.

Relative condition factor

To trace the temporal change of the nutritive condition of an individual in respect to reproduction or hibernation, an index was diviced as follows. As the point of an adult moves only vertivally on the figure of relative growth, the vertical deviation from an regression line (E-line, Hst-line or Rt-line) must show the relatively better or worse nutritive condition in respect to the related stage (emergence, starting to hibernate or starting to reproduce). The deviation (Δd) is represented as

$$\Delta d = \log W - (\log a + b \log L) = \log (W / aL^b)$$

Here, W and L are the live weight and the width of elytra of an adult respectively at any time, and a and b are the constants specific to the regression line. All the values of a and b of the lines which were proposed hitherto are shown in Appendix 3. In other words, the deviation was the logarithm of the ratio of live weight at any time to live weight specific to the size at the stage chosen as a standard. This index was born from a discussion with my colleagues, and Yuma (1981) applied it to assess the nutritive condition of the mature firefly larvae (*Luciola cruciata* Motschulsky).

Le Cren (1951) already proposed the same index, but not in logarithm, to represent the nutritive condition of perch, as

$$K_n = W / aL^b$$

and called it as relative condition factor. As the presentation in logarithm is rather incomprehensible, it may be better to use the index of Le Cren itself and then to use its name (Rcf) in our analysis. But it must be noticed that the size does not change in the adult stage of this species and probably in most of insects in contrast with fish. Le Cren (1951) used the index as the ratio of a value at any time to the maximum value. But the ratio may be uncertain to detect the nutritive condition, because the maximum value may change among years or places. On the contrary, our usage of the index is based on the developmental stages which have been ascertained by another aspect, and therefore may be more well-grounded biologically.

When we want to use Rcf, the standard of it should be mentioned together, such as Rcf to Rt or Rcf to Hst. But it may be convenient to use Rcf to E as a general index to compare the nutritive condition of an adult in different times or adults in differnet stages. The index in this usage will be called as only Rcf.

Growth and development referred with Rcf

Rcf in autumn

Fig 49 shows the temporal change of Rcf in Rearing-I for the individuals of both sexes which could be traced from its emergence to the end of September.

The males which had emerged early increased their Rcf rather rapidly at first, but slowly from mid-August to early September. During this period, the preys were often left uneaten, especially in the males which were provided with large number of preys. On August 20 all the males could inseminate the females effectively, so long as the condition of the female was ready. It is natural, because Rt of male is from 1.17 to 1.18 in respect to Rcf. All of them got over Hst (from 1.32 to 1.50 in respect to Rcf) without difficulty by the end of September.

The males which had emerged late increased their Rcf also rapidly, and got over Hst without any standstill by the end of September. As these males were not contacted with female, their abilities to inseminate was not clarified. But, as most males had sperms at the end of September in field (Fig. 37), even the lately emerged males may have the ability, so long as they get over Rt.

The females which had emerged early increased their Rcf rapidly, and then oviposited. They finished oviposition and got over Hst (from 1.38 to 1.46 in respect to Rcf) by the end of September.

The females which had emerged late also increased their Rcf rapidly, and entered hibernation without oviposition by early or mid-October. Generally in both sexes and in both groups of emergence times, the more the preys were provided, the larger their Rcf were at any time.

Rcf to Hst, survival and oviposition in the following year

From the definition, Rcf to Hst of any adult must be above unity to enter hiberntion. In Rearing-I, Rcf to Hst of all the individuals got over unity eventually. In Rearing-IV and -V, Rcf to Hst of some females were forced to be lower than unity by poor food supply even at mid-October, and their survival to the following year and whether the females could oviposit again or could not were checked.

Table 11 summarized the results of these two rearings. The relation between Rcf to Hst and the survival (A) was highly significant ($P<0.001$), while the relations between the oviposition in autumn and the survival (B) and between the ovipositions in two seasons (C) were insignificant ($P> 0.7$ and $P> 0.4$ respectively). So, the females were not necessarily apt to die as a result of oviposition in autumn itself, but ones whose Rcf to Hst were below unity were more easy to die than the others.

It turned out that most females oviposited in early summer even under the poor food conditions, though they had not oviposited in autumn under the same condition. The result is attributed to the phenomenon that once the reproductive period begins the female oviposits regardless of the level of Rcf to Rt, as shown in the preceding chapter. It also proved that the female which had oviposited in autumn could do again in early summer.

In the natural condition the adult which entered hibernation could all survive to the following spring, as suggested in Chapter III. In these rearings the result was somewhat illegible. As adults which had entered hiberntion in the rearing cages were removed into the outdoor cage, some disturbance on physiological condition might happen. On the other hand, some adults whose Rcf to Hst was below unity at the onset of the hibernation period might be able to eat within the outdoor cage to get over the threshold.

Some females were reared from their emergence without any contact with male in Rearing-V, and they never oviposited. In

Rearing-IV the females had never oviposited in early summer till they contact with male, in spite of being inseminated in autumn. So, the copulation is necessary to oviposit in each season. In this connection, the dissection of hibernating females at early November suggested that the sperms in the spermatheca was ineffctive no longer.

Rcf in early summer

Figs. 50 and 51 show the temporal change of mean Rcf of each division in Rearing-III (male) and in Rearing-II (female) respectively. Mean Rcf of male in each division was maintained within relatively narrow range compared with the change in autumn, though it fluctuated and had large variance. Mean Rcf of Division a was consistently below the others. But in female, the more the preys were provided, the larger the mean Rcf was, though all the females in every division continued to oviposit at any rate. Mean Rcf of Division a decreased gradually, suggesting that the amount of food as 1 maggot every 3 days was insufficient to compensate for the expense of continual oviposition.

As Rt-line of female is not parallel with E-line, Rcf does not indicate the exact nutritive condition in respect to oviposition. Fig. 52 shows the temporal change of mean Rcf to Rt of female in each division and that of mean number of laid eggs every 3 days. In general, Rcf to Rt and the number of eggs were large in order of the amount of food supply, though the both much fluctuated with large variance. The mean number of laid eggs in Divisions a, b and c from May 14 to June 30 were 42.0, 119.7 and 139.1 respectively. Even the value in Division c is much smaller than the fecundity of this species (about 310), which turned out from the outdoor rearing (Chapter III). So, the amount of food as 6 maggots every 3 days must be insufficient to perform the maximum reproduction.

Effect of food amount on growth and number of laid eggs

Food amount and growth in autumn

Fig. 53 shows the relation between Rcf of each individual at late September and its total dry weight of food eaten from emergence to the time in Rearing-I. The more the individual ate, the larger its Rcf was in both sexes. The female seemed to need an amount of food more than aout 300 mg to hibernate, judging from the level of Hst in respect of Rcf.

The small-sized adults could have larger values of Rcf than the others with the same amount of food in both sexes, suggesting that small-sized adults can get over Hst with relatively small amount of food. It may be an important process, because small-sized adults emerge relatively late and have short period of foraging.

Food amount, growth and number of laid eggs in early summer

Fig. 54 shows the effect of food amount taken by each female on the number of laid eggs, mean Rcf and mean Rcf to Rt in Rearing-II. The number of eggs increased linearly as the amount of food increased. Mean Rcf and mean Rcf to Rt were also increased as the amount of food increased, though it is neither so clear nor linear. As Rcf and.Rcf to Rt did not increased temporarily even with large food supply in this season in contrast with the process in autumn, the income must be invested entirely in eggs. And the female which was making many eggs should, as a result, maintain large value of Rcf and Rcf to Rt.

The small-sized females laid eggs more than large-sized ones with the same amount of food. It is reasonable, because the maintenance of individual of the former must be smaller than that of the latter.

Fig. 55 shows the mean number of eggs laid by each female on the figure of relative growth. Though there were some exceptions, the smaller the size of female was, the more it could oviposit with the same level of body weight. This process may have important meaning for popultion dynamics. Because the small-sized females are apt to appear in the year or place of poor food condition. If they survive to the following year, they can oviposit eggs more than the large-sized ones with the same amount of food.

Fig. 56 shows the relationship between the both directly. When the value of Rcf to Rt got over unity, the number of laid eggs increased sharply. The individuals which had the lower Rcf to Rt than unity was those whose body weight decreased gradually, except for one female. It means that oviposition of these females exhausts their nutritive condition itself, and that the efficiency of reproduction is also low. The mean survival period of Divisions a, b and c from May 14 were 56.2, 71.6 and 68.3 days respectively. So, the exhaustion seemed to affect the length of survival period.

Fig. 56 also shows the relationship in Rearing-I. The female in autumn oviposited only when its Rcf to Rt was larger than unity, and its number of eggs per day is always smaller than those in early summer with the same level of Rcf to Rt. These results suggest that nutrition is reserved for hiberntion in autumn, and only the excess is used for reproduction. The process may be advantageous to survive to the following year and to oviposit, though the survival rate of adult and of two cohorts of larva must be compared each other in detail to assess its meaning on population dynamics.

Fig. 57 examines the effect of food amount on Rcf of male in early summer. The more the food was eaten, the larger the value of Rcf was within a same grade of size. The small-sized males had larger value of Rcf than large-sized ones with the same amount of food. But all of them are considered to maintain the ability of insemination, as Rt of male is about 1.17 to 1.18 in respect to Rcf. Thus, reproduction of male may be not so affected by the food amount.

The process of growth and reproduction of adult may be summarized as follows. The emerged adults of various sizes feed as much as possible to get over Hst by early October. Only if the nutritive condition was enough, the female oviposits in autumn. The male, whose burden of reproduction is far lighter than that of female, are all ready to inseminate. The females which survived to the following year oviposit as much as possible, even though their body weights decrease. In these processes the burdens of small-sized adults are lighter than that of large-sized ones. The number of eggs laid by a female depends on its size and the amount of food eaten.

Chapter VIII Study of larval population by mean of burrow-labelling

Methods

Working stations, burrow-labelling and survey of food

From 1972 to 1978, 7 stations were settled within Field-I of Kamigamo Station. All the larval burrows which appeared within each station were labelled, and the development or death of each larva was traced by periodical observations. The details of the method were already described in Chapter I.

The food condition was investigated by collecting the leftovers in 5 stations for 2 years. The method was described in Chapter II.

Survival period of each individual in each instar

For all individuals of each instar, the survival period was assessed as the number of days from opening to closing the entrance of burrow. The period was calculated as follows.

i) The opening the entrance after hatch or molting, the death and the closing the entrance for molting or pupation were all regarded to have happened at the middle day between the recorded day and the latest survey.

ii) The survival period of 1st instar was calculated as the number of days between the hatch and closing the entrance. With the same procedure, the survival period of 2nd or 3rd instar was obtained as the number of days between the opening and closing the entrance at the related instar.

Examination of the interval of survey

The number of individuals in each instar at any time and the total number of emerged adults were known exactly, but the total number of individuals which attained at each instar would be underestimated, if the interval of survey had been long compared with the survival period of the instar. Especially, as the survival period of the 1st instar was relatively short, some individuals of the instar might have died before their burrows were labelled.

To examine this problem, the survey was carried out every day from late May to mid-July except for rainy day, and every 3 to 5 days after then in St. A for the cohort of 1974. Fig. 58 shows that the survival period of both the dead and the survivors in each instar varies much among individuals except for the survivors of the 3rd instar larva. It also indicates that the survey must be done at least every 2 days in order to follow almost all the 1st instar larvae which may newly appear. The survey of every week and 10 days may follow virtually all the 2nd and 3rd instars respectively.

The survey was carried out actually every 3 or 4 days in the period when the 1st instar larvae might newly appear, and after then every about one week in the other years. Judging from the data of 1974 in St. A, the portion of the overlooked 1st instar larvae might be about 1.2 % at most when the survey was done every 3 days, or 2.7 % when 4 days. So, there might be not so large error in practice.

Death in pupal stage

The death in pupal stage was included in that of the 3rd instar in Chapter I. Here, the both are separated each other, considering as follows. The rearings in laboratory and the outdoor experiments revealed that the 3rd instar larvae tolerated rough treatments during their activities and can survived under the poor food condition. But individuals just before and after pupation were sensitive to any disturbance and easy to die.

The difference of survivorship in the two stages was also suggested in the natural condition. Figs. 5 and 6 show that the number of death is small in most parts of the 3rd instar stage, while it increases rapidly after the period of pupation. The observation in 1974 which was done every 3 or 5 day also revealed that almost all the individuals which died during the period of pupation had already closed the entrances of their burrows for themselves. They must have died in pupal stage, including the period just before pupation.

Thus, all the records of the larval survey were re-examined, and the death after the period of pupation was treated as the death in pupal stage.

Spatial and temporal change in density of larva and key stage

The numbers of individuals which attained each developmental stage from hatch to emergence were obtained in 7 stations (Sts. A to G) from 1972 to '78. The individuals which prolonged their stage of 2nd or 3rd instar and hibernated again, were neglected entirely from their hatch in the analyses, because they might be affected by any factors twice and/or by different kinds of factors. The two cohorts of early summer and autumn were analyzed separately. As the early summer one constituted the main flow of life cycle, the analyses were concentrated on it.

Density at each stage and its change among stations and among years

Fig. 59 shows the larval densities at each stage in logarithm in each station for the cohorts of early summer in every year. In every station the change of density was large in general between the 1st and 2nd instar and between pupa and emerged adult, while it always small between the 3rd instar and pupa. The density of each stage was also much different among stations (sometimes more than 10-fold).

The same data were rearranged to see the change of density at each stage among years in each station (Fig. 60). The change is also large, but less than the change among stations in each year (about 6-fold at most). It suggests that the number of hatched larvae in a station was apt to be maintained in relatively narrow range every year, and also that the intensity of mortality factor on each stage varied not so large year by year in a station.

Assessment on the importance of initial density and mortality in larval stage

As shown in the following chapter, the adults which emerged from these relatively small stations spread over the whole area of Field-I till the period of reproduction. So, the number of females ovipositing in a station may never be related directly to the number of adults emerged from there in the preceding year. There is a possibility that the change of density in each stage depends not only on the change of mortality in larval stage, but also largely on the change of the number of hatched larvae, and thus on that of eggs laid there itself.

Southwood (1966) proposed a method which compares the degree of importance of initial number with that of mortality in developmental stage. Using this method, the importance of both on the number of emerged adults was compared with each other among stations or years (Fig. 61).

The comparison among stations (Fig. 61; A) shows that the initial number caused fundamentally the change in number of emerged adults in every year except for St. F, though the mortality looked also to affect at any rate. Therefore, assuming that the mortality of egg was not so different among stations, the selection of ovipsition site by females might play a great part for the change of number of emerged adults.

The comparison among years in every station (Fig. 61; B) suggests that the both processes affected the change in number of emerged adults. And the change of initial number was apt to be compensated by the change of mortality in larval period except for in Sts. D and E. Especially in St. A, as the result of compensation, the number of emerged adults was kept rather constant. It suggests that the mortality in larval period operated density-dependently.

Key stage analysis

Using the method of key factor analysis proposed by Varley & Gradwell (1960), the key stage whose change of density affected most the number of emerged adults was searched. The total mortality from hatch to emergence (K) and the age-interval mortality (k_i), following the definition of Varley & Gradwell (1960), were compared with each other among stations in every year (Fig. 62). The mortality of the 3rd instar (K_3) was always small, and its change was little related to K. The other three (k_1, k_2 and k_p) changed all violently, and looked to be responsible together for the change of K. The comparison of the changes of K and k_i with each other among years (Fig. 63) shows that k_3 again little affected K, and that k_p looked to be most corresponding to the change of K, though both k_1 and k_2 also affected K to some extent.

These results proved that the number of emerged adults in a station was dependent primarily on initial number and secondarily on the mortality in developmental stage except for the 3rd instar, especially in pupal stage. The intensity of mortality in the 1st and 2nd instar much varied among stations in each year compared with the variation among years in a station.

Regression analysis

To see the effect of density on the survival of larvae, the density of each developmental stage in logarithm was plotted against that of the preceding stage (Fig. 64). As no slope of the regression line differs significantly from unity, and density-dependent mortality did not operate in every stage. The relation between the densities of pupa and emerged adult in St. A has a gentle slope. As the density of the 3rd instar larvae in this station was not always high and the food condition was not poor compared with other stations (Fig. 11), it is hard to consider that a density-dependent mortality operated only in this station.

Factors affecting larval survival

Amount of food taken

The minimum number of preys taken by each larva and its fate were known in Sts. A, D and G from September 1975 to July 1977. For the 1st and 2nd instar larvae in the early summer cohort of 1976, the effect of the number of preys taken during each instar on the survival rate to the following stage and on the portion of larvae prolonged their stage to the following year was examined (Table 12). The larger the number of taken preys increased, the higher the survival rate was. So, the effect of starvation on the survival might be present. The prolongation of the stage to the following year arose also in the 2nd instar larvae which took small number of preys.

For the 3rd instar larvae which survived from September to the following June in the early summer cohort of 1975, the rate of pupation within the year, the rate and the time of emergence and the size of emerged adult were examined in relation to the number of preys taken during the 3rd instar (Table 13). The prolongation of the stage to the following year arose also in the larvae which had taken small number of preys. Even if they could pupate, the mortality during the pupal stage was high. Of course, the survival rate of the individuals which prolonged their stage must be low at all, if considered for the long period till emergence. Therefore food shortage during the 3rd instar also affects largely on the survival till emergence, even if the 3rd instar larva tolerates it.

When the number of taken preys increased more than 5 or 6, the rate of emergence itself was not so different with each other. But the less the number of taken preys was, the smaller the size of emerged adult and the later the emergence time was in general in both sexes. These small-sized and lately emerged adults might be the individuals which had continued their feeding even in July and could have gotten somehow over the threshold to pupate. However, as shown in the following chapter, the adults which emerged late may suffer the higher mortality than the others, because they have relatively short period of time to prepare for hibernation. If so, these larvae merely delay the negative effect of food shortage till adult period.

Table 14 examines the effects of the density around a larva of the 3rd instar on the number of preys taken by the individual for a month and the emergence rate in the following year. The result shows that the density around one never affect the feeding condition of the individual. As shown in Chapter II, the larva catches not only preys of walking but also ones from the air. And the outdoor experiment of larva suggested that the subtle unevenness of the ground surface make the number of preys taken by each larva much variable. Both of them must be responsible for the result mentioned here.

Other factors and conclusion

During the survey the 1st instar larva was often observed dead after a heavy rain. Fig. 65 shows an example. Nevertheless, I failed in detecting any significant relationship between number of the dead per days or in a season and the precipitation or number of times of rain with a certain heaviness during the period. I also could not find any appreciable effect of mean or minimum temperature in various period on the survival of larvae.

Thus, it is likely that the larva which was almost died of starvation could not reopen the entrance of burrow closed by a heavy rain. If so, the meteorologic factors merely affect the survival of the 1st instar larva subsidiarily.

As an stage-specific mortality factor, the parasitoid wasp (*Methoca yasumatsui Iwata*) attack only the 2nd instar larva. As the entrance of burrow was stopped up with sand grains of even size, the parasitized larva could be distinguished from those which closed it for themselves and those which died with their entrance left open. But, once it rained heavily, the discrimination between those before the rain was impossible.

For the early summer cohort of 1974 in St. A, almost all the larvae of the 2nd instar could be discriminated in respect to the fate (Fig. 66). One wasp was only found at most every time, and the ratio of parasitism to all of the dead in larval stage was low as 0.048 (0.220 to the dead of the 2nd instar).

In the other stations and years, the number of parasitism could not be counted entirely on account of interval of survey, though the record was kept if possible. Assuming that the recorded ratio of parasitism to the death of the other cause in some days was maintained all over the death of the 2nd instat, the mortality of the parasitism was estimated (Table 15). The estimated value to the total number of 2nd instar larvae was always not so high, though it varied from 0 to about 0.20 among stations and among years. When "stage-specific" mortality of the parasitism (following the usage of Varley & Gradwell, 1960) was calculated, the change of it among stations or years was no longer parallel to k_2 or K. So, the effect of parasitism by the wasp was not so important to the change of larval population.

These results prove that larvae of all the three instars suffer mainly the effect of amount of food on their survival. But they become to delay the effect as the stage proceeds. It may be adapive for a certain type of predator such as this species. Because, surviving till adult stage has a possibility to reproduce, and moreover, the food condition might turn to be favorable.

The change of K among stations in every year was larger in general than that among years in every station. It is a parallel pattern to the change of the number of taken preys among stations or years, which was shown in Chapter II. It is a circumstantial evidence that the amount of food affects the survival of larva. And it suggests that both a heterogeneity of habitat (a difference in condition among parts of habitat) and the selection of oviposition site by females affects largely the survival of larva. However, as the change of the initial number of larvae did not correspond significantly to the change of K, it is unlikely that adults select the favorable place in respect to larval food condition.

Chapter IX Study on adult population by marking and recaputure

This chapter treats the seaonal change of adult population size and spatial structure of population in its habitat, and analyzes how the processes of growth and reproduction affect the seasonal change of population size. Factors which affect the yearly change of population size will be analyzed in the last chapter, after the change of overall larval population size is examined.

Methods

To estimate the population size and other parameters, the marking and recapture method was applied to 7 adult generations in Field-I from 1972 to ´79, and to 4 generations in Field-II from 1973 to ´77. To see the exchange of members, the method was also applied in 1973 to adults on a road which connected these two fields. The forest roads and the bare grounds inside and outside of Kamigamo Station were surveyed with the same method once in every autumn and early summer for these 8 years to see the migration between the fields and these remote habitats.

The routine work of capture in Field-I and -II was done in a calm day with interval of 1 to 2 weeks during the period of adult activities over the whole study area. It was done by myself in most times, but with the help of another person when the adults were abundant. The nylon net with a diameter of 42 cm attached to a stick of 1.5 m in length was used. The all captured adults were kept in cages during the capturing, and then brought to the laboratory in Field-I.

Each newly captured adult was given an individual mark coded to represent a number with the method described below. The records were made of sex, width of elytra, live weight, and injury if any for each individual in every time except for the generation of 1972, for which only the sex was recorded. After these operations, the cages were settled with their lids left open at the fixed releasing points. The release was done within 7 hours after the capture at most.

For the generations of 1972 and ´73, the adults were captured from Field-I as a whole, and released in a lump at the center of the field. After the generation of 1974, Field-I was divided into 6 blocks (Bl. 1 to Bl. 6, Fig. 67). Each block was systematically searched, and the point of capture was recorded for every individual on detailed map (1/1,000). The marked adults were released in a lump at the center of block in which they were captured. The division of block was done as that within a block a series of bare grounds were connected together and the adults might move freely, but as that between blocks the movements of adults might be prevented to some extent by the presence of bush or grass, though any block connected the other directly or with a path.

The double marking system was applied to the generation of 1972, i.e., the individual mark with vinylose-lacqure paint and the uniform mark with cutting-in by file at a certain position of elytral edge fixed in each time of capture. After the generation of 1973, only the individual mark was branded by soft touch of a burning neelde on the surface of elytra. Fig. 68 shows the code system of individual mark.

When the survey were done in Field-II, same method were applied as Field-I of that year. Table 16 summarizes the methods applied to each generation. The obtained data were analyzed by Jolly-Seber model (Seber, 1973).

In the course of survey in Field-II, I noticed that the area of bare grounds (roads, paths and seedbeds without dense grass) decreased gradually year after year. To know the density in respect of the width of habitat, the area of bare grounds was recorded in this field once in late spring and in late summer of 1975 and '76. The area during 1973 to '74 was evaluated by some personal informations from the staffs of Kamigamo Station and by the records on points of capture. The area was regarded as constant during the period of a generation, i.e., from August to the following June, as it looked to change largely only during the growing season of grass, June to August. Table 16 shows the estimated area for each generation. The area of bare grounds in Field-I (7,913 m^2) could be regarded as constant during this study, because the seedbeds were relatively small and the removal of weed had been made frequently in this field.

Some examinations on effectiveness of estimation

Detachment of marks

Jolly-Seber model assumes no mark is detached. The operation of double marking proved that the lacquer paint began to detach within two or three weeks judging from the mark of cut by file. Thus, this painting method is unsuitable for this beetle, and the data concerning each individual in the generation of 1972 should be unreliable.

Marking effects

On the other hand, there are some possibilities that marks of cut or brand has some effects on survival, activities or catchability. To examin the effects, a rearing experiment was done.

On April 24, 1976, 23 females and 15 males were collected from a sampling locality, and divided into two groups for each sex. One group was branded with 2, 4 or 6 points, and another group was the control. The both groups were reared together in the outdoor cage (Plate 8) till early July. This experiment revealed that both the survivorship and the change of mean Rcf were not different significantly between two groups (Fig. 69).

Manly (1971) proposed a method to detect the effect of marking operation on the survival or catchability, when the effect was limited only in the initial marking time. This method can be also used to detect the possible difference in mortality in relation to age, as pointed out by Iwao (1977).

The method was applied to 72 survey times which were total possible cases for calculation, and only 9 times were significantly different (5 % significance level) in catchability. Four cases out of the nine occurred when very small number of individuals were captured during the initial or final period of generations. So, there must be the biases caused by small samples. The remaining 5 cases occurred in the period just before (early or mid-October) and just after (mid-April) hibernation. Because the cases fell in the specific period, the difference were not caused by the effect of marking operation, but by the age dependent mortality.

These two examinations prove that the marking effects are negligible.

Equal catchability and age-dependent mortality

Jolly-Seber model also assumes i) the catchabilities of marked and no-marked individuals are equal, and ii) every marked individual has the equal probability of survival. In this study the intervals between the times of capture are relatively long (more than a week in most cases). Considering the adult activities (Chapter III), the adults may mingle with each other during the period. Iwao (1977) pointed out that the assumption of equal catchability seemed to be satisfied at least approximately in many cases in insects. There is no proof to deny this suggestion on our species at present. Thus, the first assumption may be held.

The second assumption falls down if the age dependent mortality happen. Manly (1970) showed that Jolly-Seber estimates would be seriously biased if mortality change sharply with age. In our species the age dependent mortality might happen as suggested above, though limited during the periods just before and after hibernation.

Fig. 70 shows the minimum survivorship of the newly captured individuals at every time for the generation of 1974. The pattern of disappearance was different among seasons. As the newly captured individuals must be composed mostly of the young members, the age dependent mortality really happened. The pattern of disappearance looks to be approximately the same among each of three periods, i.e., from August to September, from May (except for the beginning) to July and just before and after hibernation. In the former two periods the survivorships in logarithm may be regarded as linear, with similar inclinations within each period. In the third period the survivorship cannot be regarded anyway as age-independent.

This result indicates that it must be better to estimate the population parameters for two periods separately. Then the data were treated as if the marking and recapture had been operated twice independently from August to September and from the second week of May to July for each generation. The estimation for the period just before and after hibernation was despaired, and the data concerning this period were neglected.

Iwao et al. (1966) and Manly (1968) have derived independently the methods which are applicable to the case where mortality is dependent on age. As these methods depend on the re-recapture data, the bias tend to be large when the sample sizes are small (Manly, 1970). In this study the sample sizes and their recaptures were both not so large. So, these methods were not applicable.

Test of immigration

Jolly (1965) proposed "death but no-immigration" model as a special case of the general model. The model may give better estimates (smaller variance) than general model (Iwao, 1977). In this study the model is applicable in the period from May to July, because there is neither the emergence of adult (Chapter I) nor immigration from the outside of the study area, as shown below, in this period.

On this subject, Leslie (1952) proposed a test of no dilution. The method was applied to the period of every generation, and no significant difference (5 % level) was detected.

Sample size

Some authors noticed that Jolly-Seber estimates tend to be biased if the sample size was small, even when the other assumptions are fulfilled (Manly, 1970, Bishop &Sheppard, 1973, Gilbert, 1973). Iwao (1977) pointed out that Jolly-Seber model would yield reliable estimates if the sampling fraction is larger than 0.2 when every individual has equal catchability, and than 0.5 when there is some heterogeneity in the catchability.

In this study the sampling fraction seldom attained above 0.5, but it was more than 0.2 in most times except for the initial and final periods of each generation. As the heterogeneity in the catchability was almost negligible as mentioned above, it may be sufficient.

Seber (1965, 1973) proposed the small-sample formulae to reduce biases and also recommended that the number of marked individuals in a sample and their recapture should be greater than 10 for satisfactory application even when the small-sample formulae were used. Though our sample sizes were not so large at any rate, the limit was overcome except for the initial and final period of each generation.

Based on these considerations, the small-sample formulae of general Jolly-Seber model were used for the period from August to September, and the small formulae of special Jolly-Seber model (with death but no immigration) were from the following May to the dying out of adult in every generation (Appendixes 4, 5).

In some cases it is neccessary to know the size of sub-population, such as the number of adults in each block or each sex. In these cases the application of the model was almost impossible on account of the smallness of their sample. These size was obtained to divide the estimated overall population size by the proportion of individuals concerned in the sample.

To examine the reliability of this method, a comparison was made in a few cases when the sample size was large and then the size of sub-populatons could be effectively estimated by the model. the both methods yielded similar results with each other.

Estimation of population interchange between areas

Some authors have devised the methods to estimate population interchange between areas (Richards & Waloff, 1954, Iwao, 1963, Arnason, 1972a, 1972b). The Method of Richards & Waloff assumes the same survival rate between two areas, though allowing different sampling intensities. In this population the assumption was never held as shown below.

Iwao (1963) extended this method to include the case where survival rate differed between any two areas. Thus, his method can be applied to areas different in suitability or quality (Iwao, 1963, 1977).

Arnason (1972a) confirmed that the method of Iwao was valid from a stochastic point of view. But Arnason (1972a, 1972b) pointed out its restriction in that if return migration occurred between areas, and he constructed a more extended model allowing return migration with variance formulae. But his method is rather complicated. In this population the return migration occurred not so frequently at least within each period as shown below. Thus, the Method of Iwao was applied to estimate the number of individuals which interchange between blocks.

Spatial extent of the natural populations

The two study areas for adult (Field-I and -II) were defined as that a series of bare grounds was connected each other within an area. And the two neighbors separated in both sides of a small hill, about 50 m of width, though a shady and curved road connected them (Fig. 2).

The marking and recapture method was applied in Field-I and -II with a similar intensity and intervals for the generation of 1973. Table 17 shows the number of individuals which interchanged between the two fields and the total number of individuals recaptured within each field, with results of the other generations. The number of interchange was very small and negligible in practice compared with the total number of the recaptured.

On the road which connected the two fields, some number of adults often appeared from early to mid-September, though no larva was present. In September 1973, the marking and recapture was also applied to these adults. As the appearance was short and in small number (12 adults was captured at most), the number of individuals could not be estimated. But it proved that some adults were those which had been marked before in one of the two fields, and some ones were recaptured later in one of the two fields. The points where these adults were recaptured within a month were always close to the road.

These observations and the fact that the adult populations in the two fields attain their maximum number at mid-September (as shown in the following section) indicate that the interchange between the two fields are not usual, but some adults occasionally come into the road when the population size increases in each field and then go back or into the other field.

Besides the road, there are small bare grounds and some roads which surround the two fields, and a few adults appear there. The marking and recapture was also applied to them twice in each generation. But no adult marked in Field-I or -II was captured there, and no one released at these places was captured within the two fields. Therefore the small populations on these places have no relation with those of Field-I and -II.

Fig. 71 shows the released and recaptured points of each individual in Field-I for the generation of 1975. They moved around rather freely within the field at least during their long period of activities. It proves that the two populations subjected to marking and recapture in Field-I and -II are the two local populations which are independent each other but self-contained within own members.

Population size and other parameters in Field-I

Appendix 6 shows the popultion size and other parameters estimated by Jolly-Seber model. Though the variance is relatively large in autumn, these estimates are, checking with the observations and considerations mentioned hitherto, reasonable and has no confliction, except for the survival rate in June which rather fluctuated. But the estimates concerning the initial and final periods of each generation should be unreliable to some extent from the reasons considered in the previous section.

Population size and its seasonal change

Fig. 72 shows the seasonal change of estimated population size. In every generation the adults appeared from August and attained its maximum number about September 10th. The number of adults at the peak fell down in relatively narrow range between 340 and 460. After then it decreased gradually, and they entered hibernation. They appeared again at following mid-April, and the number of individuals at the beginning of their reproductive period, early May, was from 200 to 300. The value was again in relatively narrow range, and equivalent to 42-88 % of those of the peak for each generation. After then it decreased rather rapidly, and almost extincted by the end of June.

Thus, the population was much stable among generations. It is worthy of special mention. When the attention is paid in detail, however, there is some differences in population size at each period among generations, such as the period of their maximum (1.4-fold) or beginning of reproductive period (1.5-fold). The speed of increase or decrease was also different with each other.

The sex ratio in each sample was almost maintained at 0.5 during the most period of every generation. The records from the emergence traps revealed that the number of emerged adults was not different between sexes in every period of time (see Table 21).

Total number of emerged individuals

As the immigration was negligible in this population, the number of recruited individuals estimated by Jolly-Seber model means only the number of emerged adults, and should be calculated only for the population in autumn. But the value is not the real number of emerged adults, because some mortality operates. Iwao (1970) and Dempster (1971) devised independently the methods to estimate the real number of recruited individuals. Checking up the formulae of both, it revealed that the estimated values do not so much fiffer from each other, if the survival rate is relatively high and constant as shown below in this population. So, the real number of emerged adults and its total value were calculated by the method of Dempster, because it had been proposed with formula of variance (Appendix 6).

The calculated value, however, does not show the total number of adults emerged in a generation, because the marking and recapture was not applied all over the emergence period, and the estimate can not be calculated for the first one and the last two times of capture.

The number of emerged adults in working stations of larva and its periodical change all over the period were known. So, the number of emerged adults all over the period in Field-I was calculated by proportional allotment, assuming that the periodical change of emergence was the same between the stations and the overall area (Appendix 8; F). Among these values, that for the generation of 1973 may be not so reliable, because the survey was carried out only in one station and the number of recruited adults was estimated over a relatively short period.

The total number of adults emerged in Field-I varied form 710 to 1,360, about 1.9-fold. The stability of the adult population among generations seems to be caused partly by this relatively stable number of emerged adults.

Survival rate

As emmigration was negligible in our population, all the disappearance can be regarded as the death. As the intervals of recapture were not the same except for the generation of 1974, all the estimated values were converted into the rate per week, assuming that the daily survival rate were constant within each interval (Appendix 6). The weekly survival rate was relatively constant both in autumn and in early summer, and the former was a little lower than the latter in most generations.

Jolly (1970) derived formulae to give the average survival rate and its variance over the period of sampling (cited from

Carothers, 1973). The average weekly survival rate was calculated over various length of period in each season for every generation (Table 18). It varied between 0.81 and 0.56 in autumn, and between 0.88 and 0.62 in early summer among generations.

With the total number of emerged adults and the population size at early May, the survival rate from emergence to onset of the reproductive period varied between 0.37 and 0.18.

Population size and density in Field-II

Appendix 5 summarizes the data obtained from marking and recapture of adult in Field-II, and Appendix 7 shows the estimates by Jolly-Seber model. In this field the population size at any season decreased gradually year after year. The degree of change among generations was larger than that of population in Field-I, though the similar seasonal change was seen.

As the area of bare grounds in Field-II decreased year after year, comparison between the two fields was made in respect of the density to the total area of bare grounds in each field (Fig. 73). The density and its seasonal change in both fields were in good agreement, about 5.0 to 3.5 per are in late September and 3.8 to 3.8 2.5 in early May. It suggests that in the population process there are some mechanisms which maintain a certain level of adult density to the area of habitat. This problem will be considered in the last chapter.

Growth, maturity and mortality

Reproduction in autumn and survival to the following year

As shown in Chapter VII, the ovipositing females in autumn should be the individuals which had emerged early and fed enough. Then a subsequent question may arise as whether the oviposited females can hibernate to participate the reproduction in the following year.

Whether an adult is in reproductive stage or not at a certain time can be assessed from the value of its Rcf to Rt. Fig. 74 shows the frequency distribution of Rcf to Rt of each sex in each sample for generation of 1974 as an example. The individuals with Rcf to Rt ≥ 1.0 before September 19 can be regarded as in reproductive stage. After May all the adults should be considered as reproductive regardless of their Rcf to Rt level as mentioned in Chapters VI and VII.

In autumn the females with low value of Rcf to Rt grew fast, but grew scarcely or even lost weight as approaching or exceeding the level of unity. The standstill of growth between September 12 and 19 might be caused by a long spell of rain during the period. About 10 to 30 % of females in every time were ovipositing, and they were mainly the individuals which had emerged early. As a number of them were recaptured in the following year, the oviposition in autumn may not prevent the survival during winter. Most males were in possible state to reproduce, and some of them were recaptured in the following year.

To see the problem more precisely in both sexes, the recapture rate to the following year was compared with respect to the level of Rcf to Rt for all the individuals captured from August to mid-September in each generation (Table 19). Though the females whose Rcf to Rt were larger than 1.1 were scarcely recaptured, the recapture rate of females whose Rcf to Rt were between 1.0 and 1.1 was not necessarily lower than the rest. So, the oviposition itself does not affect the survival during winter, which agrees with the result of rearing experiment (Chapter VII). The phenomenon is reasonable, because Rt of female is higher than Hst and the ovipositing females keep their weight above Rt in this season.

In male, there is also no appreciable difference of the recapture rate among individuals with respect to the level of Rcf to Rt, though the individuals with the lowest and highest level of Rcf to Rt were apt to die. Because most males can reproduce actually or potentially and the burden on nutritive condition is far lighter than preparing for hibernation, their survival to the following year should be little affected by reproduction in autumn.

The reason why the recapture rate of adults with the highest level of Rcf to Rt was low may be that they emerged earlier than the others and then the period concerned was longer. It will be examined again in the following section.

Nutritive condition for wintering and survival

As shown in Chapter III, all the adults which once enter hibernation should survive during winter. The collecting of carcases (Chapter IV) has suggested that a considerable number of adults die without entering hibernation. Thus, the adults which died before the following April must have insufficient nutritive condition to exceed Hst and never hibernate even when the climate is getting hazardous.

The recapture rate in the following year was compared in respect of Rcf to Hst of all the individuals which were released between late September and mid-October in every generation for each sex (Table 20). The individuals with Rcf to Hst $\geqq$ 1.0 were recaptured more in number than the others, i.e., their survival rate was high, in both sexes. Especially, the adults whose Rcf to Hst were much smaller than unity seldom survived to the following year. On the other hand, some adults whose Rcf to Hst were a little smaller than unity could survive. It is probable that these individuals could have exceeded the threshold by feeding after the release and hibernated.

The critical limit looks somewhat different among generations. It may be attributed to partly that the days of capture were not the same period among generations, but mainly to that the different climatic conditions among generations affected the feeding processes, such as the feeding time and amount of prey insects.

Most of the adults which had low level of Rcf to Hst might be the individuals which had emerged recently. The survival rate of adults which emerged early may be lower than that of those emerged late. Therefore the survival rate to the following year of adults which emerged in middle period of emergence must be higher than those emerged early or late. For the generations of 1975 and ′76, in which an amount of records on emerged adults and their fates were kept, the relation between the time of emergence and the recapture rate in the following year was examined (Table 21). The result agreed with the expectation.

The peak of emergence and the survival looked different between the two generations. Dreisig (1981) has proved that the feeding rate of C. hybrida is strongly dependent on the ambient temperature. The feeding also must be prevented in rain day. So, it is probable that the feeding condition caused by the climatic condition is also different between generations. Under a good feeding condition, the number of adults which emerged early would be increased, while their suvival rate to the following year would be low. The number of adults which emerged late and entered hibernation successfully would be increased under this condition. Under the poor condition, the reverse process may be expected. The poor feeding condition may be also arisen by the high density of adult population itself, which will be examined in the last chapter.

Relation between population process and structure of habitat

Usage of habitat

The habitat of both the adult and larva of this species is the bare ground except for the roost of adult. So, even an area is defined for a local population, the members inhabit only in bare grounds within the area. For an example, Fig 75 shows the spatial distribution of adults and larvae at each maximum population size (see also Fig. 67). Adults scattered rather evenly all over the bare grounds, while larvae concentrated on certain places. As larvae seldom move from the sites where they were born, the difference between the two stages indicates that adults emerge from relatively limited places, scatter over the whole area probably for foraging, and prefer some restricted places as oviposition site. It means that there is some difference in quality among bare grounds at least with respect of oviposition, and that the adults use these different kinds of places properly in the course of their activities.

Seasonal change in usage of habitat

The marking and recapture had been operated in each of 6 blocks (Fig. 67) from the generation of 1974. The population size was estimated over the whole area with lumped data, and was allotted for each block in proportion to sample size. Utilizing a detailed map, the density in each block could be assessed. As an example, Fig. 76 shows the seasonal change of density in each block and the number of individuals which interchanged between blocks for generation of 1976. The similar pattern resulted from each of the other generations.

The pattern of adult distribution can be divided into three periods, i.e., from the appearance to the peak in number, from then till hibernation and after hibernation to reproduction in eary summer. In the beginning of the first period the adults appeared mainly in Bls. 1 and 3, and a little in Bls. 2 and 5. After a while the adults also appeared in Bls. 4 and 6, and the density of each block rose gradually. The pattern of rising was different among blocks. But the discrepancy between the maximum density and the actual one in each block looked to be kept equal among blocks at any time. In other words, the density was rose as if to maintain the room equal.

In the second period the density became lower only in Bls. 4 and 6. In the third period the tendency continued, and adults within these two blocks disappeared at all as the reproductive preiod began. In Bls. 1 and 3, on the other hand, density was maintained at high level, and in Bls. 2 and 5 the situation seemed to be neutral.

Thus, Bls. 1 and 3 are used continuously by adults, and Bls. 4 and 6 are used temporarily during the population size is large. In this generation the density of Bls. 1 and 5 in early May was higher than the density at the peak of population size in autumn. In other generations the former was about the same as or a little lower than the latter. So, I am inclined to consider that the result of this generation was exceptional event or a bias caused from the somewhat complicated procedures of assessment.

As seen in Fig. 75 and will be shown in the following chapter, the larvae inhabited Bls. 1 and 3 most, and Bls. 2 and 5 in some amount, but in Bls. 4 and 6 a little. Therefore most adults which appeared in Bls. 4 and 6, and some ones in Bls. 2 and 5 might be the immigrants from Bls. 1 and 3. It was supported by the pattern of interchange estimated. The adults move between blocks more often in autumn than in early summer, and some individuals returned from Bls. 4 and 6 to the other blocks as the population size decreased.

Thus, the increasing period of population size is the spatially expanding period, and the decreasing and reproductive period is the contracting and concentrating period. At least in this field, the favorable places for oviposition seems also favorable for other adult activities, because the density in these places is maintained at high level in spite of the frequent interchange.

Heterogeneity of condition in habitat of adult

Fig. 77 shows the density in each block at the peak of population size for every generation with the same manner as Fig. 76. The density in Bls. 1 and 3 was always high and the difference among generations was not so large, while the density in the other blocks was always lower than Bls. 1 and 3 and the difference among generations was large. But the number of adults in Bls. 2 and 6 was larger than that in Bls. 1 and 3 in some generations in spite of the low density. Therfore most of the difference of population size at peak among generations was presented in Bls. 2 and 6. It indicates that the Bls. 2 and 6, and probably Bl. 4, were utilized as a space of accommodation for adults which overflowed the favorable places.

Fig. 77 also shows the rate of recapture after then within the whole area for the adults in each block. As the effort of recapture was not the same among generations, the comparison between generations may be meaningless. But the difference in the condition of each block which affect the survival may be assessed, assuming that the rate of recapture is parallel with the survival rate. The condition for survival is the best in Bls. 1 and 3, where the density was high, the worst in Bls. 4 and 6, which were utilized temporarily, and is variable year after year in Bls. 2 and 5. The most probable factor which affects the survival and is variable among blocks should be the nutritive condition, as suggested in the preceding section.

Only for the individuals which were released in any block at the peak of population size and recaptured in the same block after a week, the Rcf at the peak and the increment of Rcf in a week was compared among blocks in the generation of 1976 (Fig 78). Only the result of male was examined, because even when the food condition is favorable the female may decrease her Rcf by ovipositing. The average Rcf of male was small in Bls. 1, 2 and 3. It can be attributed to that the newly emerged adult were present most in these blocks. The increment of Rcf of male was large in Bls.1, 2 and 3, and was a little or negative in the other blocks. Thus, there was a heterogeneity of food condition among blocks, and it must be the main cause for the difference in survival rate among blocks.

From these results, the population process in this period in relation to the habitat heterogeneity can be considered as follows. As the density becomes high, some adults are driven into the unfavorable habitat of poor food condition. They suffered high mortality during the starting of hibernation at least and probably another period. The capacity of favorable habitat is maintained at rather constant and much lower level than the total population size. This capacity and the process of overflow may be achieved by, as an actual mechanism, the spacing of each individual, which was shown in Chapter III.

On account of the capacity, the larger the number of emerged adults is, the larger the number of adults driven into unfavorable habitat is, and therefore the mortality of the overall population becomes high. The change of survival rate among generations will be analyzed in the last chapter.

Chapter X Estimation of larval population size by means of belt-transect census

As shown in Chapter VIII, the number of hatched larvae, the pattern of larval survival and the number of emerged adults were more or less all variable among stations and also among generations. To see the number of larvae in each instar in the whole study area and the change of population size among blocks or among generations, the census was done periodically in Field-1 for four and a half years.

Methods

Counting the larval burrows

During the period of larval activities from April 1975 to July 1979, the census was made by belt-transect method with interval of one to four weeks. The interval was set as short during the season when larvae developed fast, and rather long during the other seasons. Each census was done in a day all over the bare grounds in Field-I.

The rate of discovery might be varied more or less among instars and also among the bare grounds of various situation. Thus, each block were further divided into several sub-blocks as that within each sub-block the surface of ground was regarded as uniform in respect to the efficiency of discovery. Walking evenly within every sub-block, I looked for any larval burrow and recorded the number of each instar larvae discovered in it.

Efficiency of discovery and estimation of population size

To know the efficiency of discovery for each instar in each sub-block, all the sub-blocks were grouped into four categories as follows, according to the situation of their surface. i) The bare ground of smooth surface without any obstacle for discovery; ii) The pebbly bare ground of uneven surface; iii) The bare ground with thin grasses; iv) The bare ground with thin turf.

Picking out four sub-blocks of each category as typifiers, a complete survey was done on each just after a routine census, and the efficiency of discovery was measured for each typifier. This survey was carried out once at early June 1975, when all the three instars of larva appeared about same in number. The efficiency of discovery for each instar and for each category was calculated by the weighted arithmetic mean of four typifiers (Table 22).

Dividing the census data by the related value of efficiency of discovery, the population size of each instar in each sub-block was estimated. For the station in which all the larval burrows had been marked, the number of each instar larvae was known precisely.

Seasonal and spatial change of larval population size

Fig. 79 shows the seasonal change of population size estimated for each instar in Field-I from 1975 to '79, with the seasonal change of adult population size. The result was, of course, the summation of each cohort, and never conflicted with the results for the life cycle which was clarified in Chapter I.

The pattern of seasonal change in every instar was similar among years, and the abundance of them was not different so much among years. The 1st instar of larva appeared most in mid-June, and its maximum number varied from about 1,400 to 2,300 among years. This instar appeared again in autumn, and its number was from about 150 to 500, though the peaks of appearance were not so clear. The 2nd instar had almost one peak of abundance at late July. The number of individuals at the peak was from about 1,000 to 1,300. The 3rd instar had two gentle peaks of abundance in late May or early July and in autumn, whose number varied from about 700 to 1,200 in both seasons among years.

The seasonal change of abundance became smaller as stage progressed. Especially, the 3rd instar larvae were always present in every season, and the range of their number was between about 400 and 1,200 for four and a half years. The moderation of seasonal change should be caused by the two reasons as that the span of larval instar becomes longer as stage progresses, and that the developmental speed becomes more variable among individuals. For example, some larvae of the 3rd instar in midsummer was the individuals which had not pupated in the year, and the remainder was those which were born in early summer of the year and developed fast.

These data of abundance were separated into 6 blocks (Fig. 80). The number of the 1st instars appeared in early summer was generally large in Bls. 1 and 3, intermediate in Bls. 2, 5 and 6, and small in Bl 4. This order is the same as the degree of usage of adult in early summer.

The number of the 1st instars appeared in this season was different year by year even in one block. For example, the number was large in Bl. 3 from 1975 to ′77, but it decreased rapidly after 1978. Bl. 4 had been utilized a little till 1977, but abandoned at all after then.

In spite of such variabilities, the overall larval population size in Field-I changed not so much among years. Because the adults use the field as one continuous habitat at any rate, this phenomenon may be attributed to a process as follows, assuming that the mortality of egg is not so much different among blocks and among years. The total number of eggs laid in Field-I differs not so much among years, while the proportion of allotment to each block may altered year by year, though the discrimination between favorable and unfavorable block is kept. Such alternation may correspond to the change of the relative condition in every block.

In this connection, some species of Cicindela in North America discriminate the difference in the quality of bare ground for oviposition site, such as humidity or composition of soil (Shelford, 1911). Though no data was taken on the change of such kind of quality, some suggestive observations were kept as follows. A number of the 1st instar larvae hatched both in the seedling bed which was newly settled and plowed before the reproductive period, and in the places where the canopy was removed. In some seedling beds, on the other hand, the number of hatched larvae decreased gradually year by year as the seedling grew. Thus, the change of abundance of the 1st instar larvae appeared in a block may be partly attributed to the factors cited by Shelford.

Estimation of the number of larvae appeared in Field-I

In order to analyze the dynamics of population in Field-I, the total numbers of larvae hatched both in autumn and in early summer and that of mature larvae in this field were estimated for generations of 1975 to ′78 as follows.

The 1st instar larvae of early summer cohort appeared in early June and disappeared by mid-August, as shown in Fig. 5. Most of the 1st instar larvae which had hatched in the preceding autumn disappeared by the early June (Fig. 6). Assuming that the number of the former individuals was zero on June 1 and August 1, the cumulative number of the 1st instar larvae during the period was calculated from Fig. 79 for every generation. Dividing the cumulative number by the mean survival period of the instar of each generation which was known from the survey in larval stations, the total number of hatched larvae were obtained for each summer cohorts (Appendix 8; U, V and W). As the mean survival period for generation of 1979 was not known, the weighted average for generations from 1975 to '78 was used. The total number varied between about 3,950 and 7,740 (about 2.0-fold).

With the same procedure, the total number of larvae hatched in autumn was estimated, assuming that the 1st instar larvae hatched from August 20 till September 30 (Appendix 8; L, M and N). The mean survival period of each generation was taken from the data of burrow-labelling, assuming that any larva of the 1st instar died on October 1. The total number varied from 441 to 773 (about 1.8-fold), which was equivalent to 9 - 25 % of the total number of larvae hatched in the following early summer.

Most of the 3rd instar larvae in both cohorts survived during May and pupated from June, as shown in Figs. 5 and 6. No individual of the 2nd instar grew into the 3rd instar yet in May. So, the number of the 3rd instar larvae in May can be regarded as the total number of the mature larvae itself (Appendix 8; A).

A small portion of them, however, never pupated in the year, but hibernated again. And a small portion of the 2nd instar larvae which developed fast into the 3rd instar could pupate within the year. So, it is necessary to estimate the number of both to know the number of mature larvae which were ready to pupate within the year.

From the records on larval stations, the proportion of individuals which were still in the 3rd instar at the period when the others pupated successfully was known. Assuming that the proportion was held all over Field-I, the total number of the 3rd instar larvae which prolonged their span of the instar was obtained for each generation (Appendix 8; B). The similar procedure was applied to know the number of the 2nd instar larvae which pupated within the year (Appendix 8; C). Taking away the former value and adding the latter, the corrected total number of mature larvae was obtained for each generation (Appendix 8; D).

The number of mature larvae varied only between about 870 and 1,030 (about 1.2-fold). The analysis of the change among generations will be done in next chapter, being related with the total number of adults which emerged or participated in reproduction in Field-I.

Chapter XI Population dynamics and general discussion

As shown hitherto, both adult and larval populations were much stable among generations within an area which was used as an continuous habitat by adults. In this chapter the processes which may be responsible for the stabilization is analyzed in connection with the heterogeneity of members in a population.

The studies on population dynamics of insect have been concentrated upon those whose densities change largely from generation to generation (for examples, Varley & Gradwell, 1958, Morris (ed.), 1963). These studies have developed own methods, in which a change of population is contrasted with that of an environmental factor or the density at any stage is compared with that of the following stage.

In this species, on the contrary, only a little change was observed among generations. For example, an estimated density of adult at any season often included those of the other years within its range of variance (Appendix 6). And the population size of larva at any stage never changed among years more than 2-fold. Considering the error of estimation, even the difference may be not so definite.

Nevertheless, some steady trends were also observed in the yearly change of some stages as shown below, though these were subtle too. Using these stages as clues, the relations between consective population processes were analyzed. Appendix 8 summarizes the data described already but concerned to the subject here.

Change of adult population size among years

Population process in autumn

As shown in Chapter IX, when the overall density became high, the number of adults driven to unfavorable place increased. So, the nutritive condition of population as a whole may grow worse as the density becomes high. Fig. 81 shows the relation between mean Rcf of each sex at some periods and the density or the total number of emerged adults. Mean Rcf did not change clearly according to the change of density at the period of peak in number. But the larger the total number of emerged adult was, the lower the value of Rcf of each sex was. The trend was more clear at the end of emergence period than at the period of peak in number.

Thus, the density affected the nutritive condition cumulatively, and the effect extended equally over both sexes.

As a result of this process, the overall survival rate may become low when the number of emerged adults is large. Fig. 82 shows the relation between the weekly survival rate averaged for various period in autumn and the total number of emerged adults. In general, the larger the total number of emerged adults was, the lower the survival rate was. The trend was most clear in the period from late August to mid-September during which density was maintained high.

These results anticipate that in the year when the density had been maintained high, the adults which survived till late autumn had poor nutritive condition as a whole and suffered high mortality on account of Hst. It cannot be ascertained directly, because the population size in late autumn could not be estimated in most years. But Table 20 already showed that the individuals of poor nutritive condition at late autumn were likely to die. And Fig. 72 indicated that the larger the population size at the peak was, the smaller the size at early May in the following year was. Fig. 83 shows directly the relation between the population sizes of both periods in each generation. A clear inverse relationship reveals, which makes the anticipation quite probable.

The population size at beginning of reproduction was not related any longer to the total number of emerged adult in the preceding autumn (Appendix 8; O and E). It must be attributed to that the two successive processes operate on the population density-dependently.

Population process in early summer

The adults continue to reproduce from early May till they die out in late June or early July. Therefore, in respect to the amount of reproduction made in this period, the cumulative number of adults over the period must be more meaningful than the number of adults at beginning of the period. Using the data concerned in Fig. 72 and assuming that the adult died out on the following day of the survey time when the last adult was observed, the cumulative number of adults (no. of individuals x days) from May 8 to the day was calculated (Appendix 8; P).

Fig. 84 shows the relation between the number of adults and the total number to hatched larvae in early summer. The inverse relationship revealed.

The expected total number of laid eggs in Field-I was estimated as follows. A relationship between the daily number of eggs laid by a female and her Rcf to Rt in early summer was known (Fig. 56). Assuming that a frequency distribution of Rcf to Rt of female obserbed in each survey time was held all over the female population till the following survey time, the relationship was applied to the females captured in each survey time in Field-I, and the taken number in each interval was summed up over the reproductive period for each generation (Appendix 8; T). The expected total number of laid eggs increased as the cumulative number of adults increased (Fig. 84).

There is no evidence that the hatchability of egg is not different among years, though it was not affected by the nutritive condition of female. If the change in number of hatched larvae in this figure resulted only from the change of hatchability, we must presume a change of about 3.0-fold. It may be unreasonable. Moreover it is hard to consider that the hatchability is inversely related to the cumulative number of adults. Therefore the change in the number of hactched larvae must show that of eggs laid actually. It suggests the presence of a mechanism which controls the process of reproduction density-dependently.

Fig. 85 shows the relation between the cumulative number of adults and mean Rcf of each sex during the reproductive period or rate of the injured (the ratio of cumulative no. of adults which had any injury on their appendages or elytra to that of all adults). Though Rcf of each sex changed at any rate among years, it was no longer related to the cumulative number of adults. So, it may be difficult to prove the ill effect of high density on nutritive condition.

On the contrary, the rate of the injured of male grew as the cumulative number of adults increased, suggesting the presence of some interference between individuals. In the female, the relationship was not shown any longer. The females may be injured not only by the interference with the other individuals, but also by the oviposition itself, which was often observed in the rearings of female. The latter cause may increase as the interference decreases.

This consideration was supported by other observations. As shown in Chapter III, about 9 minutes was necessary for female to lay an egg, while an adult was walking about 0.6 to 1.5 m every minute in daytime and could find the other individual apart from about 1 m. After finding, it approched positively, and the chasing, grappling or copulation followed. The density was often maintained nearly to 10 individuals per are (equivalent to an adult within a radius of about 1.8 m around) in oviposition site. So, where the density is high, some behavioral disturbance on oviposition must happen frequently. Thus, the inverse relationship between the cumulative number of adults and the number of laid eggs must be attributed to the direct disturbance on reproduction.

The change of mean survival rate during various periods in this season was neither so variable among years (Fig. 86) nor related any longer to the number of adults (Appendix 8; O to S).

The total number of hatched larvae in early summer changed about 2-fold among the five years, which was a little larger than the change in cumulative number of adults in the period. But the important point is that the process operated density-dependently. The change of the former was not related any longer to the total number of emerged adult in the preceding autumn. It is natural as a result from at least three density-dependent processes which operates one by one.

Relationship between amount of reproduction in autumn and in early summer

Murdoch (1966a) studied on some ground beetles (Agonum, Abex and Pterostichus), which reproduce before and after winter. He found that their population sizes were fairly stable (2- or 3-fold in 2 years), and also that the amount of reproduction was a function of food supply. Murdoch (1966a, 1966b) suggested that other mortality factors being equal intensity, the survival of adult, especially female, from near the end of one breeding season to the start of the following was inversely proportional to the amount of reproduction in the first breeding season. He considered that this was one of the compensatory mechanisms leading to population stability in Carabidae and might be widespread in other insects. Because of the similarity in life history and other biology, his hypothesis should be much important to our species.

Fig. 87 shows the relation between the total number of larvae in autumn and some estimates. The total number of hatched larvae was small when the total number of adults emerged till mid-September, which might be responsible for the reproduction in autumn, was large. Both the survival rate from emergence to the following May and the number of adults at early May changed contrary to Murdoch's hypothesis, though the former was not the actual survival rate during winter. All these results are reasonable, because the more the adults emerged in number, the worse both the nutritive condition and the survival rate of adult became as shown already. The poor nutritive condition should affect badly both the reproduction in autumn and the preparing for hibernation.

The total numbers of hatched larvae in autumn and the following early summer, on the other hand, related inversely to each other. It must be another causality which is responsible for the stability of this population. But the relationship was never caused by single and direct compensatory mechanism. There were at least three processes as shown above. The total number of larvae hatched in both seasons changed only 1.3-fold among 4 generations.

Fig. 88 summarizes the relations among population processes and factors, all of which have been proved hitherto to affect the stability of this population.

General discussion

I make considerations here on some prominent features of life history, development and population processes in this species, i.e., on hibernation, response to food amount, and individual difference such as size and nutritive condition. Some considerations are also made on the mechanism of stabilization and habitat structure of this species.

Hibernation and life cycle

Nakane (1955) treated *C. japonica* Thunberg as a species, which had been considered as a variety of *C. chinensis* De Geer (Horn, 1915). As this treatment has been widespread in our country, I followed him in this paper. But some taxonomists have not recognized this form as a species (for example Rivarier, 1961). At any rate, *japonica* is closely related to and might be derived from *C. chinensis*. Though *japonica* is only found in Japan, *chinensis* is distributed widely in Korea, China and Tonkin, and all the related species to the latter are widely found in continental part of Oriental reagion (Horn, 1915, Schilder, 1953, Rivalier, 1961). Thus, *chinensis* and *japonica* might originate from Oriental stock and advance into the Far East, regardless what time the speciation occurred.

In any season except for the period around winter, the larvae of all three instars are present and the molt can take place. The adults reproduce before and after winter. These phenomena can be interpreted as natural, if the hibernation was inserted into its life cycle afterward. In other words, the wintering must be a burden which ought to be born when this species or its ancestor preceeded nothword. This hypothesis must be confirmed by comparison with the related species in low latitude.

If the hypothesis is held, the burden might modificate the process of development as follows. Both adult and larva were forced to make up a physiological resume for wintering, especially in nutritive accumulation. And the development and reproduction were refrained from in the period around winter.

The emergence was limited in rather short period in contrast with the other period of development and reproduction. It was suggested that the latest time of emergence was defined as to maintain a certain length of time which was necessary for adult to prepare for wintering. It was also shown that the later the adult emerged, the lesser its size was. It should be attributed to the fact that the small-sized adult may accumulate nutrition lesser than large-sized one to get over the threshold to enter hibernation. It is probable that the fastest time of emergence is also defined by a period of time in which the physiological resume is reset and the exhaustion during winter is made up for.

Response to food amount

Though the growth, development and reproduction are continued loosely in time, there are a number of thresholds to nutritive condition between successive stages in both larva and adult period. Especially in larva, if an individual cannot get over the threshold, it forced to stay in the same stage regardless its age.

On the problem of insect life cycle, the attentions have been paid mainly to the seasonal timing of development or reproduction in herbivors, which grow on food plant. In the polyphagous predator such as this beetle, it must be important not how long time they can eat, but what amount of food they can eat actually. For this reason, the threshold for nutritive condition may appear prominently on the growth and development.

The presence of such threshold was already indicated by Palmer & Gorrik (1979) between stages of the 1st and 2nd instar of *C. repanda* under rearing condition. This study proved that the threshold was present not only in all stages of larval development but also in starting of reproduction and hibernation of adult. The threshold of adult was a function of its size. It may be reasonable, because the nutritive condition is defined with both the weight and size. So, in study on tiger beetles and other polyphagous insect predators, more attentions must be paid to the individual difference, such as the difference of size and nutritive condition among individuals. This subject will be considered further below.

Because of their sessility, the effect of food shortage may be definitive for the larvae. But they also show the counter responses to the food shortage in various ways. Firstly, as referred above, they prolong the period of their stage, or emerge as small-sized adults. Secondly, as seen in Figs. 26 and 27, the lighter the body weight of larva was in each instar, the shorter the period of their burrow closed during winter, i.e., the longer the larva have feeding time. Thirdly, rearing of larva proved that the lighter the body weight of larva was, the smaller the ratio of weight of leftover to that of taken preys was, i.e., the more the larva consumed efficiently. All of these responses may moderate the effect of food shortage, and then are responsible to the stability of larval population.

In this connection, Takahashi (1977) suggested with a mathematical model that if a fraction of members prolong their life cycle, the population became stable by the reason itself. This may be also true for our population, but it must be more important that the phenomenon is caused as a response to the food shortage. Łomnicki (1980) has shown with a mathematical model that unequal resource partitioning among individuals makes the population very stable.

Individual difference

Wellington (1957, 1960) suggested that the individual difference such as the difference of larval activities played much important part to stabilize the population. It has been also well known that phase variation in locust and phase polymorphism in moth operate as the main promoter in population process. This study shows that the individual difference which is found ordinarily in an insect population such as size and weight also promotes the population process.

The difference of size among adults originates from the food condition in larval period. The size is fixed in each adult at emergence and then it is, in turn, responsible to the difference of nutritive condition among individuals together with the food condition in adult period. The individual difference seems not to be succeeded to the eggs produced by them, though hereditary aspect could not be investigated any longer.

Both the difference of emergence time and of size among adults cause the difference of their fates after then. And the difference of nutritive condition among adults affects both the reproduction in autumn and the survival to the following year. As the nutritive condition is sensitive to the density in autumn, the difference is also responsible to both the yearly change of adult population size in this period and in the following reproductive season.

The number of eggs laid by a female is a function of its nutritive condition, which is defined by its size under a given food condition. So, the distribution of the individual difference in a population again may be responsible to the amount of reproduction. But, in this season the direct interference among adults was so prominent, I could not find any effect of individual difference to the amount of reproduction.

Stabilization of number and population processes

It is obvious that the stability of this population is acheived by a number of processes instead of one strong factor or process. Some authors (Voûte, 1943, Milne, 1962, Wilson, 1968) have suggested that natural insect population should be regulated by different kinds of factors which operate one by one at different densities. For example, Milne (1962) has considered that the increase of a population is controled by the combined operation of density-independent and imperfectly density-dependent environmental factors. In the rare cases when this combined operation fails, increase to the point of collective suicide is prevented by the one and only perfectly density-dependent factor, i.e., intraspecific competition. The extinction of population is prevented ultimately by density-independent factors alone. But he refered nothing to the actual mechanism of the control at the ordinal level of density.

I tried to understand the dynamics of this species as the result of a series of population processes. The stability of this population was caused not by the factors which operate one by one at different densities, but by the compensatory operation of successive population processes in the adult stage. In other words, it was performed by a number of the adjustment mechanisms which were built in the population processes themselves and operated at any ordinal level of density.

Both the structure of habitat and the behavior of adult must be fundamentally important to the population dynamics, because the former provides the actual field in which such mechanisms operate and the latter is a main performer of the mechanisms.

Iwao (1963, 1970) have already emphasized the importance of the actual structure of habitat, such as patchness or heterogeneity of it, on the population dynamics. This study make some further considerations possible on this subject. The structure of habitat may be treated at the two aspects, qualitative and quantitative one.

Habitat of a self-containing population should be composed of a set of sub-habitats. It is considered here that each sub-habitat has a kind of resources or property which is indispensable to the corresponding activities of a stage, such as foraging, oviposition, roosting and hibernation. In actual state, it may be possible both that an area (or a patch) serves as more than two kinds of sub-habitats, and that more than two areas provide the same kind of sub-habitat. The members of a population use properly these sub-habitats according to the physiological demand of their stage. Thus, uneven distribution and the reorganization may involved in the course of seasons. If a sub-habitat is not so broad for all the members of related stage, some kind of density-dependent process may be involved, even when the others are broad enough. An examle of this process was given at the adult concentration into the oviposition site in early summer.

There is also quantitative difference in suitability among the same kind of sub-habitats. The population process which proceeds over the sub-habitats of various degrees of suitability may also involve the density-dependent process. An example of this process was seen in the adult dispersal over the peripheral areas in autumn. The higher the density became in the favorable areas, the larger the number of individuals driven into the unfavorable ones was. The nutritive condition and the survival rate of these individuals became worse.

The behavior of adult plays an important part in the mechanism of the stabilization of this population, and its operation is also closely connected with the structure of habitat. Especially, the spacing of adult, i.e., excluding the others from a range around him, seems to be the most responsible to both the expansion of the population in autumn and the control of the amount of reproduction in early summer.

The larval population size was also much stable among generations. But I failed to find any density-dependent process in the larval stages. The prominent feature of larval stages is, as mentioned above, the toleration to unfavorable condition, mainly to food shortage, and some counteractions of larva which moderate the ill effect of the shortage were observed. Thus, the stability of larval stages must be resulted chiefly from the passive preservation of the initial number of hatched larvae which has been maintained within a relatively narrow range.

Den Bore (1968) and Reddingius & Den Bore (1970) suggested that the heterogeneity among habitats in which each sub-population inhabited was important for the stability of overall population, and also that the interchange between the sub-popuation might accelerate the stability. The first statement may be partly true in our larval population. But the most important matter for the stability of this population is that the adult utilizes the habitat as a whole and use these properly according to relative condition of each oviposition site, instead of the interchange between independent sub-populations.

Summary

1) The subjects of this paper are to describe the life history, growth and development, and structure of population of a tiger beetle, *Cicindela japonica Thunberg*, and to analyze its population dynamics. The study was carried out mainly at Kamigamo Experimental Forest Station, Kyoto City, over the period of 8 years, 1972-'79. The laboratory or outdoor rearing and the sampling of materials were also done abreast.

2) In Kamigamo Station, a main study area (Field-I, about 2 ha) and subsidiary one (Field-II, about 1 ha) were defined. Both of them consist of a series of bare grounds and neighbore each other. For study of larva, 7 working stations were settled in Field-I. All the larval burrows appeared within the stations were labelled. Observing the width of and the opening or closing the entrance of every burrow regularly, the development and the death of each larva were traced. Collecting the leftovers of prey from every larva for 2 years, the sort of prey animals and its amount were assessed. Newly emerged adults were caught by emergence trap. The marking and recapture method was adopted for adult population in Field-I over the whole period and in Field-II for 5 years. Adult was marked individually with brand at initial time, and its size, weight, and captured point were recorded at every time. Population size and other parameters were estimated by Jolly-Seber model.

3) Rearing both the larva and adult under the control of food condition throughout the stage, the growth and development and/or the reproduction in adult were observed. Moreover, a number of adults were collected regularly from various places in Kyoto City. Then some characteristics, such as body weight, the state of maturation, and rate of copulation, and its seasonal change were investigated.

4) Adults emerge in August to September, and enter into hibernation under the ground by mid-October. They use the period from emergence to enter into hibernation for foraging, but some individuals reproduce. The adults appear on the ground at mid-April. After early May they reproduce by their extinction, about early July. The egg is laid under the soil, and the period of egg is 10 to 19 days.

5) There is three larval instars. The larvae which were born in early summer hibernate once and pupate about July in the following year. The period of pupal stage is about two weeks. The larvae which were born in autumn hibernate twice and pupate about July in the same year to those born in early summer.

6) Then it takes two years for one generation regardless when the larvae is born. But there is large difference in developmental speed among individuals. Some individuals grow into adult one or, in rare case, two years later than the ordinary.

7) The larva ambushes the prey at the entrance of burrow day and night. Whenever any small animal enters within a range around the entrance, he catches it. The more the instar advances, the larger the prey he can catch.

8) The adult prowls for foraging on the ground in the daytime, and roosts on the bush or under the stone at night. They prefer the more soft preys than that of the larvae. The adult is willing to approach on foot to any kind of object moving within about 1.5 m around him. When two adults come face to face, the grappling and/or chasing happen. As a result an individual sends the other away from a range around him. The adults hibernate in the soil usually in group.

9) The amount of prey taken defines the speed of the growth and development of larva. The larva of any instar grows into the next stage only when his body weight amounts to a definite level. But the threshold of body weight become lower as season proceeds. The large difference in developmental speed among larvae observed in the field was attributed to the difference in the amount of preys taken among them.

10) The feeding condition of larval period defines both the emergence time and the size of adult. The body weight of each adult at the time has a linear relationship in logarithm with its size in each sex.

11) The ovary or testis of adult is in immature stage at emergence, and its development depends upon the feeding after then. To start the reproduction, each adult must have a heavier body weight than a threshold which is defined by its size in each sex.

12) There is also a threshold of body weight to enter hibernation for each male or female of any size.

13) As a criterion to judge the nutritive condition of each adult of any size at any time, the relative condition factor (Rcf), i.e., the ratio of body weight to the standard weight of the stage concerned, was used. The relationships as follows were shown. The number of eggs laid by a female for a period is a function of its Rcf to reproductive threshold. The individuals of each sex whose Rcf to hibernation-starting threshold was below the unity is likely to be die during winter in the field.

14) The number of emerged adults in a station is dependent both on initial number and on the mortality in developmental stages. Among the latters, mainly the mortality in the pupal stage, and secondarily in the 1st and 2nd instar were responsible for.

15) The death of the larvae is mainly caused by the food shortage. The 3rd instar larvae can endure the food shortage by reserving the effect into the later stages, the pupal or adult stage.

16) Any density-dependent process was not found in the survival and the developmental speed of larva. Though a parasitoid wasp (Methoca yasumatsui Iwata) has attacked only the 2nd instar larva, the effect was no longer large on the total mortality of the larval stages.

17) The seasonal change in larval population size was much stable in Field-I for 5 years. The change in total number of the 1st instar appeared in it was only 2.0-fold among years.

18) Because the adults interchanged little between Field-I and -II but mingled with each other in each field, the population in each was considered as a local population.

19) The seasonal change in adult population size was also much stable in Field-I for 7 generations. The change in number is 1.4- and 1.5-fold at peak in autumn and at onset of reproductive period in early summer respectively. The adult population size in Field-II was lowered gradually during 4 generations. But the density to the total area of bare grounds was maintained equal at about the same level to Field-I.

20) The adults use properly the different quality of habitat in the course of seasons as follows. They scatter widely over any kind of the bare ground in Field-I mainly for foraging in autumn, and concentrate upon some restricted area for oviposition in early summer.

21) The individuals in the marginal area in autumn was considered as those which were driven from the central as the density became high. Their survival rate was low, probably because of the poor food condition there.

22) The more the total number of adults emerged was, the lower the survival rate of the population in autumn was. The survival rate to the following year of the females which had oviposit was lower than the other.

23) There was a reverse relationship between the number of adults in autumn and in early summer. The reason is considered as that the number of adults which can enter the hibernation becomes small according to the poor nutritive condition when the density is high.

24) The number of the 1st instar larvae appeared in early summer in Field-I was reversely related to the cumulative number of adult during the period. It was suggested that the direct interference between adults was most responsible to this relationship.

25) From these results and considerations, I think that the stability of this population is achieved with a series of compensatory processes of adult population which operate successively. Both the behavior of adult and the structure of habitat are bound up with these processes, as well as actual food condition of each part of habitat.

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Appendix 1. List of preys of the larva, *C. japonica*.

This list consists of preys which were found in leftovers of each instar of larva within all the stations in Field-I of Kamigamo Station from 1972 to 1979. The scientific name and their systematic order followed the books;

1) Uchida, T., Fundamentals of systematic zoology (5th ed.),1968, Hokuryukan Co., Ltd., Tokyo, Japan. (in Japanese)
2) Hokuryukan's illustrated encyclopedia of the fauna of Japan (revised ed.), 1947, Hokuryukan Co., Ltd., Tokyo, Japan. (in Japanese)
3) Hokuryukan's iconographia insectrum Japonicorum colore naturali edita, Vol. 1-3, 1959-1965, Hokuryukan Co,. Ltd., Tokyo, Japan. (in Japanese)

The ants and the other preys without any proviso denote the workers and adults respectively.

Phylum Class Order Family	Species	No. of preys Instar		
		1st	2nd	3rd
MOLLUSCA				
GASTROPODA				
STYLOMMATOPHORA				
Philomycidae	*Incilaria confusa*			1
Bradybaenidae	*Acusta despecta*			1
	sp.			1
ANNELIDA				
OLIGOCHAETA				
NEOLIGOCHAETA				
Lumbricidae	*Allolobophora* spp.			2
ARTHROPODA				
ARACHNIDA				
ARANEAE				
Ctenizidae	*Kishinouyeus typicus*			8
Segestriidae	*Ariadna lateralis*			1
Scytodidae	*Scytodes nigrolineata*			1
Argiopidae	spp.			2
Lycoidae	*Lycosa coelestis*			1

Appendix 1. (continued)

Thomisidae	spp.			2
Saltícidae	spp.		1	3
Unidentified spiders		5	18	163
ACARINA				
Unidentified mites		2		
CRUSTACEA				
ISOPODA				
Oniscidae	*Armadillidium vulgara*	1	5	79
DIPLOPODA				
POLYDESMOIDEA				
Strongylosomidae	*Oxidus gracilis*	2	16	395
	spp.		2	63
CHILOPODA				
GEOPHILOMORPHA				
Mecistocephalidae	sp.			1
INSECTA				
COLLEMBOLA				
Unidentified springtails		6	9	3
THYSANURA				
Machilidae	*Pedetontus nipponicus*			1
EPHEMEROPTERA				
Ephemeridae	*Ephemera strigata*			2
ODONATA				
Libellulidae	*Sympetrum frequens*			1
PLECOPTERA				
Unidentified stonefly				1
ORTHOPTERA				
Phalangopsiidae	*Homoeogryllus japonicus*			1
Nemobiidae	*Pteronemobius fascipes*	1		10
Gryllidae	*Gryllus yemma*			4
	Gryllus minor			2
	Gryllodes aspersus			10
	Loxoblemmus arietulus			2
	Loxoblemmus doenitzi			6
Gryllomorphidae	*Scleropterus coriaceus*			6
Unidentified crickets	(adult; large)			32
idem	(adult; small)		5	24
idem	(nymph)		1	4
Stenopelmatidae	*Diestrammena japonica*			3

Appendix 1. (continued)

Tettigoniidae	sp.			1
Tridactylidae	*Tridactylus japonicus*	1	2	7
Tetrigidae	*Acrydium japonicum*	1	6	232
	Euparaterrix histricus			3
Locustidae	*Acrida turrita*	1		9
	Atractomorpha bedeli			5
Unidentified grasshoppers (large)				4
idem (small)				8
Mantidae	sp. (nymph)			1
Blattellidae	*Blattella niponica*			7
ISOPTERA				
Rhinotermitidae	*Reticulitermes speratus*		1	
PSOCOPTERA				
Unidentified lichen lice				1
HEMIPTERA				
Cydnidae	*Geotonomus pygmaeus*			2
Plataspidae	*Coptosoma punctissimus*			1
Pentatomidae	*Halyomorpha brevis*			1
	spp. (adult)		2	5
	spp. (nymph)	1	1	23
Lygaeidae	spp.			2
Largidae	*Physopelta cincticollis*			1
	spp.			2
Tingidae	*Galeatus spinifrons*	1		
Reduviidae	*Velinus nodipes*			2
	spp.		2	6
Miridae	sp.			1
Deltocephalidae	spp.			2
Flatidae	*Geisha distinctissima*		2	3
Delphacidae	spp.	1		4
Aphididae	spp. (alate)	11		5
	spp. (apterous)	15		1
	spp. (nymph & unknown morph)	62	2	
Unidentified bugs				7
NEUROPTERA				
Mantispidae sp.				1
Chrysopidae sp.				1
MECOPTERA				

Appendix 1. (continued)

Panorpidae	*Panorpa japonica*			1
TRICHOPTERA				
Unidentified caddis flies				2
LEPIDOPTERA				
Psychidae	*Nipponopsyche fuscescens* (larva)			39
Pyralididae	sp.			1
Geometridae	spp.			2
Notodontidae	sp. (larva)			1
Noctuidae				1
Unidentified moths				7
Unidentified caterpillars		3	5	38
DIPTERA				
Tipulidae	spp.	2	2	28
Culicidae	*Anopheles* sp.			1
	Arimigeres subalbatus			1
	sp.	1		
Chironomidae	spp.		1	2
Mycetophilidae	spp.	2		
Empididae	spp.		1	10
Syrphidae	*Eristalomyia tenax*			4
	spp.			4
Trypetidae	sp.			1
Drosophilidae	spp.			2
Muscidae	spp.			2
Calliphoridae	spp.			5
Sarcophagidae	spp.			3
Unidentified Diptera (large)		21	19	424
idem (small)		7	4	56
COLEOPTERA				
Cicindelidae	*Cicindela japonica* (larva)	1		
Carabidae	*Apotomopterus yaconinus*			2
Harpalidae	*Ophonus* spp.			17
	Pterostichus spp.	1		31
	Calathus halensis			1
	Chlaenius spp.			20
	Planetes puncticeps			2
	Panagaeus japonicus			5
	Tachys laetificus	1		

Appendix 1. (continued)

	Chlaenius virgulifer			5
	Chlaenius naeviger			1
	spp.	1	2	100
Haliplidae	sp.			1
Silphidae	sp.			1
	spp. (larva)			2
Staphylinidae	spp.		1	6
Scarabaeidae	*Maladera* spp.			3
	Sericania sp.			1
	Anomala daimiana		1	6
	Heptophylla picea			2
	Lachnosterna sp.			1
	Blitopertha orientalis		1	4
	Apogonia amida			58
	spp.		1	16
Elateridae	*Colaulon scrofa*		1	11
	spp.			7
Cantharidae	*Athemus suturellus*			1
	spp.			2
Dermestidae	sp.			1
Coccinellidae	*Propylaea quatuordecimpunctata*			1
	Epilachna vigintioctopunctata			1
	Chilocorus kuwanae			1
	sp.			1
Tenebrionidae	spp.	1	1	3
Lagriidae	*Arthromacra viridissima*			3
	Luprops cribrifrons			1
Alleculidae	*Allecula fuliginosa*			17
Oedemeridae	*Xanthochroa waterhousei*			2
	Xanthochroa hilleri			1
	Xanthochroa spp.			16
Meloidae	*Meloë* sp.			1
Cerambycidae	*Ceresium* sp.			1
	Cephalallus unicolor			1
	Pterolophia zonata			1
	Pterolophia rigida			1
Chrysomelidae	*Atrachya menetriesi*			22
	Gallerucida nigromaculata			1

Appendix 1. (continued)

	Linaeidea aenea			1
	spp.			9
Attelabidae	sp.			1
Anthribidae	sp.			1
Curculionidae	*Phyllobius* spp.			11
	spp.		3	14
Ipidae	*Platypus lewise*			1
	spp.	1		1
Unidentified beetles		6	5	34
HYMENOPTERA				
Tenthredinidae	spp. (adult)	1		2
	sp. (larva)			1
Argidae	*Arge similis*			2
	Arge pagana			1
Ichneumonidae	sp.			1
Bracodidae	sp.			1
Chrysididae	*Chrysis* spp.			2
Leucospidae	*Leucospis japonica*			1
Formicidae	*Brachyponera chinensis*			4
	Proceratium watasei (♀)			1
	Aphenogaster famelica			2
	Messor aciculatum			2
	Pheidole fervida	7	2	54
	Crematogaster sordidula		1	10
	idem (♀)			3
	Monomorium nipponense	5	1	12
	Pristomyrmex pungens	22	7	38
	Tetramorium caespitum	46	12	82
	idem (♀)		3	2
	Iridomyrmex itoi	4		1
	Camponotus japonicus		13	126
	Camponotus obscuripes (♀)		1	
	Camponotus caryae (♀)			1
	Polyrhachis moesta (♀)			1
	Formica japonica	1	19	193
	idem (♀)			11
	Paratrechina sakurae	1	1	

Appendix 1. (continued)

	Lasius fuligonosus (♀)			4
	Lasius niger	67	23	132
	idem (♀)	6	24	43
	lasius umbratus (♀)		1	
	spp. (worker)	7	3	26
	spp. (♀)	1	4	21
	spp. (♂)	1		4
Scoliidae	*Campsomeris* sp.			1
Tiphiidae	spp.		1	1
Vespidae	*Eumenes micado*			5
	Eumenes fratercula			1
	Discoelius japonicus			1
	Vespula lewisi			3
	Parapolybia indica			1
	Polistes mandarinus			2
	Polistes jadwigae			1
	Anterhynchium flavomarginatum			1
	Vespa sp.			1
Pompilidae	sp.			1
Sphecidae	*Sceliphron inflexum*			1
	Sceliphron deforme			1
	spp.			2
Andrenidae	*Andrena prostomias*		1	56
	sp.			1
Halictidae	spp.			6
Apidae	*Bombus ignitus*			1
	Apis mellifera		2	105
Unidentified wasps		9	1	51
Unidentified insects		11	12	97
VERTEBRATE				
AMPHIBIA				
ANURA				
Bufonidae	*Bufo vulgaris* (young)			1
Ranidae	*Hyla arborea*			1
The other unidentified animals			2	5

Appendix 2. List of preys of the adult, *C. japonica*.

This list consists of preys which were found to be eaten by adults during marking and recapture work in Field-I of Kamigamo Station from 1972 to 1979. The scientific name and their systematic order follow those mentioned in Appendix 1.

Phylum Class Order Family	Species	No. of preys
(Animals)		
ANNELIDA		
OLIGOCHAETA		
NEOLIGOCHAETA		
Unidentified earthworms		9
HIRUDINEA		
GNATHOBDELLIDA		
Unidentified leach (carcase)		1
ARTHROPODA		
ARACHNIDA		
ARANEAE		
Lycosidae	sp.	1
Salticidae	sp.	1
INSECTA		
ODONATA		
Libellulidae	*Orthetrum albistylum* (dying)	1
ORTHOPTERA		
Tetrigidae	*Acridium japonicum*	3
ISOPTERA		
Rhinotermitidae	*Reticulitermes speratus*	1
HEMIPTERA		
Cicadidae	*Meimuna opalifera* (carcase)	1
Aphididae	sp.	1
LEPIDOPTERA		
Hesperiidae	*Parnara guttata* (larva)	1
Unidentified caterpillars		6

Appendix 2. (continued)

DIPTERA			
	Calliphoridae	sp.	1
	Unidentified flies		2
HYMENOPTERA			
	Formicidae	*Aphaenogaster famelica*	1
		Tetramorium caespitum	3
		Camponotus japonicus	5
		idem (♀)	2
		Formica fusca	5
		idem (♀)	2
		Lasius fuliginosus	1
		Lasius niger	6
		idem (♀)	2
		sp.	1
	Andrenidae	*Andrena prostomias*	1
	Apidae	*Apis mellifera* (dying & carcase)	3
Unidentified animals			10
(Plants)			
SPERMATOPHYTA			
DICOTYLEDONEAE			
GERANIALES			
	Euphorbiaceae	*Mallotus japonicus* (fruit almost spoiled on the ground)	8

Appendix 3. Paramerters of regression lines in development of adult in both sexes.

A and B denote the parameters in regression line; $\log W = A + B \log L$.

Regression line	Female		Male	
	A	B	A	B
Emergence (E)	-0.2041	2.9597	-0.3324	3.1805
Reproductive threshold (Rt)	0.7259	2.0585	-0.2890	3.2140
Maturing threshold (Mt)	0.4316	2.3746	-	-
Hibernation-starting threshold (Hst)	0.2239	2.6228	0.2010	2.6843
Hibernation-ending (He)	0.3732	2.4760	0.2225	2.6994
Hibernation-starting (Hs)	0.4158	2.4331	0.6757	2.1405

Appendix 4. Data from the marking and recapture of adults for 7 generations, 1972 - 1979, in Field-I.

1. July 1972 - June 1973.

i	Date	n_i	R_i	r_i											
				1	2	3	4	5	6	7	8	9	10	11	12
1	30 July	10	10												
2	5 Aug.	10	10	2											
3	14 Aug.	40	40		2										
4	30 Aug.	107	107	2	1	8									
5	12 Sep.	71	71			2	8								
6	20 Sep.	40	40				2	3							
7	28 Sep.	31	31			1	2	3	4						
8	13 Apr.	14	14				1	1	1						
9	1 May	17	17				1		1		1				
10	5 May	43	43			1	2		1			4			
11	10 May	29	29			1	2	1	1		1	1	8		
12	20 May	28	28		1		1	1		1			3	4	
13	14 June	17	17											1	3

2. August 1973 - July 1974

i	Date	n_i	R_i	r_i												
				1	2	3	4	5	6	7	8	9	10	11	12	13
1	20 Aug.	23	23													
2	25 Aug.	19	19	4												
3	5 Sep.	40	40	2	1											
4	8 Sep.	40	40		1	4										
5	4 Oct.	49	49	1	2	3	4									
6	15 Apr.	26	26			2	3	2								
7	17 Apr.	33	33			1	1	2	7							
8	4 May	50	50				2	1	2	5						
9	16 May	43	43			1		1	2	3	12					
10	23 May	36	36			1		2		4	5	8				
11	3 June	37	37								1	6	6			
12	20 June	17	17				1			1			2	4		
13	3 July	11	11								1		1		6	
14	12 July	4	4											1		3

Appendix 4. (continued)

3. August 1974 - June 1975

i	Date	n_i	R_i	r_i																					
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	3 Aug.	16	16																						
2	5 Aug.	30	30	4																					
3	15 Aug.	56	56	3	5																				
4	22 Aug.	90	90	2	7	11																			
5	29 Aug.	96	96		2	7	21																		
6	5 Sep.	88	88		1	5	7	11																	
7	12 Sep.	123	123				5	18	23																
8	19 Sep.	93	93			1	3	7	11	24															
9	26 Sep.	88	88			1	2	3	5	11	13														
10	4 Oct.	74	74			1	3	1	5	10	13	9													
11	17 Oct.	37	37							2	3	2	11												
12	16 Apr.	47	47				2	1	1	3		2	4	2											
13	23 Apr.	37	37				2	1	1	1	2	4	3	3	7										
14	1 May	54	54			1		2		2	3	4	1	4	10	8									
15	8 May	51	51									3		2	3	2	12								
16	15 May	57	57									3	1		5	3	9	16							
17	22 May	50	50					1	2	2		2	1	2	2		4	4	21						
18	31 May	41	40					1				2		1	1	1	1	1	5	16					
19	12 June	23	23												1		1	2	2		6				
20	16 June	15	15																1	3	3	6			
21	23 June	8	8																		1	1	4		
22	27 June	9	9																	1	1	2		2	
23	30 June	13	13								1			1	1			1		2	1		2	1	3

Appendix 4. (continued)

4. July 1975 - June 1976

i	Date	n_i	R_i	r_i										
				1	2	3	4	5	6	7	8	9	10	11
1	31 July	14	14											
2	11 Aug.	52	52	3										
3	28 Aug.	91	91	1	3									
4	11 Sep.	122	122		3	14								
5	9 Oct.	80	80		1	6	15							
6	16 Oct.	10	10				1	2						
7	15 Apr.	11	11			1								
8	26 Apr.	52	52		1	2	9	9		1				
9	8 May	51	51			3	3	2			6			
10	20 May	41	41			1	2	1			5	11		
11	7 June	38	38				1	1				5	11	
12	28 June	2	2									1		1

5. August 1976 - June 1977

i	Date	n_i	R_i	r_i												
				1	2	3	4	5	6	7	8	9	10	11	12	13
1	5 Aug.	26	26													
2	23 Aug.	88	88	5												
3	1 Sep.	110	110	2	22											
4	14 Sep.	179	179		7	23										
5	23 Sep.	97	97	1	1	2	28									
6	29 Sep.	172	172		2	9	30	39								
7	5 Oct.	45	45		1	1	4	3	16							
8	12 Oct.	21	21		1	2	1	1	5	6						
9	21 Apr.	37	37		2	2	2		7	1						
10	1 May	54	54		1	2	8	3	6	3		7				
11	8 May	39	39			1	2		4	2		2	14			
12	20 May	35	35				2	2	2	1		2	7	5		
13	29 May	32	32			1		1	1			3	5	4	6	
14	5 June	13	13											1	2	4

Appendix 4. (continued)

6. August 1977 - June 1978

i	Date	n_i	R_i	r_i														
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	9 Aug.	11	11															
2	12 Aug.	46	46	3														
3	29 Aug.	59	59	1	4													
4	5 Sep.	68	67		2	14												
5	11 Sep.	98	90		2	6	17											
6	18 Sep.	61	61			3	3	10										
7	1 Oct.	65	65			2	4	6	9									
8	9 Oct.	21	21				2	5	2	4								
9	4 May	70	70		2	2	3	6	1	5	3							
10	12 May	64	64		1	2	2	2	5	2	2	26						
11	21 May	53	53			3		1	2	4	1	6	15					
12	27 May	41	41			1			2			2	6	12				
13	2 June	33	33										3	4	8			
14	10 June	15	15											3	3	6		
15	15 June	9	9											1		2	5	
16	26 June	3	3													1		2

7. August 1978 - June 1979

i	Date	n_i	R_i	r_i										
				1	2	3	4	5	6	7	8	9	10	11
1	10 Aug.	31	31											
2	13 Aug.	36	36	7										
3	26 Aug.	53	53	3	5									
4	11 Sep.	90	90	2	4	10								
5	17 Sep.	68	68	1	1	6	17							
6	25 Sep.	60	60		1	4	7	8						
7	2 Oct.	52	52	1	1	2	5	6	10					
8	29 Oct.	40	0	1		2	3	2	2	6				
9	5 May	49	49		1	1	3	2	1	2				
10	21 May	45	45			1	3	1	3			11		
11	11 June	24	24				2					2	6	
12	18 June	11	11									1	2	5

Appendix 5. Data from the marking and recapture of adults for 4 generations, 1973 - 1977, in Field-II.

1. August 1973 - June 1974

i	Date	n_i	R_i	r_i							
				1	2	3	4	5	6	7	8
1	23 Aug.	53	53								
2	27 Aug.	40	4	4							
3	7 Sep.	76	76	4	4						
4	6 Oct.	48	48	1	2	5					
5	19 Apr.	71	71		2	2					
6	11 May	69	69		1			7			
7	24 May	41	41	1		1		4	12		
8	4 June	59	59					8	12	13	
9	26 June	26	26	1		1	1	4	1	1	8

2. May - June 1975

i	Date	n_i	R_i	r_i		
				1	2	3
1	22 May	26	26			
2	23 May	63	63	12		
3	31 May	26	26	2	11	
4	9 June	16	16		4	3

Appendix 5. (continued)

3. September 1975 - June 1976

i	Date	n_i	R_i	r_i 1	2	3	4	5	6
1	30 Sep.	118	118						
2	1 Oct.	95	95	35					
3	4 Oct.	122	122	23	23				
4	15 Oct.	16	16	1	2	10			
5	10 May	47	47	3	2	6			
6	20 May	49	49	2	2	4		10	
7	28 June	17	17		1			3	5

4. September 1976 - May 1977

i	Date	n_i	R_i	r_i 1	2	3	4	5	6	7	8	9
1	18 Sep.	65	65									
2	22 Sep.	54	54	7								
3	24 Sep.	45	45	5	8							
4	29 Sep.	79	79	4	8	9						
5	5 Oct.	14	14			5	3					
6	12 Oct.	9	0		1	1	7					
7	23 Apr.	30	30	4		1	3	1				
8	8 May	32	32	1		1	1			4		
9	16 May	22	22		1		2			2	4	
10	20 May	15	15								2	4

Appendix 6. Population parameters estimated for 7 adult generations in Field-I, 1972 - 1979.

1. July 1972 - May 1973

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/r}$	$\frac{2B_i}{1+\phi_i}$
1	30 July				0.750 (0.441)		0.669	
2	5 Aug.	0.200 (0.127)	7.5 (5.1)	27.5 (35.0)	0.735 (0.368)	147.2 (184.0)	0.797	169.7
3	14 Aug.	0.050 (0.035)	12.3 (6.1)	167.4 (203.5)	0.706 (0.253)	205.2 (174.2)	0.850	240.8
4	30 Aug.	0.103 (0.029)	35.9 (16.3)	323.3 (181.2)	0.459 (0.147)	253.6 (171.4)	0.678	347.8
5	12 Sep.	0.141 (0.042)	61.4 (34.3)	402.1 (277.4)	0.416 (0.193)	202.9 (240.2)	0.467	286.5
6	20 Sep.	0.125 (0.052)	54.2 (36.7)	370.4 (360.7)				Σ:1044.4 (S.D.: 324.2)
10	5 May			244.7 (57.8)	0.875 (0.390)		0.829	
11	10 May			214.0 (80.9)	0.605 (0.371)		0.704	
12	20 May			129.5 (62.5)				

* The notation follows *Seber* (1973).

** The number in parentheses denotes error of estimation.

*** The last two columns show the survival rate per a week and number of individuals recruited respectively.

The latter follows *Dempster* (1971).

Appendix 6. (continued)

2. August 1973 - July 1974

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	20 Aug.				0.696 (0.334)		0.602	
2	25 Aug.	0.211 (0.094)	16.0 (9.7)	64.0 (57.2)	0.707 (0.379)	195.6 (212.5)	0.802	229.2
3	5 Sep.	0.075 (0.042)	23.5 (13.0)	240.9 (250.0)	0.862 (0.641)	162.7 (313.9)	0.708	174.7
4	8 Sep.	0.125 (0.052)	54.2 (36.7)	370.4 (360.7)				Σ:403.9 (S.D.:344.1)
5	4 May			284.6 (46.7)	0.825 (0.220)		0.911	
9	16 May			242.5 (48.3)	0.850 (0.280)		0.850	
10	23 May			206.2 (54.1)	0.732 (0.327)		0.821	
11	3 June			151.0 (54.6)	0.215 (0.092)		0.531	
12	20 June			32.4 (7.3)	0.432 (0.139)		0.636	
13	3 July			14.0 (3.2)				

Appendix 6. (continued)

3. August 1974 - June 1975

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	3 Aug.				0.856 (0.200)		0.579	
2	5 Aug.	0.133 (0.062)	13.7 (3.7)	84.9 (49.6)	0.858 (0.132)	144.5 (84.8)	0.898	155.6
3	15 Aug.	0.143 (0.047)	34.3 (7.0)	217.3 (85.7)	0.720 (0.100)	102.1 (71.7)	0.720	118.7
4	22 Aug.	0.222 (0.044)	59.7 (8.9)	258.6 (59.4)	0.696 (0.081)	103.7 (51.5)	0.696	122.3
5	29 Aug.	0.313 (0.047)	90.6 (12.1)	283.6 (53.3)	0.717 (0.089)	198.9 (74.0)	0.717	231.6
6	5 Sep.	0.273 (0.048)	113.0 (15.2)	402.3 (85.4)	0.896 (0.144)	60.9 (75.6)	0.896	64.3
7	12 Sep.	0.374 (0.043)	159.7 (23.8)	421.2 (76.2)	0.811 (0.201)	46.0 (56.5)	0.811	50.8
8	19 Sep.	0.495 (0.052)	193.7 (51.1)	387.4 (110.0)				Σ:743.3 (S.D.:118.2)
15	8 May			273.6 (36.6)	0.731 (0.127)		0.731	
16	15 May			200.1 (22.0)	0.837 (0.145)		0.837	
17	22 May			167.5 (22.4)	0.901 (0.222)		0.922	
18	31 May			150.8 (31.3)	0.518 (0.156)		0.682	
19	12 June			78.2 (17.1)	0.689 (0.239)		0.521	
20	16 June			53.9 (14.5)	0.775 (0.380)		0.775	
21	23 June			41.8 (17.1)	0.814 (0.469)		0.698	
22	27 June			34.0 (13.7)				

Appendix 6. (continued)

4. July 1975 - June 1976

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	31 July				0.688 (0.393)			
2	11 Aug.	0.577 (0.032)	9.6 (7.4)	127.5 (154.0)	0.362 (0.072)	349.8 (238.4)	0.658	513.6
3	28 Aug.	0.044 (0.022)	21.5 (8.8)	396.0 (300.2)	0.649 (0.161)	227.0 (218.5)	0.805	275.4
4	11 Sep.	0.139 (0.031)	70.8 (24.4)	483.9 (204.1)				Σ:789.0 (S.D.:318.7)
9	8 May			201.2 (34.4)	0.691 (0.191)		0.806	
10	20 May			139.0 (30.1)	0.413 (0.254)		0.695	
11	7 June			57.5 (33.0)				

5. Aug. 1976 - May 1977

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	5 Aug.				0.494 (0.733)		0.771	
2	23 Aug.	0.057 (0.025)	12.9 (3.8)	190.7 (102.9)	0.635 (0.074)	149.7 (76.1)	0.871	183.1
3	1 Sep.	0.218 (0.039)	61.0 (10.4)	270.8 (62.2)	0.532 (0.055)	312.2 (71.6)	0.712	407.6
4	14 Sep.	0.168 (0.028)	78.6 (10.9)	456.2 (89.6)	0.610 (0.055)	134.9 (72.8)	0.681	167.6
5	23 Sep.	0.330 (0.048)	139.1 (17.4)	413.1 (75.5)	0.835 (0.176)	21.6 (54.5)	0.810	23.5
6	29 Sep.	0.465 (0.038)	171.8 (38.4)	366.5 (85.7)				Σ:781.8 (S.D.:110.4)
11	5 May			249.9 (62.6)	0.668 (0.249)		0.790	
12	20 May			167.0 (46.1)	0.547 (0.256)		0.626	
13	29 May			91.4 (34.5)				

Appendix 6. (continued)

6. August 1977 - June 1978

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	9 Aug.				0.748 (0.401)		0.507	
2	12 Aug.	0.065 (0.036)	8.2 (5.5)	96.6 (104.5)	0.275 (0.036)	115.7 (65.5)	0.588	181.5
3	29 Aug.	0.085 (0.036)	14.2 (3.9)	142.3 (74.5)	0.750 (0.120)	101.7 (68.2)	0.750	116.2
4	5 Sep.	0.235 (0.051)	51.4 (10.0)	208.5 (58.7)	0.864 (0.221)	160.6 (77.1)	0.843	172.3
5	11 Sep.	0.255 (0.044)	89.2 (23.4)	339.8 (106.1)	0.574 (0.159)	139.3 (90.0)	0.574	177.0
6	18 Sep.	0.262 (0.056)	90.4 (33.1)	329.7 (145.7)				Σ :647.0 (S.D.:121.8)
8	4 May			299.2 (32.2)	0.935 (0.166)		0.943	
9	12 May			279.8 (39.7)	0.686 (0.142)		0.746	
10	21 May			191.9 (28.8)	0.816 (0.218)		0.789	
11	27 May			156.5 (34.7)	0.450 (0.137)		0.394	
12	2 June			70.4 (14.6)	0.403 (0.131)		0.451	
13	10 June			28.3 (7.1)	0.435 (0.178)		0.312	
14	15 June			12.3 (4.0)				

Appendix 6. (continued)

7. August 1978 - June 1979

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	10 Aug.				0.869 (0.238)		0.720	
2	13 Aug.	0.194 (0.066)	26.9 (8.2)	124.5 (59.6)	0.593 (0.118)	129.1 (74.0)	0.755	162.0
3	26 Aug.	0.151 (0.049)	33.8 (7.5)	203.0 (82.0)	0.850 (0.166)	189.2 (103.5)	0.931	204.6
4	11 Sep.	0.178 (0.040)	67.6 (13.3)	361.7 (107.1)	0.852 (0.212)	14.6 (91.3)	0.829	15.8
5	17 Sep.	0.368 (0.059)	121.6 (31.4)	322.7 (98.5)	0.607 (0.175)	103.9 (68.6)	0.646	129.3
6	25 Sep.	0.333 (0.061)	103.2 (33.5)	299.7 (114.4)				Σ:511.7 (S.D.:131.3)
9	5 May			225.7 (45.1)	0.698 (0.235)		0.854	
10	21 May			154.4 (42.7)	0.311 (0.122)		0.678	
11	11 June			49.0 (13.9)				

Appendix 7. Population parameters estimated for 4 adult generations in Field-II, 1973 - 1976.

1. August 1973 - June 1974

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	23 Aug.				0.628 (0.247)		0.443	
2	27 Aug.	0.100 (0.047)	33.3 (18.6)	272.9 (250.3)	0.634 (0.371)	224.8 (234.8)	0.748	275.1
3	7 Sep.	0.105 (0.035)	46.5 (32.2)	397.8 (343.8)				Σ:275.1
6	11 May			281.7 (39.1)	0.772 (0.185)		0.870	
7	24 May			217.4 (42.5)	0.823 (0.274)		0.884	
8	4 June			179.0 (48.2)				

2. May 1975

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	22 May			157.4 (26.1)	1.010 (0.244)			
2	23 May			159.0 (27.8)	0.715 (0.364)			
3	31 May			113.8 (54.3)				

Appendix 7. (continued)

3. September 1975 - May 1976

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	30 Sep.				0.841 (0.104)		0.298	
2	1 Oct.	0.368 (0.050)	99.3 (14.3)	264.7 (48.9)				
5	10 May			211.6 (44.0)	0.704 (0.285)			
6	20 May			149.0 (51.7)				

4. September 1976 - May 1977

i	Date	α_i	M_i	N_i	ϕ_i	B_i	$\phi_i^{7/T}$	$\frac{2B_i}{1+\phi_i}$
1	18 Sep.				0.556 (0.094)		0.358	
2	22 Sep.	0.130 (0.046)	36.1 (10.7)	248.3 (122.9)	0.808 (0.266)	23.4 (103.9)	0.475	25.0
3	24 Sep.	0.289 (0.068)	68.2 (23.7)	224.1 (97.9)				Σ : 25.0 (S.D.:109.3)
7	8 May							
8	16 May							

Appendix 8. A list of estimates concerned to population dynamics of C. *japonica* in Field-I, 1972-1979.

Season	Autumn														Early summer				
Stage	Larva				Adult							Larva			Adult				
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Generation	No. of 3rd instar larvae in early summer	No. of 3rd instar larvae prolong the stage	No. of 2nd instar larvae pupate in the year	No. of mature larvae in early summer	Total no. of adults emerged (Dempstor's method)	Revised total no. of adults emerged	Rate of emergence to no. of mature larvae	Mean weekly survival rate (whole in autumn)	Mean weekly survival rate (mid-Aug. - mid-Sep.)	Mean weekly survival rate (late Aug. - mid-Sep.)	No. of adults at peak in **autumn**	Cumulative no. of the 1st instar larvae in autumn	"Mean survival period" of the 1st instar	Total no. of the 1st instar larvae hatched	No. of adults at onset of reproductive period	Cumulative no. of adults in early summer	Mean weekly survival rate (early May - late May)	Mean weekly survival rate (early May - early June)	Mean weekly survival rate (whole in early summer)
1972-1973	.....	..	..	.....	1,044	1,358	....	.678	.645	.562	402	.....	17.8	...	245	4,492	.764	....	....
1973-1974	.....	..	..	.....	404	1,164	....	....	....	.699	370	.....	14.4	...	285	7,516	.880	.860	.735
1974-1975	.....	..	..	.....	743	929	....	.752	.764	.776	414	.....	12.7	...	274	6,643	.826	.788	.728
1975-1976	1,012	33	52	1,032	789	948	.919	.747	.728	.805	484	5,756	13.2	441	201	4,482	.806	.748	....
1976-1977	1,083	44	26	1,065	782	969	.910	.766	....	.750	456	7,224	13.5	534	250	4,760	.703	....	....
1977-1978	1,162	38	48	1,171	647	1,006	.859	.641	.680	.713	340	11,744	15.2	773	299	5,541	.822	.629	....
1978-1979	864	13	21	872	512	712	.816	.770	.784	.793	362	9,862	13.9	709	236	4,889	.854	.761	....

Appendix 8. (continued)

Season	Early summer			
Stage	Egg	Larva		
	T	U	V	W
Generation	Expected total no. of laid eggs in early summer	Cumulative no. of the 1st instar larvae	"Mean survival period" of the 1st instar	Total no. of the 1st instar larvae hatched
1972-1973	.....	......	23.5	.....
1973-1974	.....	......	16.8	.....
1974-1975	12,066	39,528	14.3	2,770
1975-1976	6,757	77,381	16.5	4,698
1976-1977	6,994	61,415	17.2	3,569
1977-1978	8,464	49,368	16.0	3,086
1978-1979	7,980	53,887	15.7*	3,437

* The value is the weighted average for generations from 1975 to 1978.

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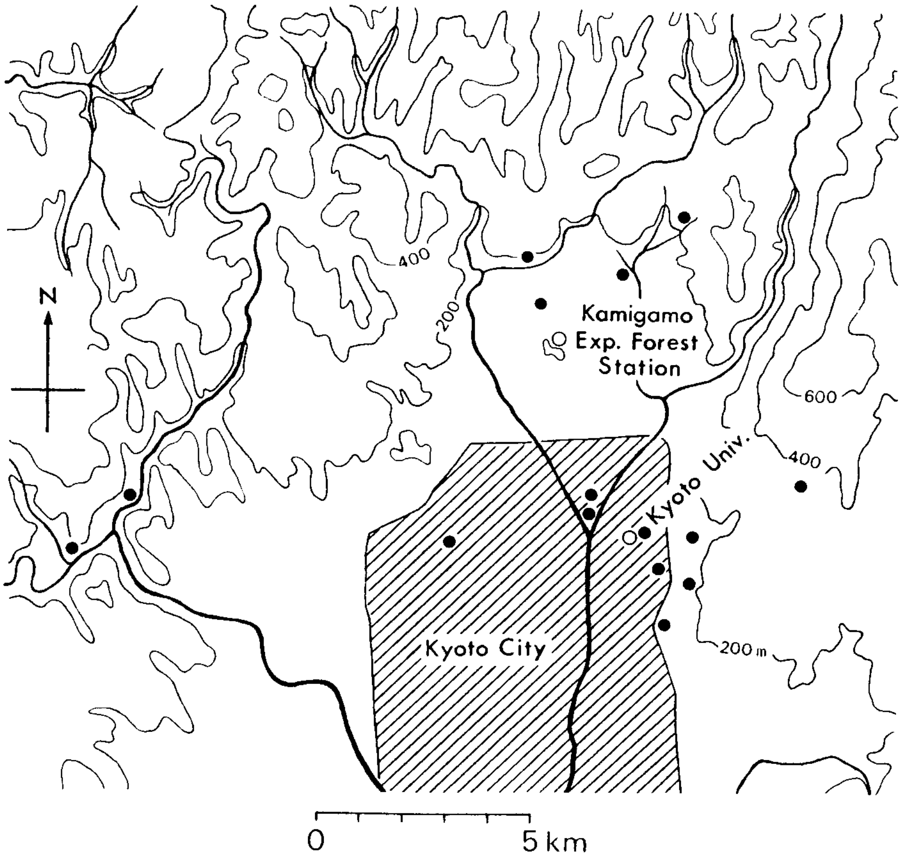


Fig. 1. Map of the northern part of Kyoto City. The open and solid circles denote two main study areas and sampling localities respectively.

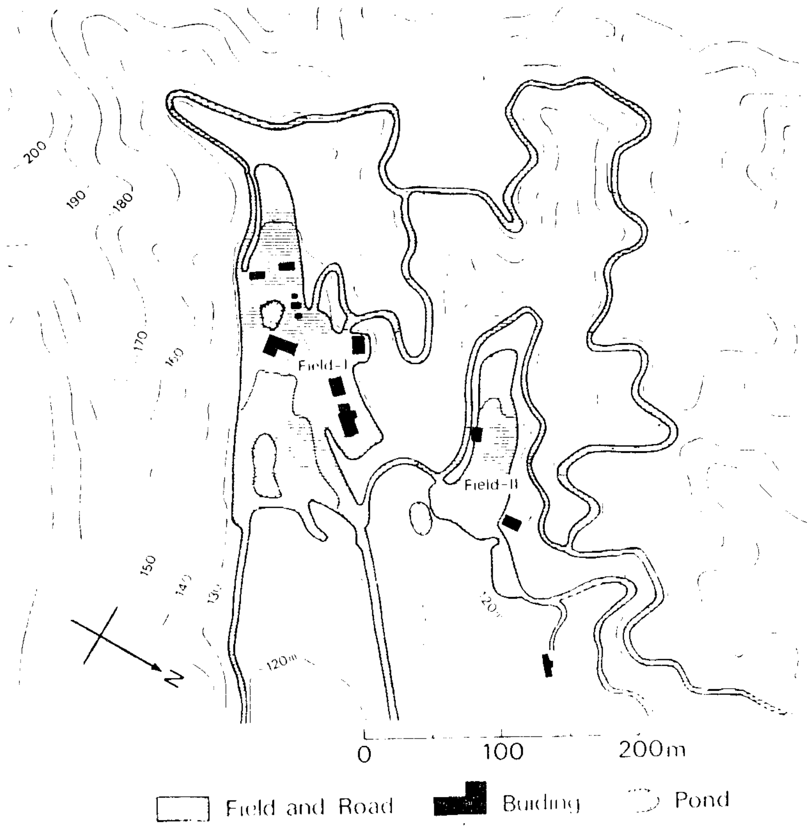


Fig. 2. Map of Kamigamo Station. The shaded area shows the bare ground.

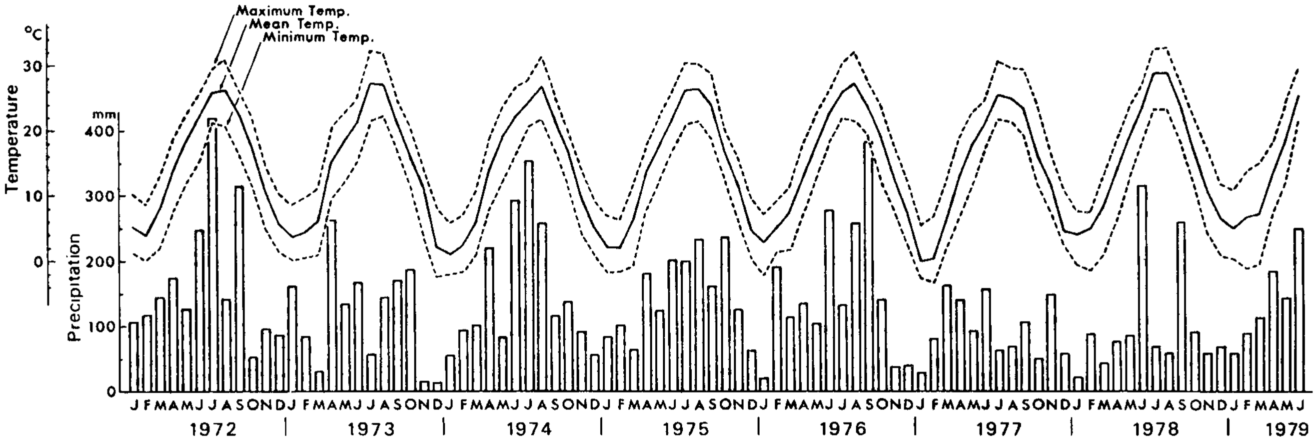


Fig. 3. Monthly precipitation and mean temperature at Kamigamo Station, 1972-1979.

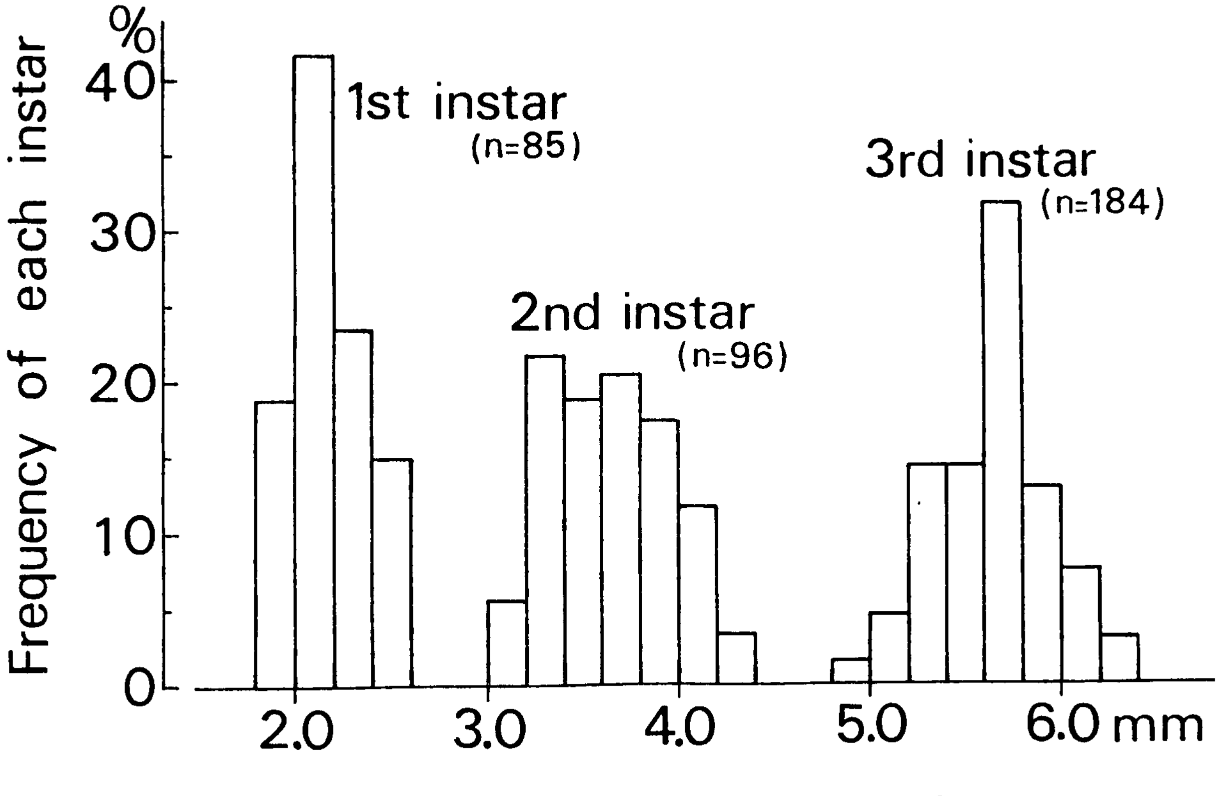


Fig. 4. The frequency distribution of diameter of burrow for each of three larval instars.

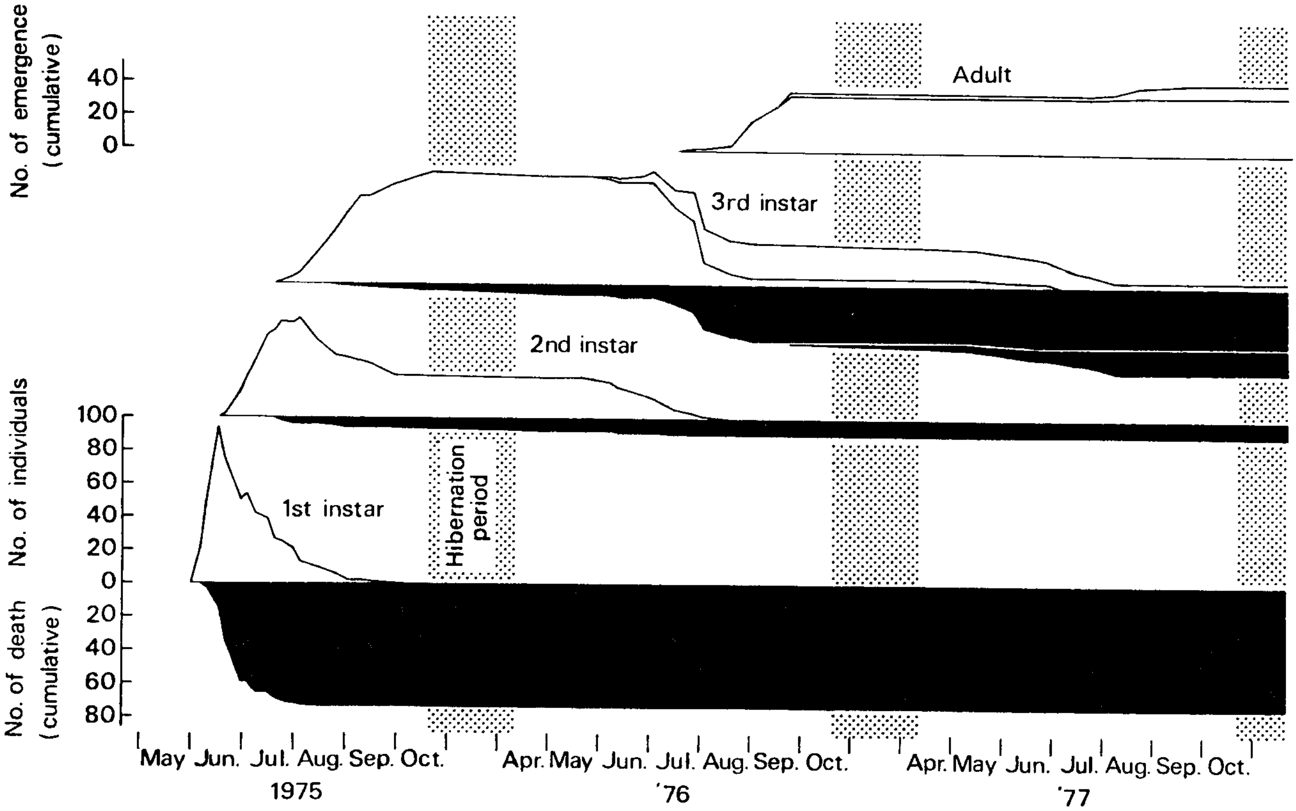


Fig. 5. The seasonal change of each stage in the early summer cohort of 1975 in St. A. The height of each instar shows the number of individuals at the time. The height of mortality and adult show the cumulative number. The dotted area means the period of hibernation. The individuals which hibernated as the 2nd instar are discriminated from the others after the 3rd instar.

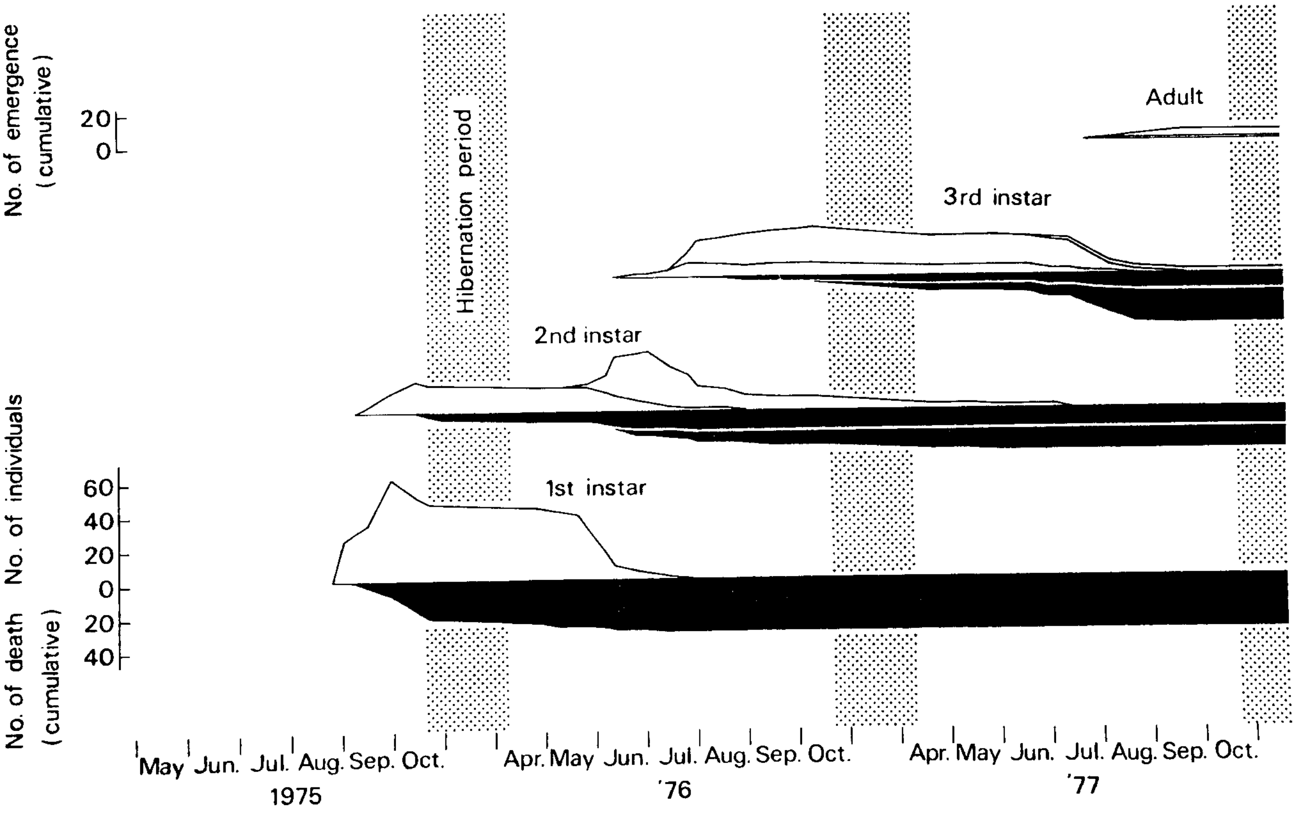


Fig. 6. The seasonal change of each stage in the autumn cohort of 1975 in St. A. The presentation is the same as Fig. 5.

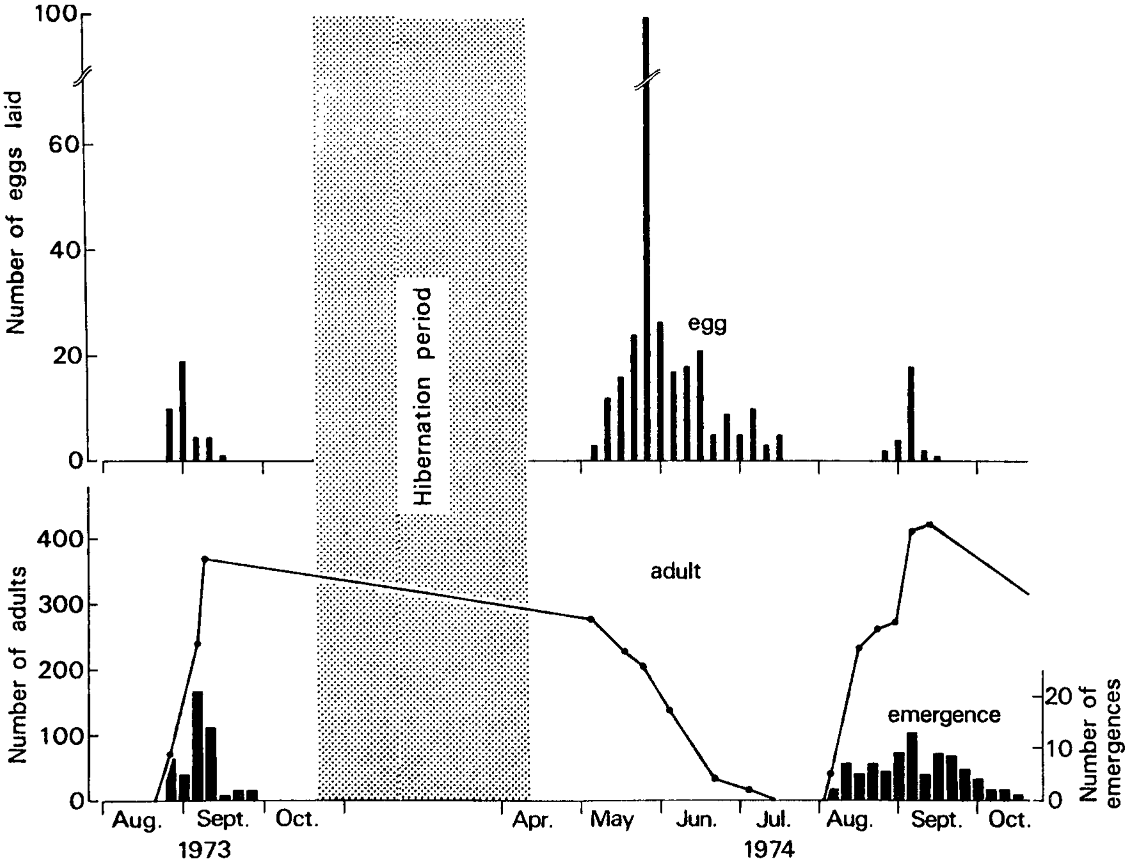


Fig. 7. The seasonal change of emergence of adults, eggs laid in St. A, and adult population size in Field-I from the autumn of 1973 to that of 1974.

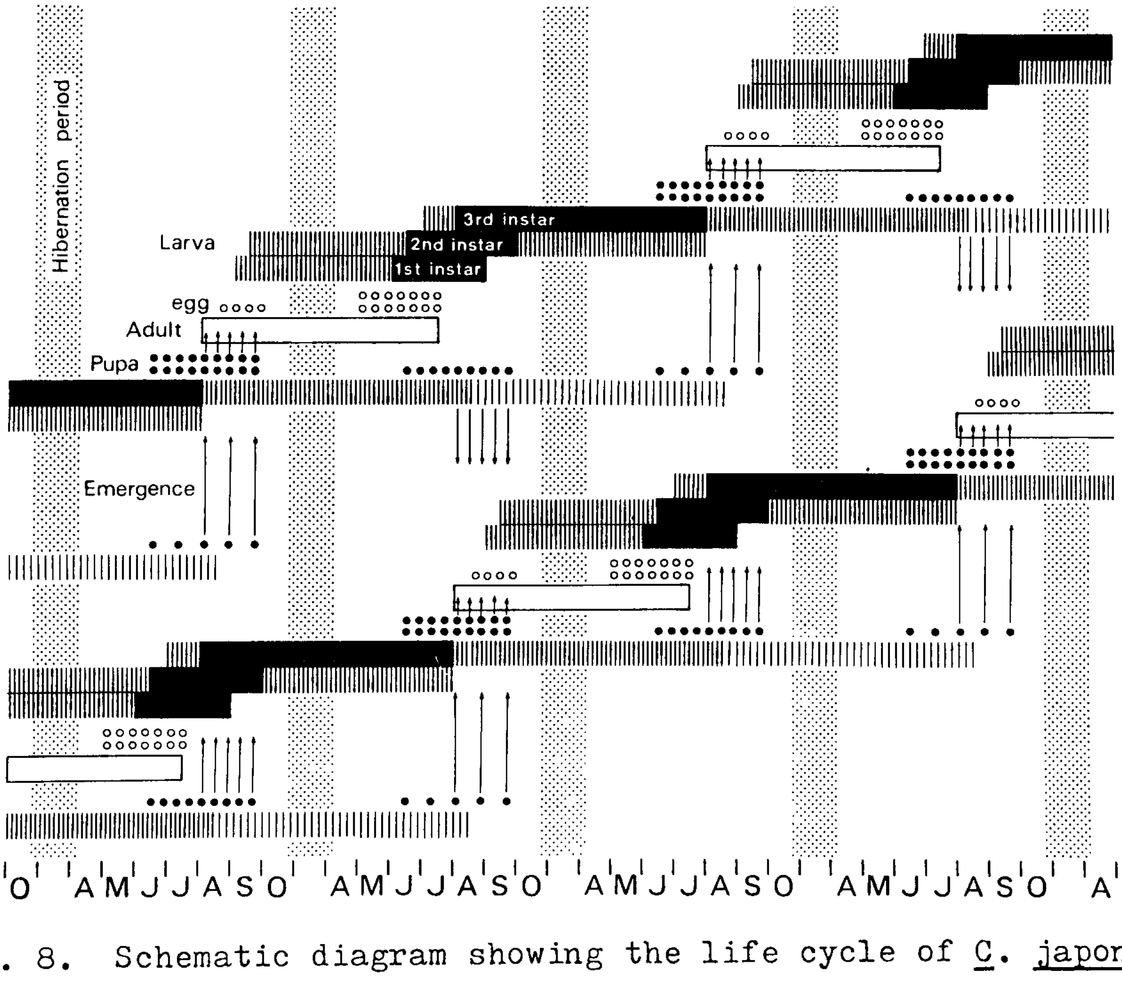


Fig. 8. Schematic diagram showing the life cycle of *C. japonica*. The arrows mean that the adults derived from the larvae of various careers join in one adult population.

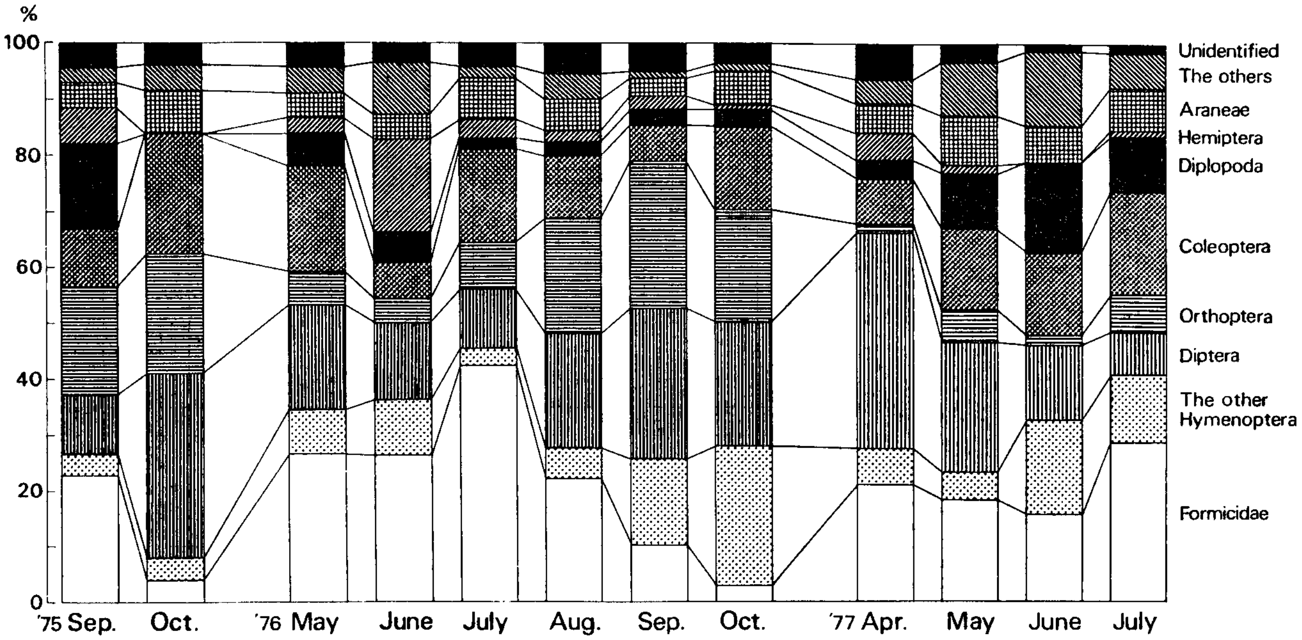


Fig. 9. The seasonal change of food composition of the 3rd instar larvae in all the stations for two years.

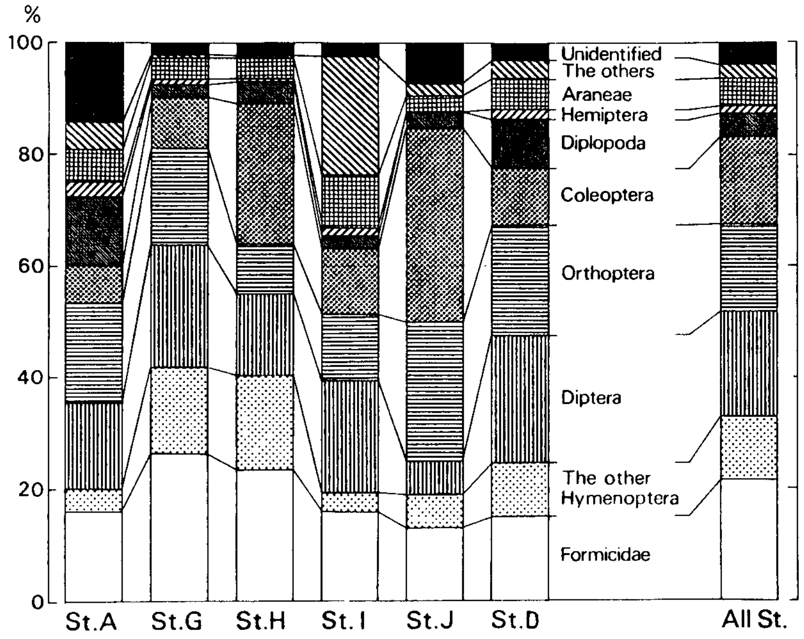


Fig. 10. The food composition of the 3rd instar larvae in each station from September 1975 to August 1976.

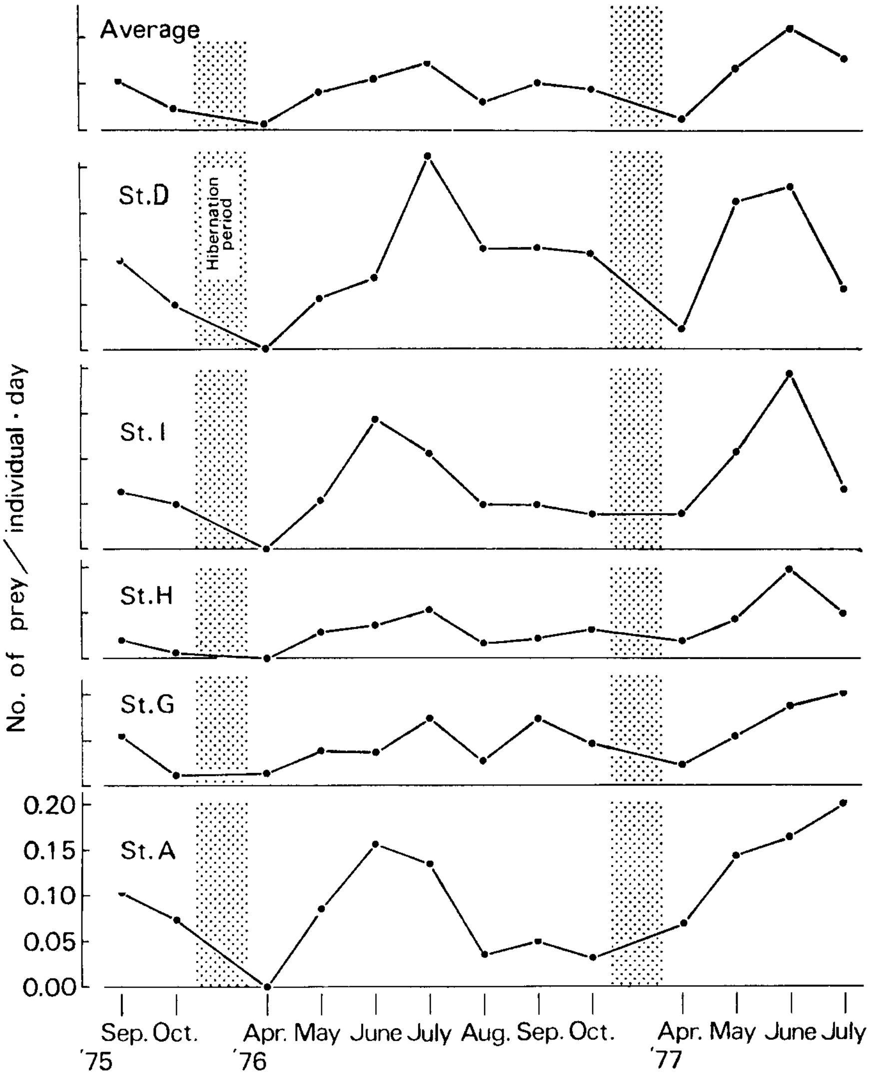


Fig. 11. The seasonal change of amount of food taken by the 3rd instar larva in each station and on average. The amount of food is indicated as the number of preys taken by an individual in a day.

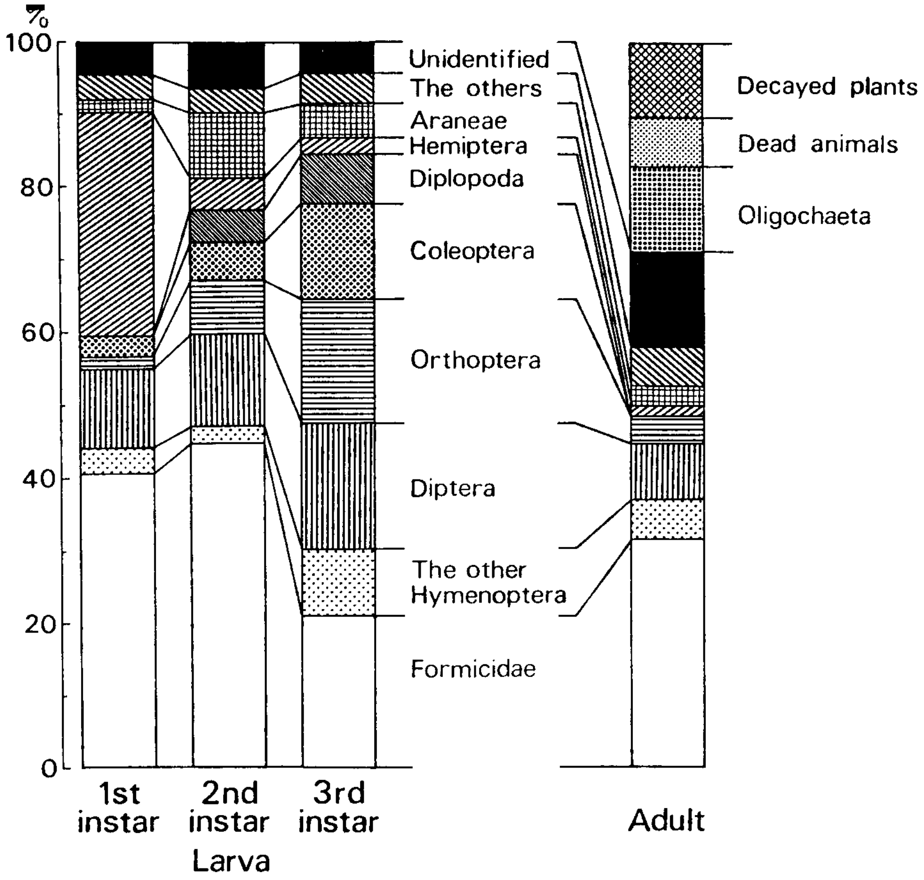


Fig. 12. The food composition in each stage from May to September 1976 (for larvae) and from April 1973 to October 1978 (for adults).

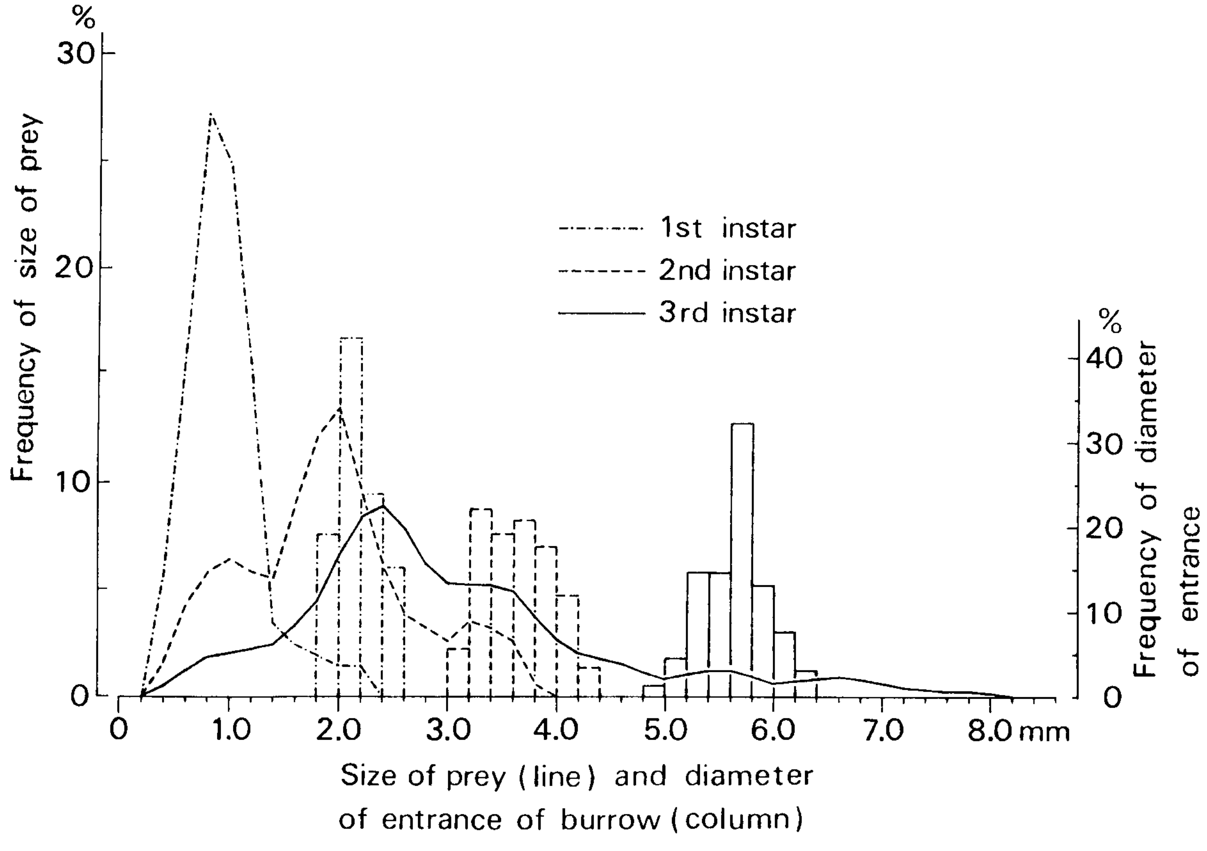


Fig. 13. The frequency distribution of size of preys (line) and diameter of burrow (column) for each of three larval instars. The former is based on the materials taken in all stations and period, and shown by moving average of 3 points. The latter derives from Fig. 4.

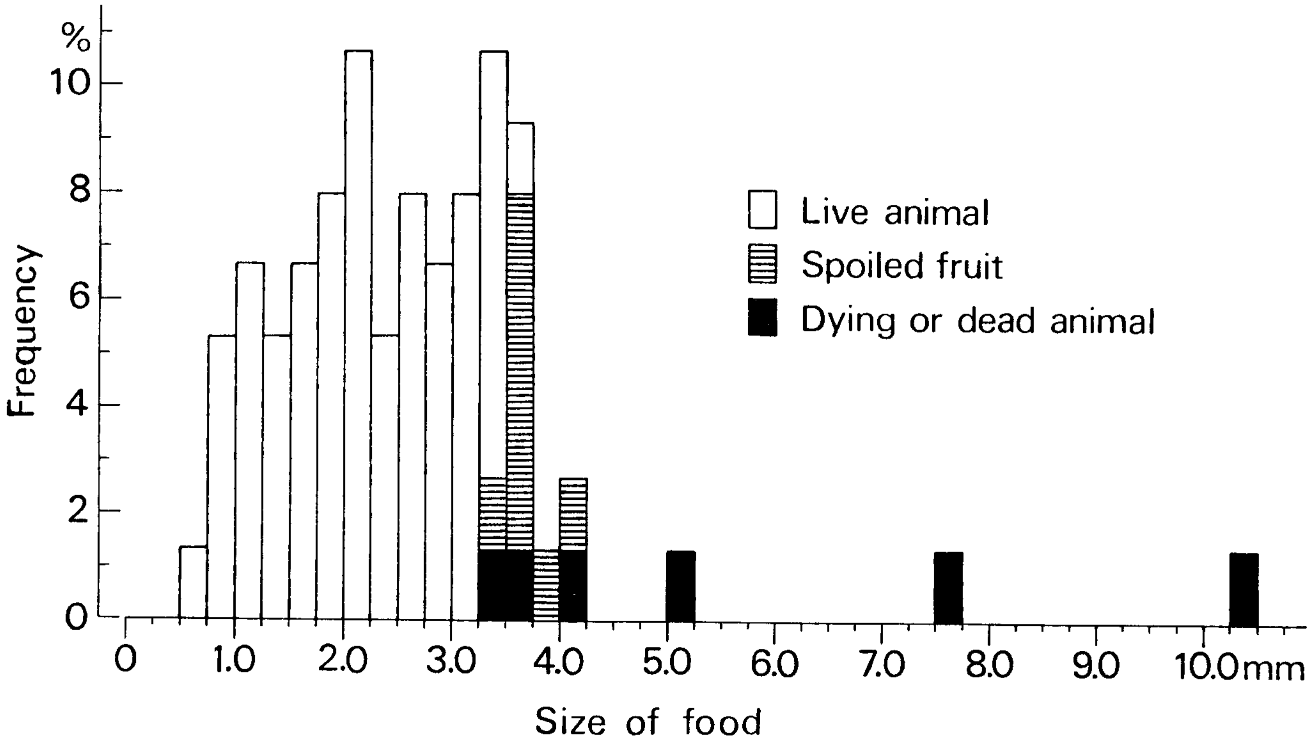


Fig. 14. The frequence distribution of size of food for the adult. the size is represented with the widest part of each material which was usurped from adult.

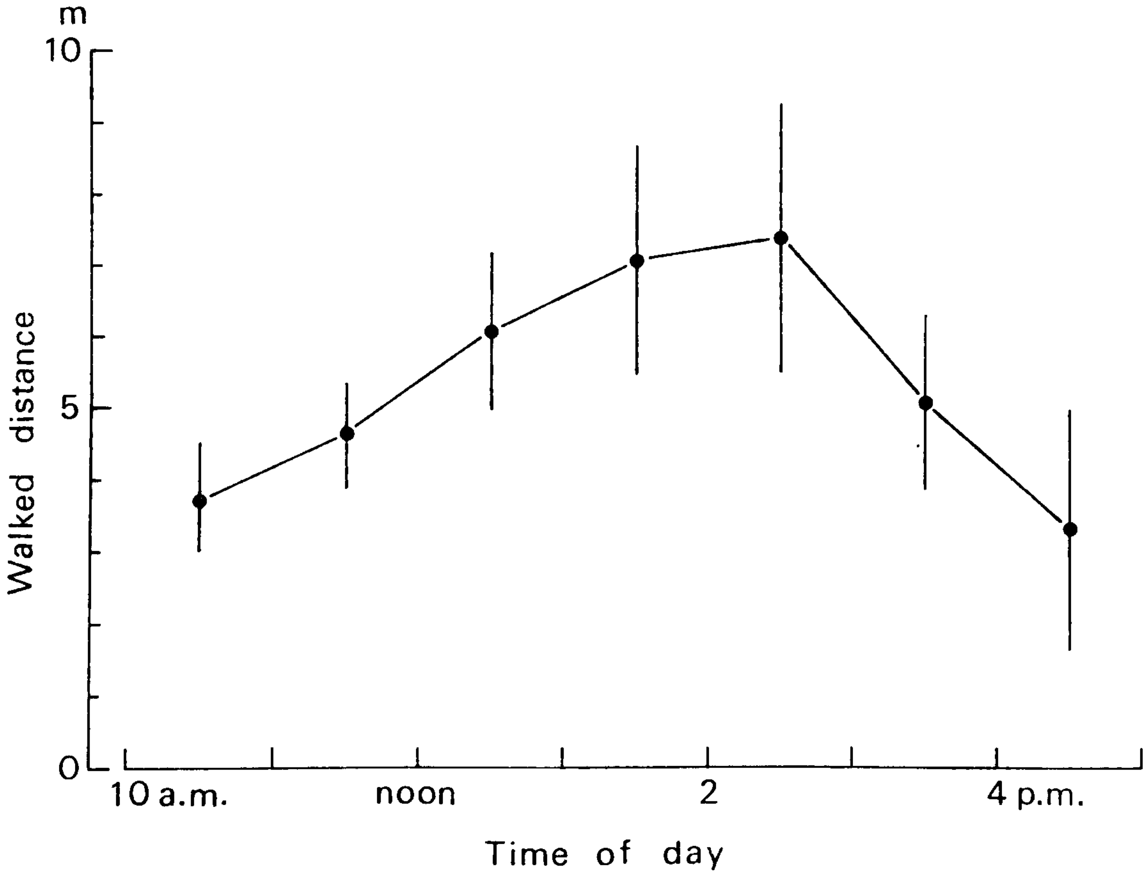


Fig. 15. Diurnal change of adult activity. The walked distance is average length of locus (m) in 5 minutes. The vertical bar shows 95 % fiducial limit of mean.

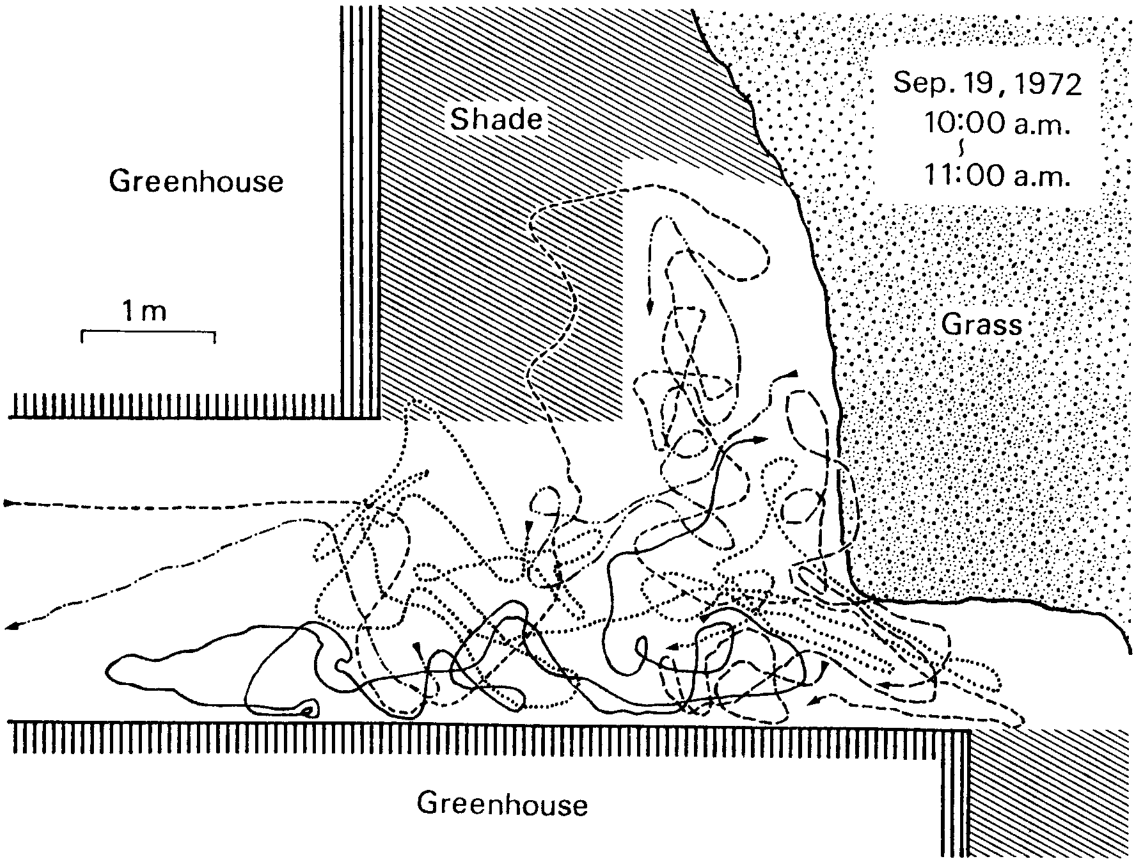


Fig. 16. An example of the trace of walking adults for an hour. In this case 6 individuals appeared.

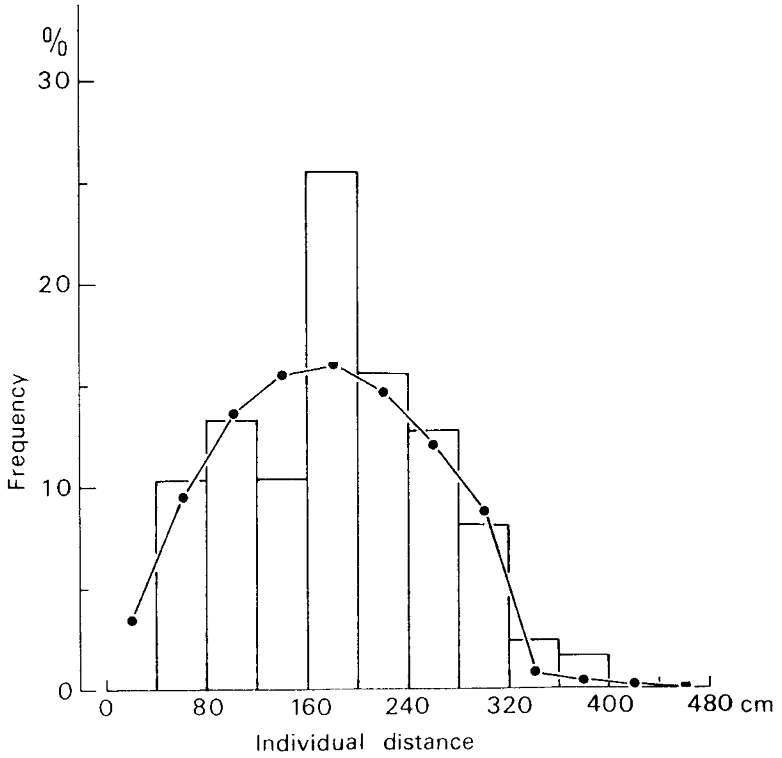


Fig. 17. The frequency distribution of the distance between two adults. The column and line show the observed value and theoretical one which is expected when the individuals disperse at random respectively.

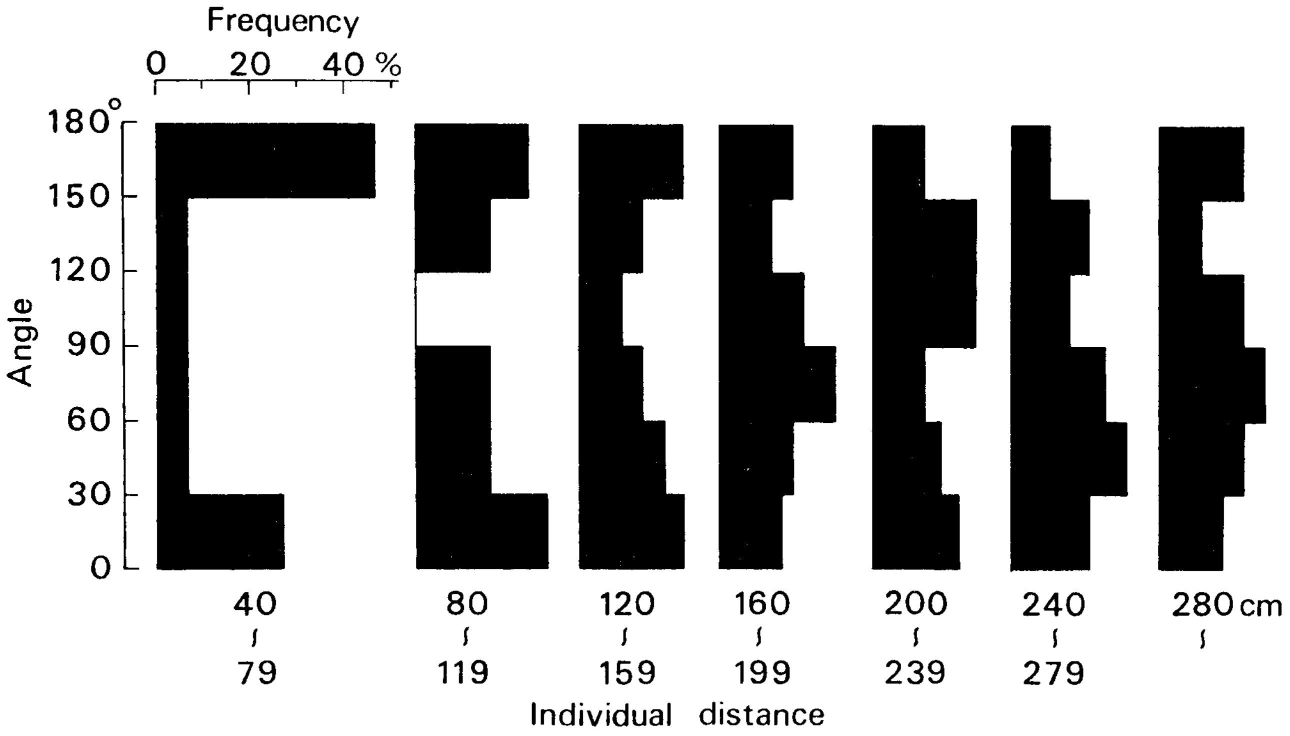


Fig. 18. Frequency distribution of angles between directions of two adults in each grade of individual distance.

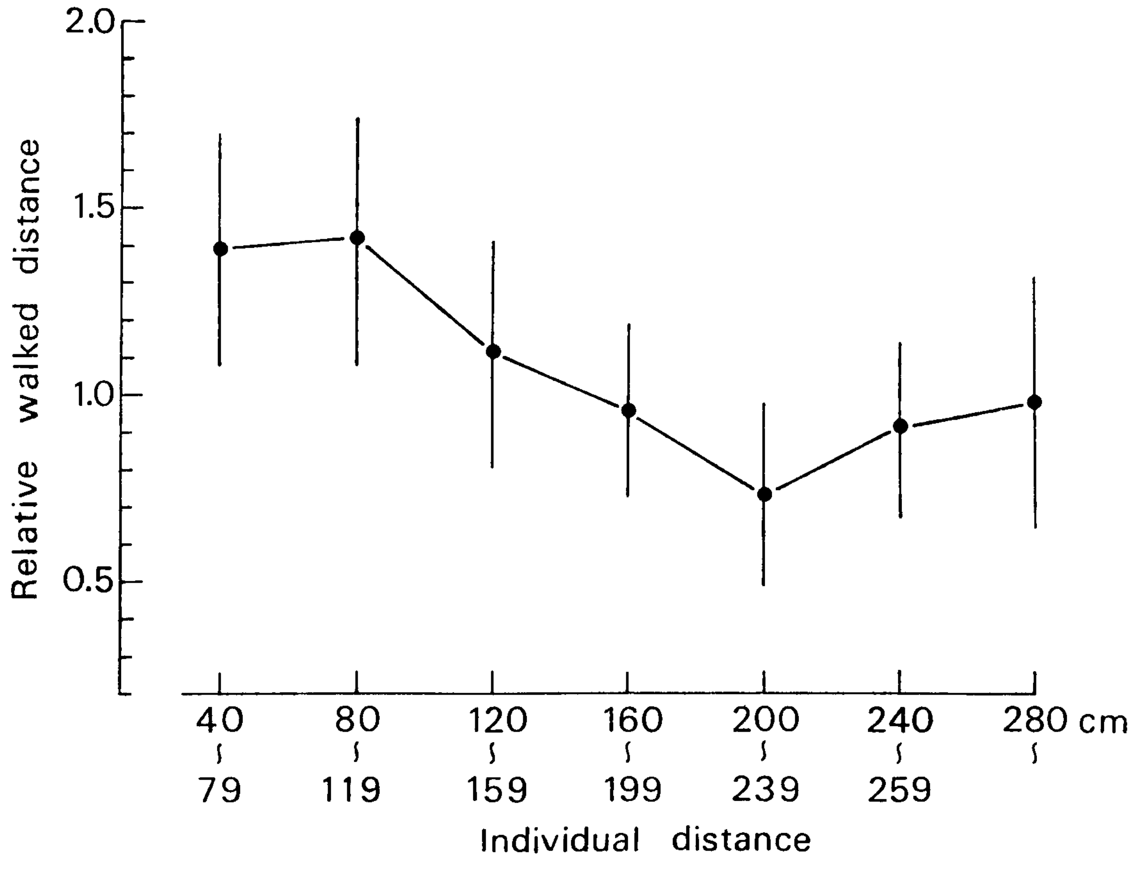


Fig. 19. The relation between the individual distance of adult and the activity after then. The latter is shown as the relative value of walked distance at the time of day. The vertical bar shows 95 % fiducial limit of mean.

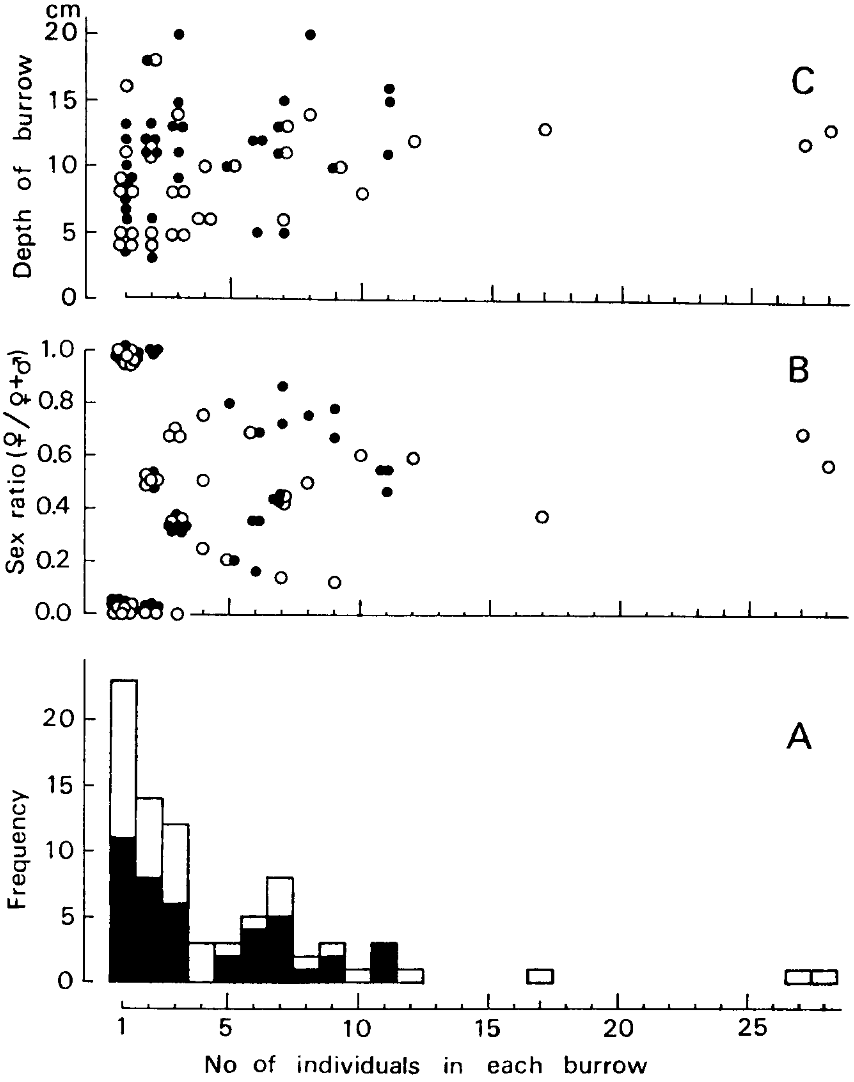


Fig. 20. The group hibernation of adult. A; the number of individuals in each burrow. B; the relation between the number of adults and sex ration in one burrow. C; the relation between the number of adults and the depth of burrow. The solid bar and circle show the instance that the entrance of burrow is clearly closed. The open bar and circle show burrow whose entrance is open.

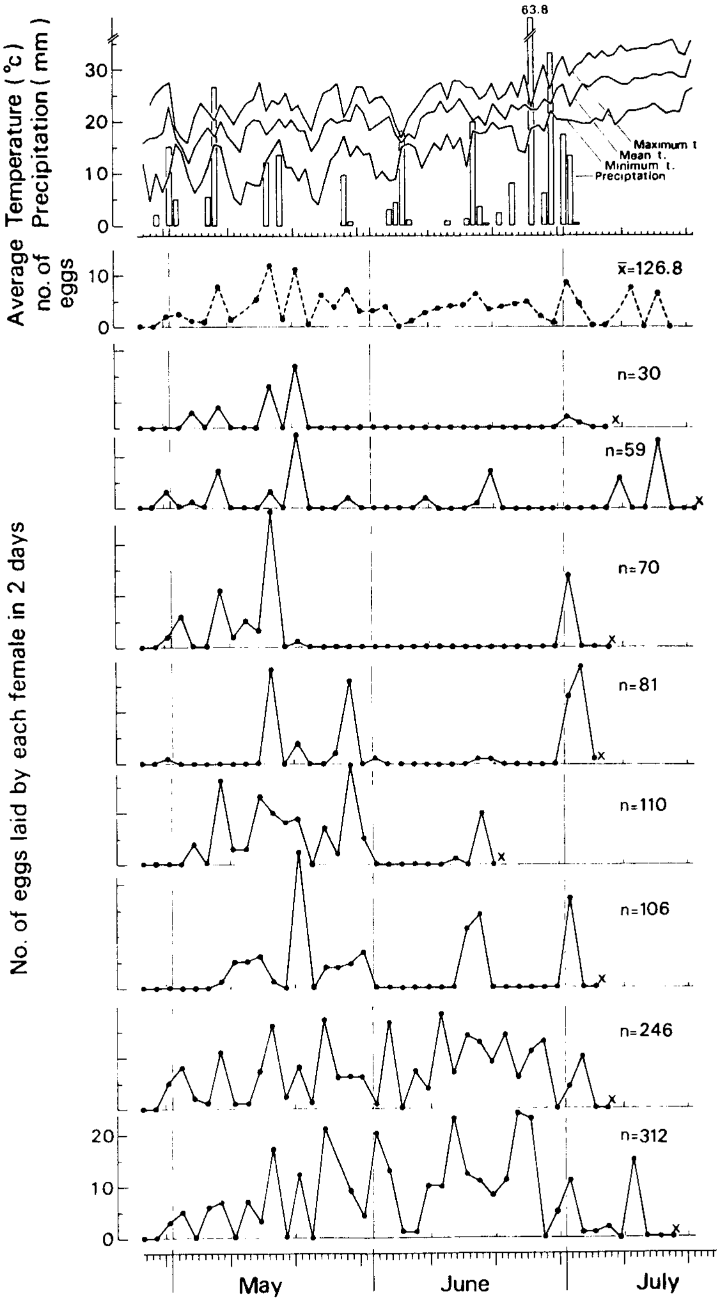


Fig. 21. The oviposition by females reared outdoors in early summer, 1973. The number of eggs laid by each female every 2 days and its average were shown with the daily meteorological data. The numerals denote the total number of eggs laid by each female, and the mark X shows the day of her death.

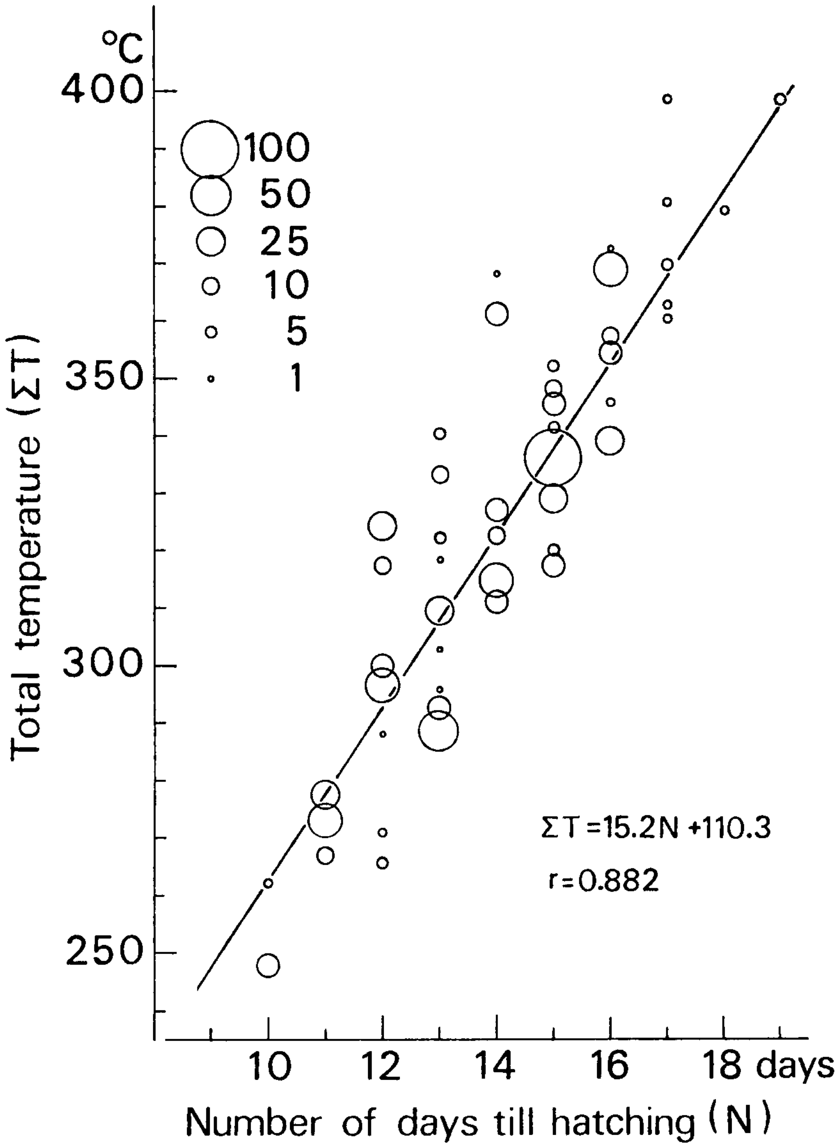


Fig. 22. The relation between the duration of each egg and the total temperature summed up during the period. The area of each circle is proportional to the number of eggs concerned.

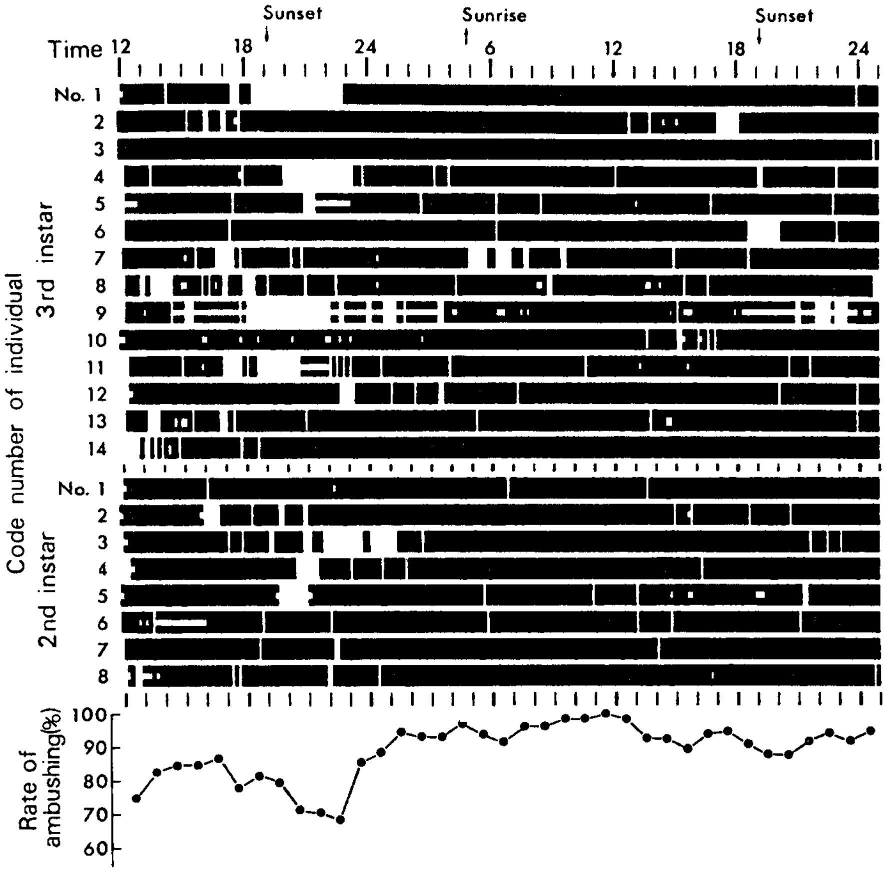


Fig. 23. The diel change of the larval ambushing behavior. The solid bar at each moment shows that the individual is ambushing, and open part shows that the individual is not seen at the entrance. The broken bar shows that the individual is repariring the entrance or merely seen there but not in ambushing posture.

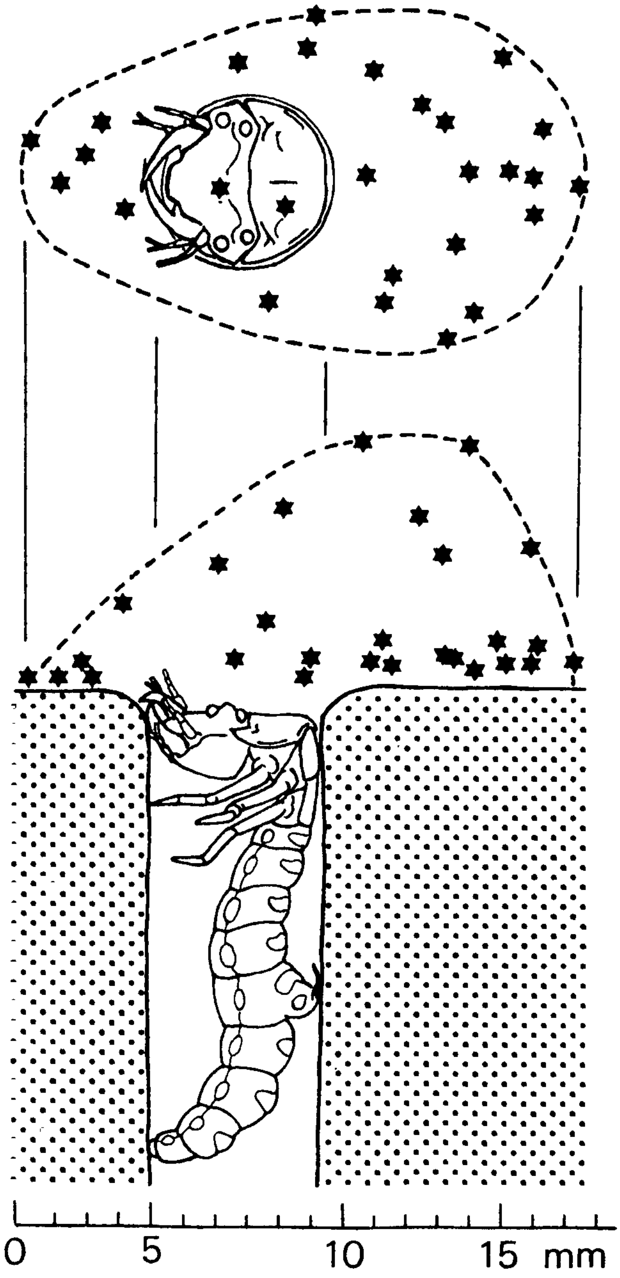


Fig. 24. The range of jumping-at and ambushing posture of the 3rd instar larva. The star shows the actual point of catching prey with the mandibles, and the broken line is the range expected.

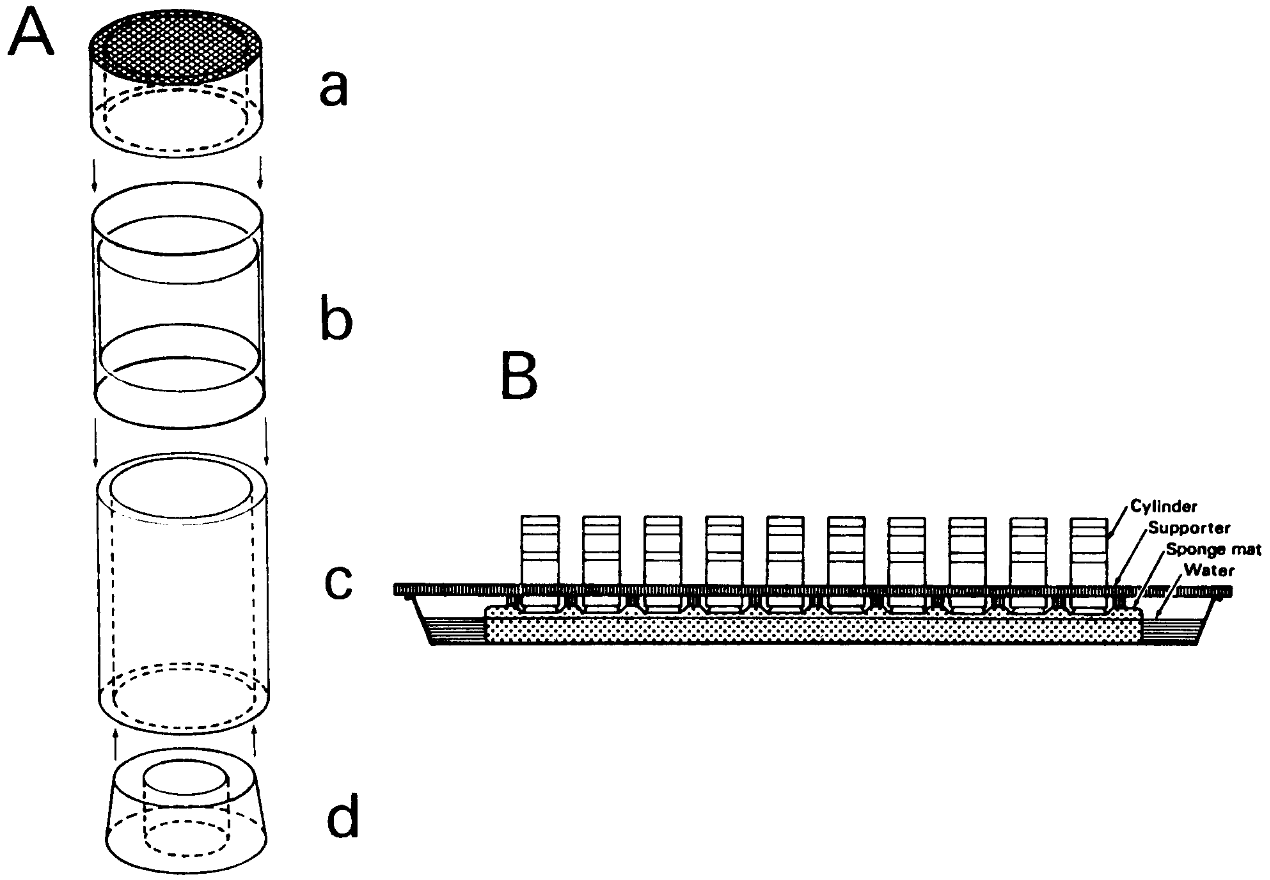


Fig. 25. The apparatus and equipment used in the rearing of larva.

A) The rearing cylinder

a) The cover; a short opaque cylinder made of vinyl chloride, and tetron net is put up on the roof for air flow. This part has been also used as the emergence trap in the field survey.

b) The lamp chimney; a transparent cylinder of 5 cm long made of vinyl chloride for lighting and observation form outside. The emerged adult appears here.

c) The main part of apparatus; a opaque cylinder of 6 cm long made of vinyl chloride with 4 cm inside diameter. It contains the fine soil sterilized by heat. Its lenght is set up as a little shorter than the usual depth of burrow of the 2nd instar in order to take the 2nd, 3rd instar larva, and pupa with little destruction of burrow by removing the stopper.

d) The stopper; made of cork. The central part is hollowed out and put the plaster into for water absorption.

B) The rearing equipment

The sponge mat is put in the large vessel filled with water. A number of the cylinders are fixed on the mat. The water level is controled according to the wetness of the soil in the cylinders. This equipment was set up in a hallyway by a window which was left open during the period of larval activities.

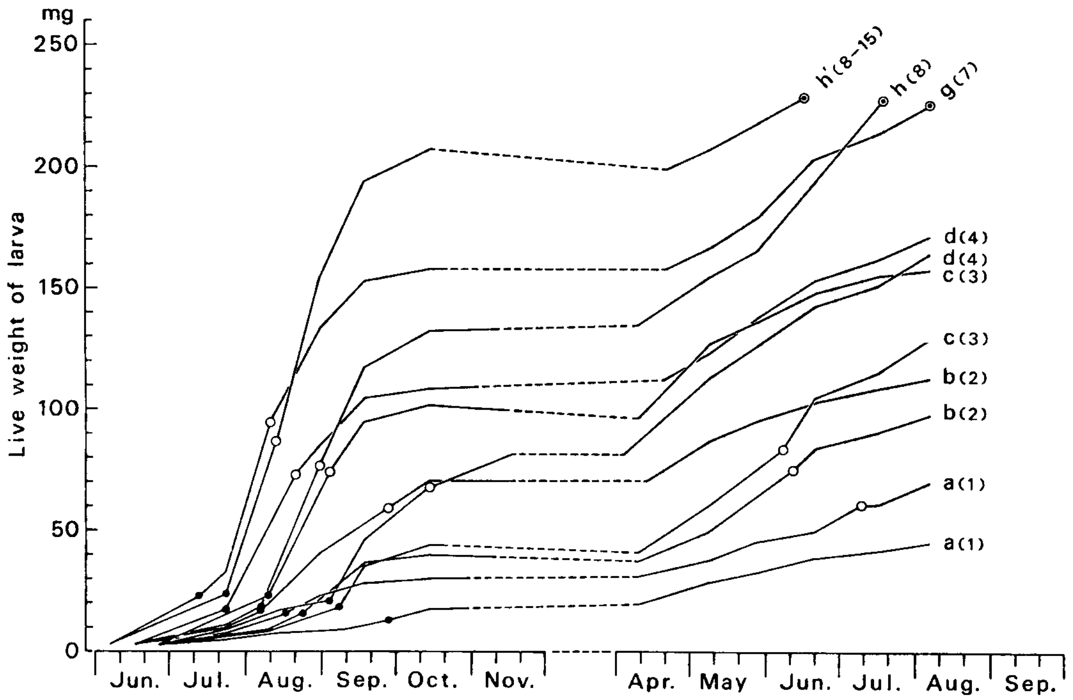


Fig. 26. The growth of larvae of Series A in Summer-I rearing. Each line shows the change of live weight of each individual and the broken line shows the period when the burrow has been closed for hibernation. The solid and open circle show the live weight at the time when the individual reopens its burrow after the molt of the 2nd and 3rd instar respectively. The double circle shows the live weight at the time of pupation. The small letter and the numeral in parentheses mean the division and the number of preys supplied twice in a week respectively.

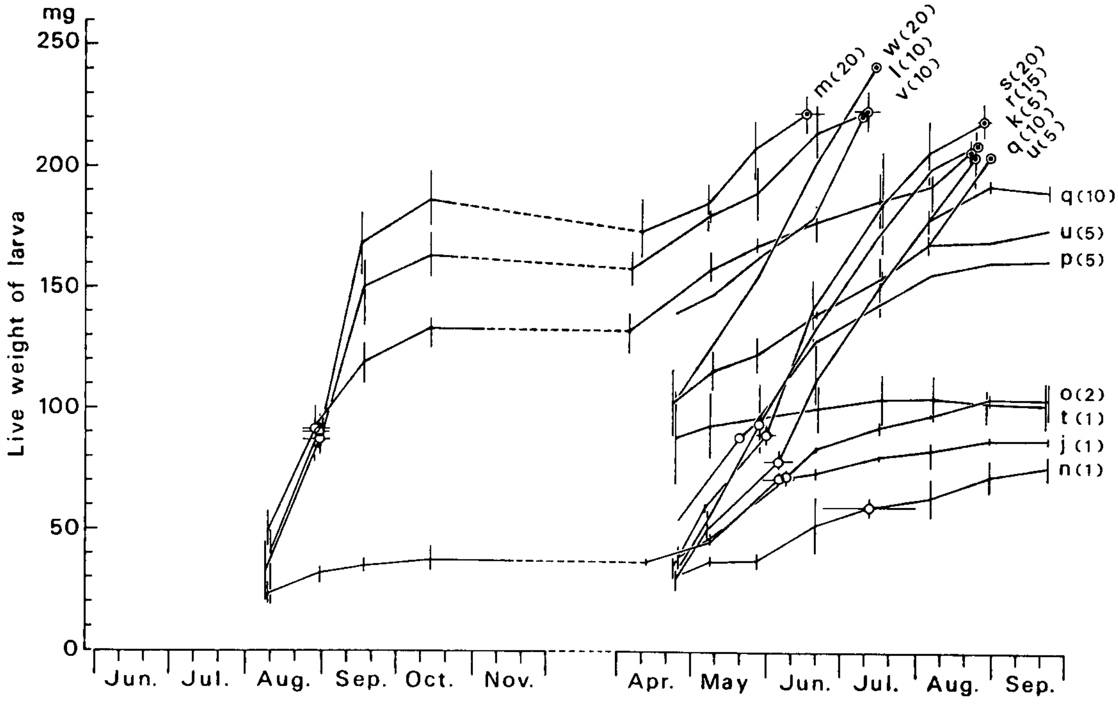


Fig. 27. The growth of larvae of Series B and C in Summer-I rearing. Each line shows the change of the mean live weight of each division, and the vertical and horizontal bar show the range of live weight and the time concerned respectively. The other designations are the same as in Fig. 26. For Division q and u, in which some individuals pupated but the others entered hibernation again as the 3rd instar, this two groups are averaged separately.

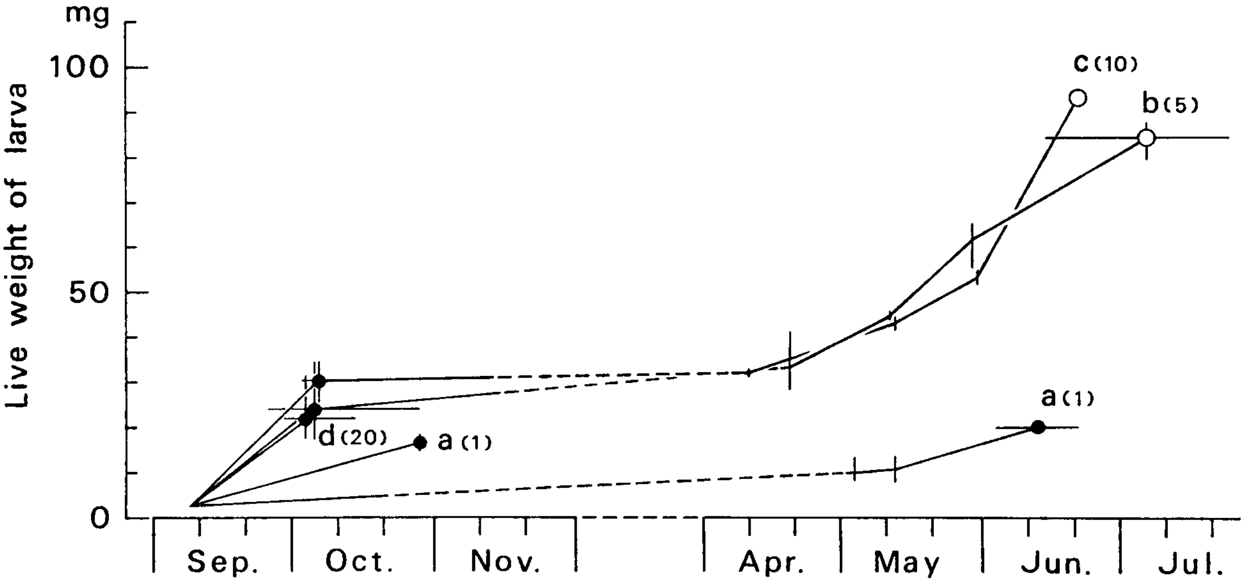


Fig. 28. The growth of larvae in Summer-II rearing. The three numerals in parentheses denote the number of preys supplied twice in a week during the 1st, 2nd and 3rd instar respectively. The other designations are the same in Figs. 27 and 28.

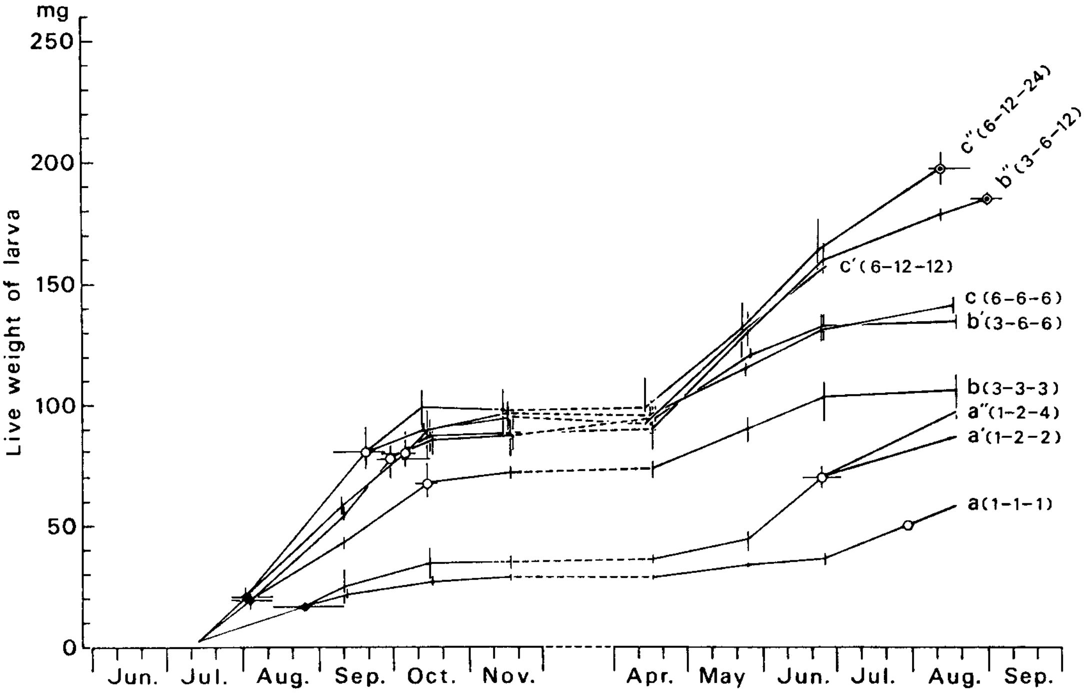


Fig. 29. The growth of larvae in Autumn rearing. This rearing was put an end in August of the second year. For Division a, in which some individuals grew into the 2nd instar during the autumn but the others entered hibernation as the 1st instar, this two groups are averaged separately. The formmer group of Division a and all of Division d died out before or during hibernation. The other designation are the same as in Figs. 26 and 27.

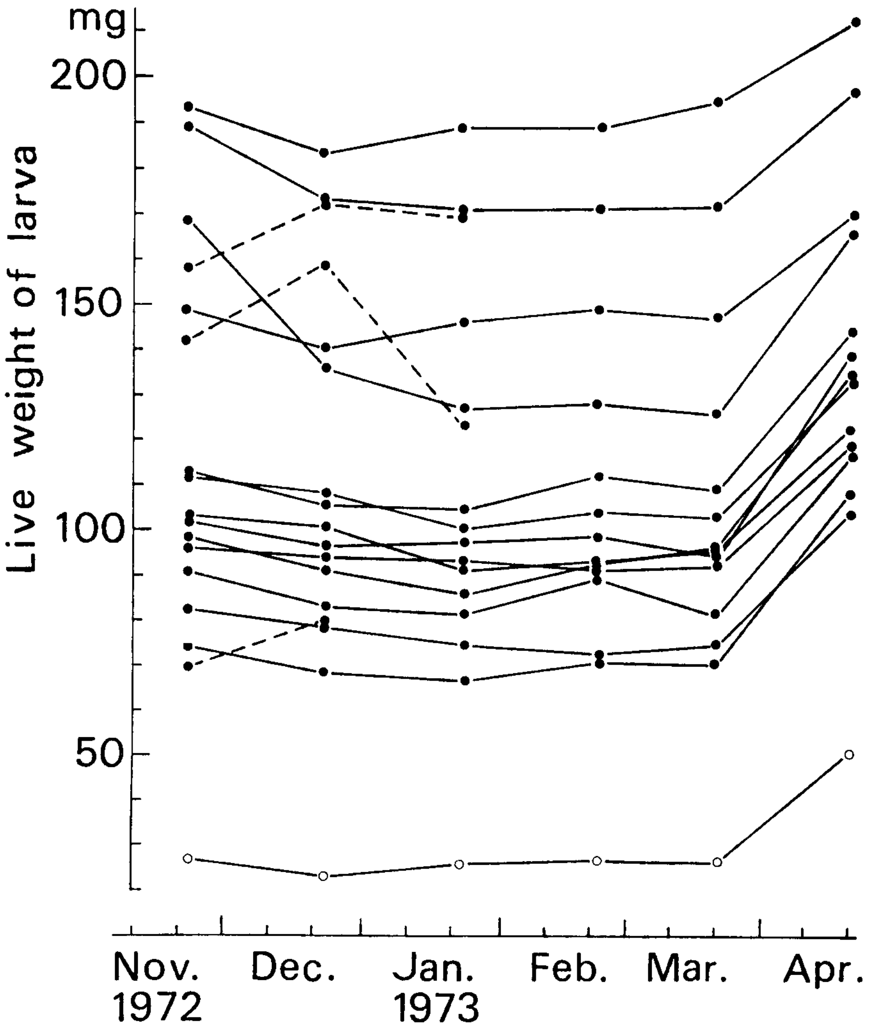


Fig. 30. The change of live weight of larva during hibernation. The solid and broken line denote the survivor and the dead during winter respectively. All the survivors opened their burrows and began to take preys from March 20th to April 19th One lightest individual (open circle) is the 2nd instar and the others are all the 3rd instar.

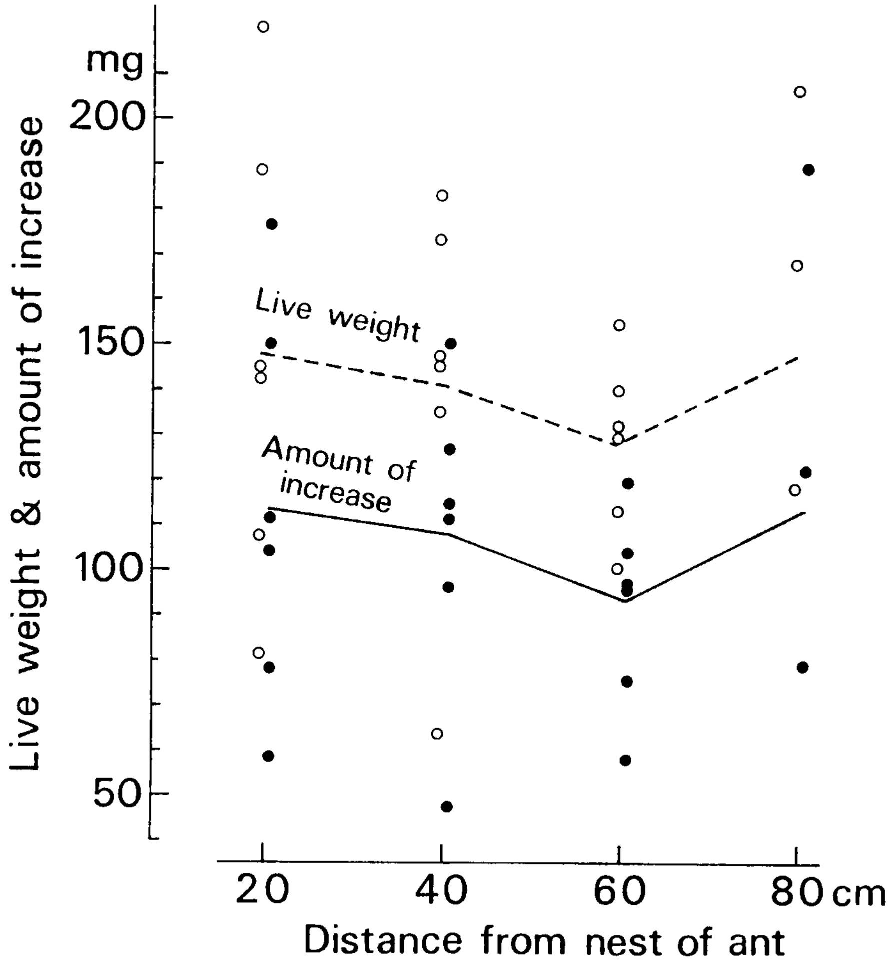


Fig. 31. The relation between the distance from the nest of ant to the burrow of the 3rd instar larva and the live weight after a month (open circle) or the amount of increase of live weight during the period (solid circle). The broken and solid line denote the change of mean live weight and amount of increase respectively.

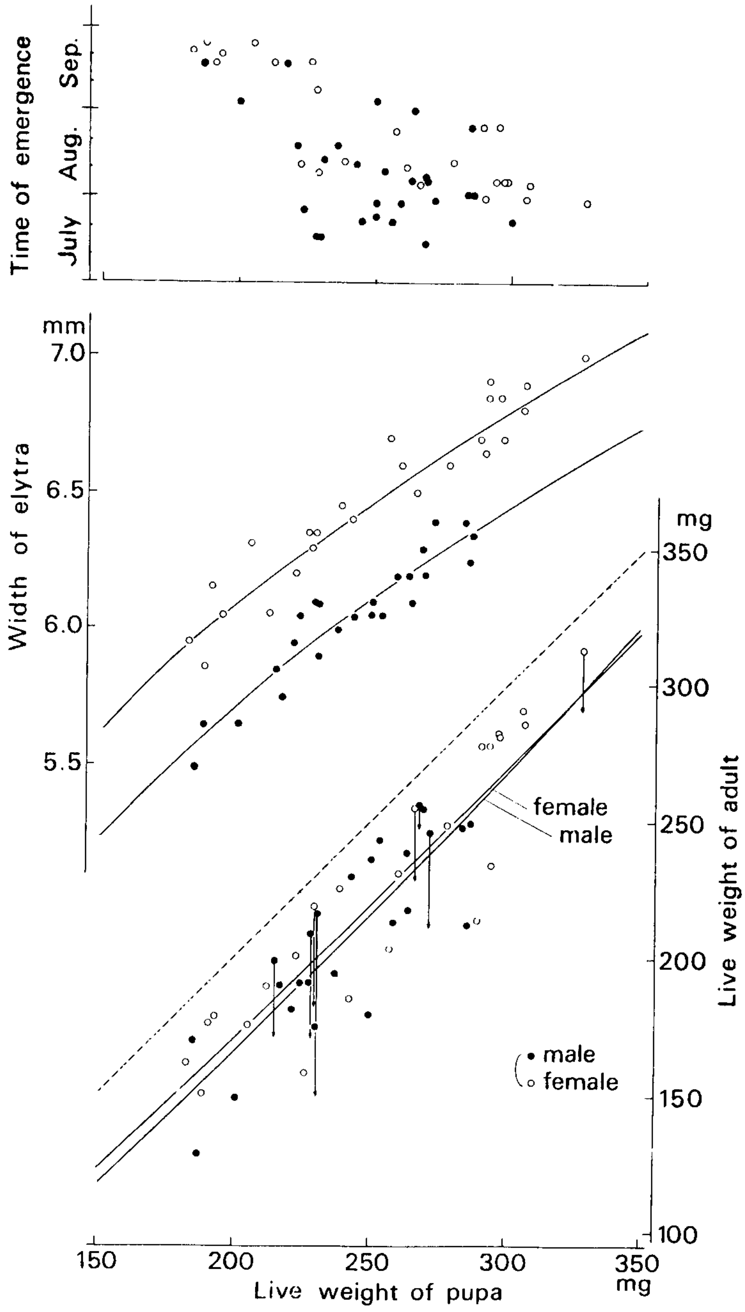


Fig. 32. The relation between the live weight of pupa and the live weight of emerged adult, its size, and the time of emergence. The data derive from the laboratory and outdoor rearings. The broken line shows the level of the same weight between pupa and adult, and the vertical arrow means the amount of decrease in adult weight from the time just after emergence to appearance above ground.

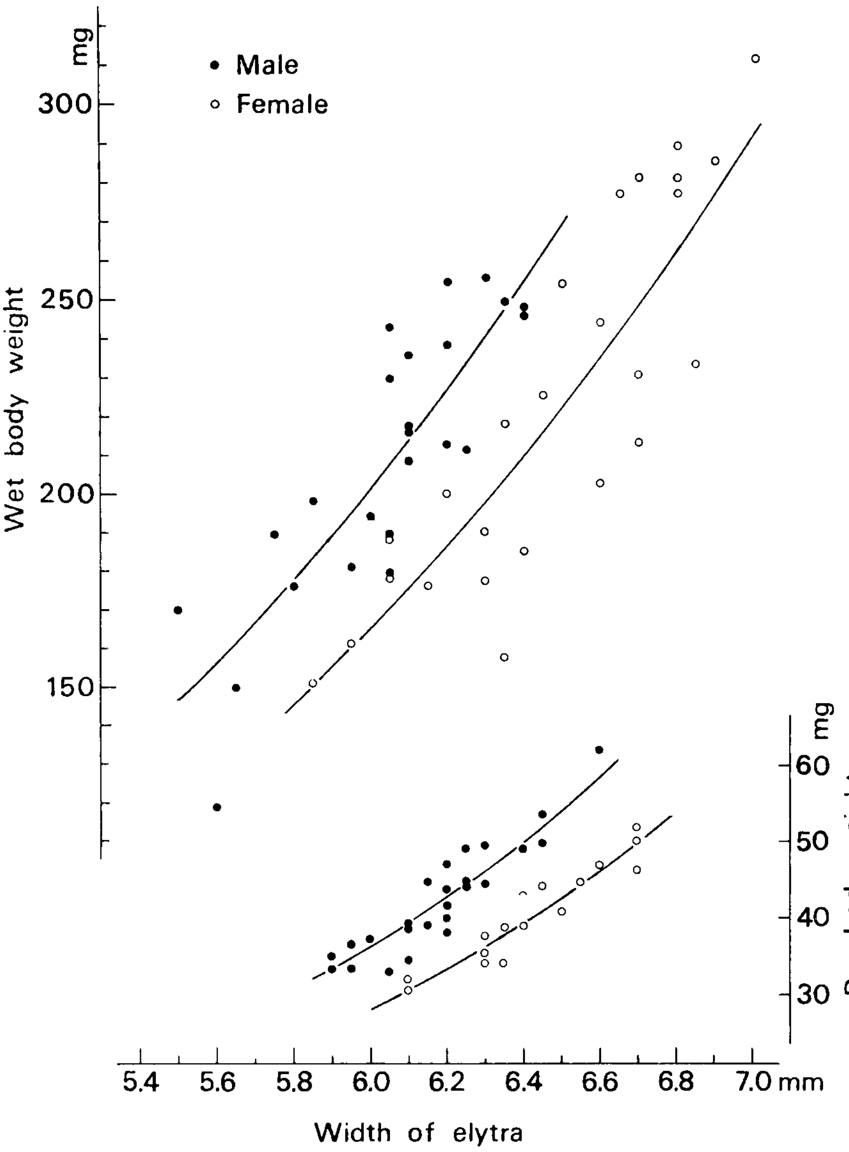


Fig. 33. The relation between the width of elytra and the dry and wet weight of emerged adult. Each regression line was culculated by the method of least squares in logarithm.

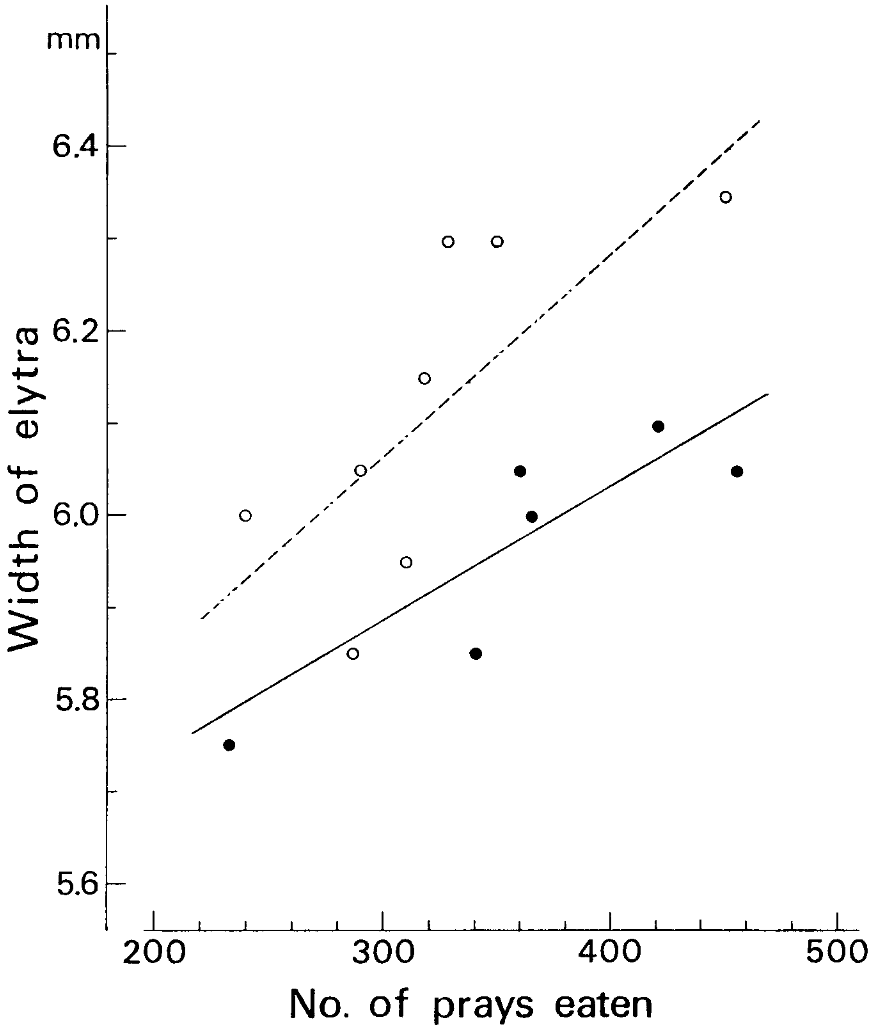


Fig. 34. The relation between the number of preys eaten by a larva during the 3rd instar and the width of elytra of the emerged adult. The open and solid circle denote female and male respectively.

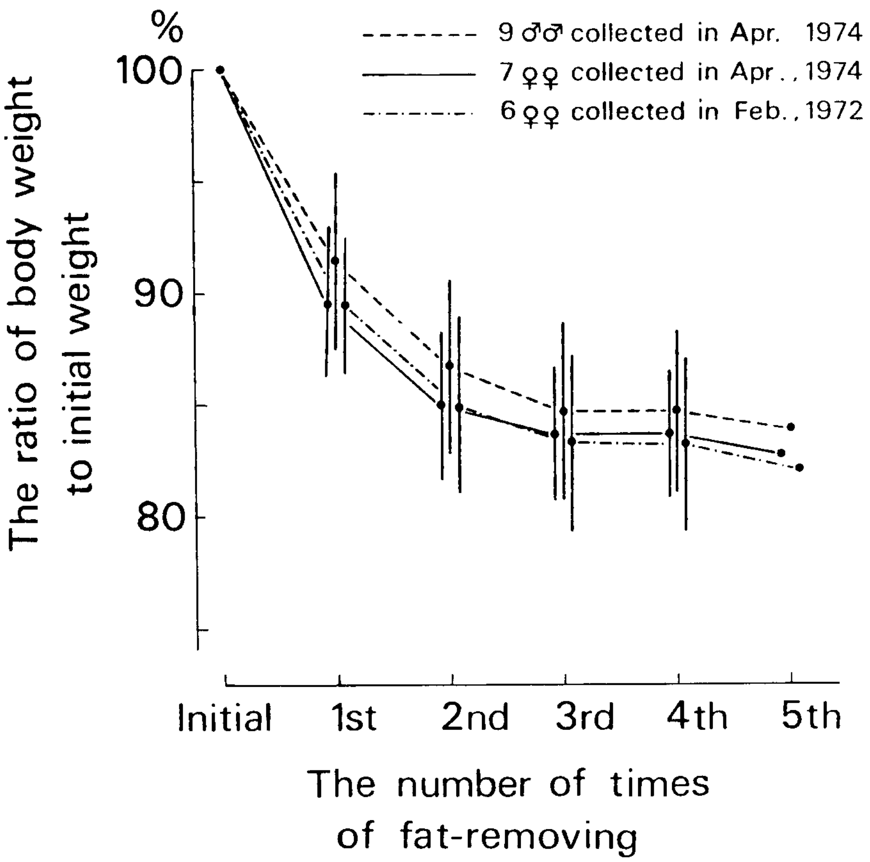


Fig. 35. The decrease of the dry weight in the course of five times of fat-removing for three sets of samples. From the first to fourth, the fat was removed by soaking in 30 ml of ethyl ether in every time, and in the fifth the Soxhlet's extractor was used in a lump for each set of samples. The vertical bar shows the 95 % fiducial limit of mean.

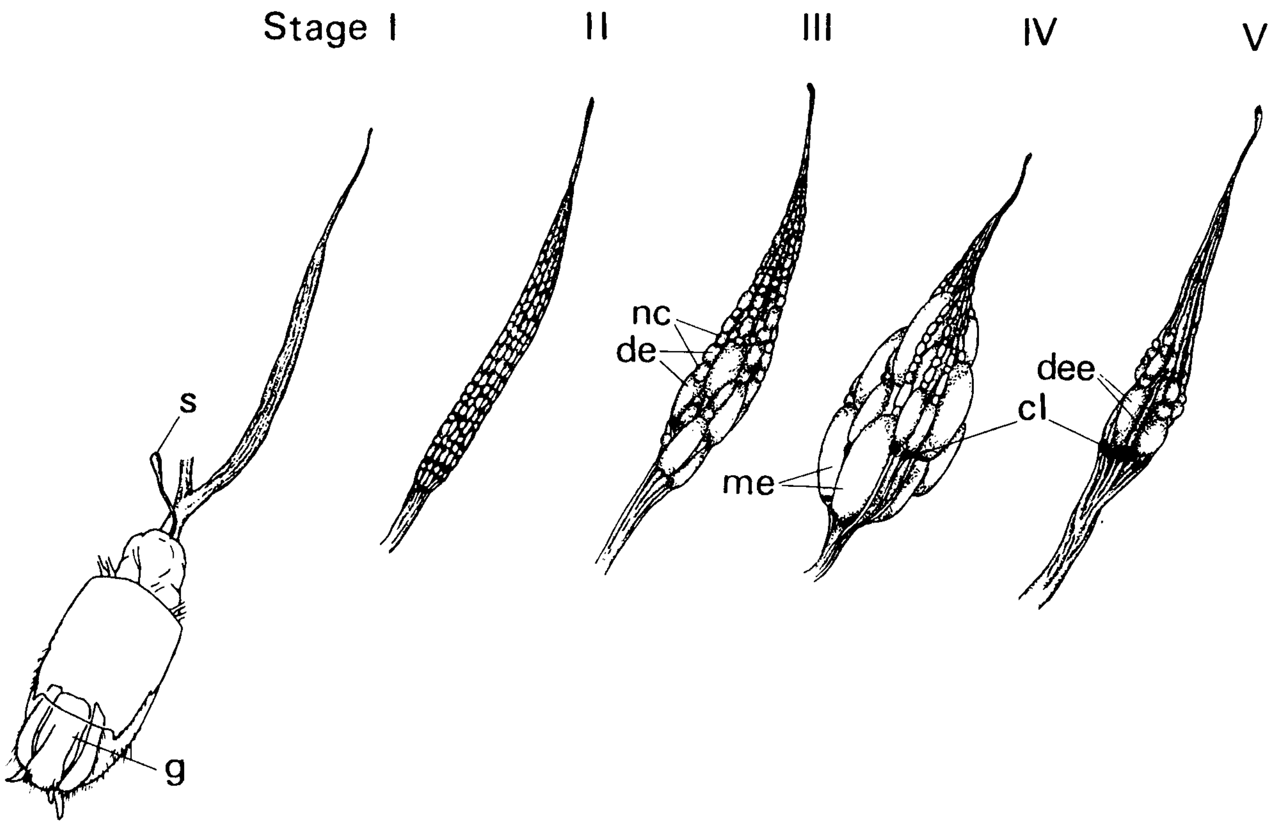


Fig. 36. Five stages of development in the ovary. The female genital organ and the spermatheca are also shown. Stage I shows the teneral state; Stage II, immature; Stage III, maturing; Stage IV, reproductive; Stage V, spent. cl, corpus luteum; de, developing egg cell; dee, degenerating egg; g, genital organ; me, mature egg; nc, nutritive cells; s, spermatheca.

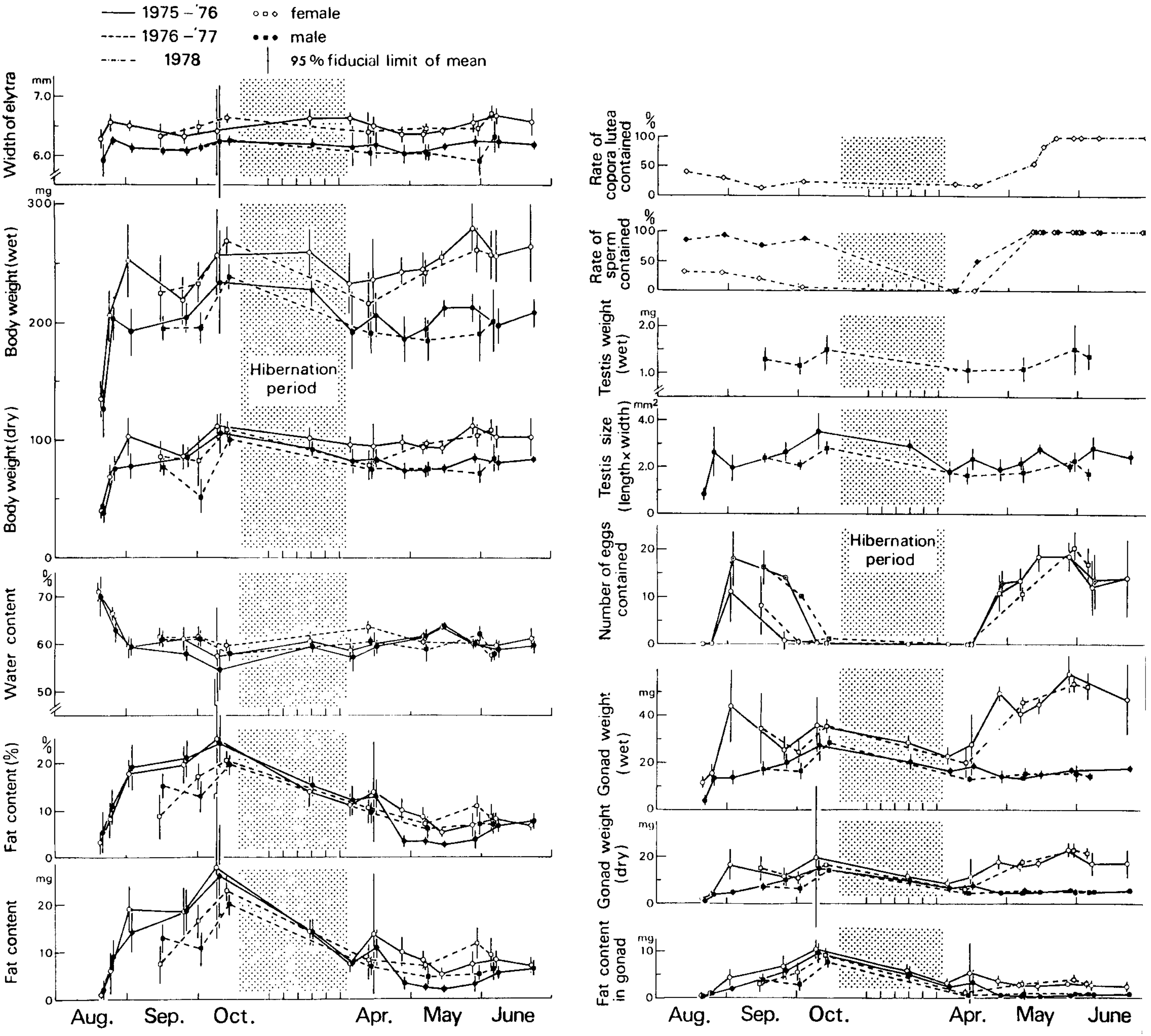


Fig. 37. The seasonal change of characteristics of adult. In 1978 the samples were taken from April to October, but the figures are drawn as if taken from August to June of the following year. The date in winter of 1976 is January 29th. "Rate of sperm contained" in female means the ratio of the individuals which have copulated. The double mark in "Number of eggs contained" denote the mean values for those only which hold eggs when some females have no egg.

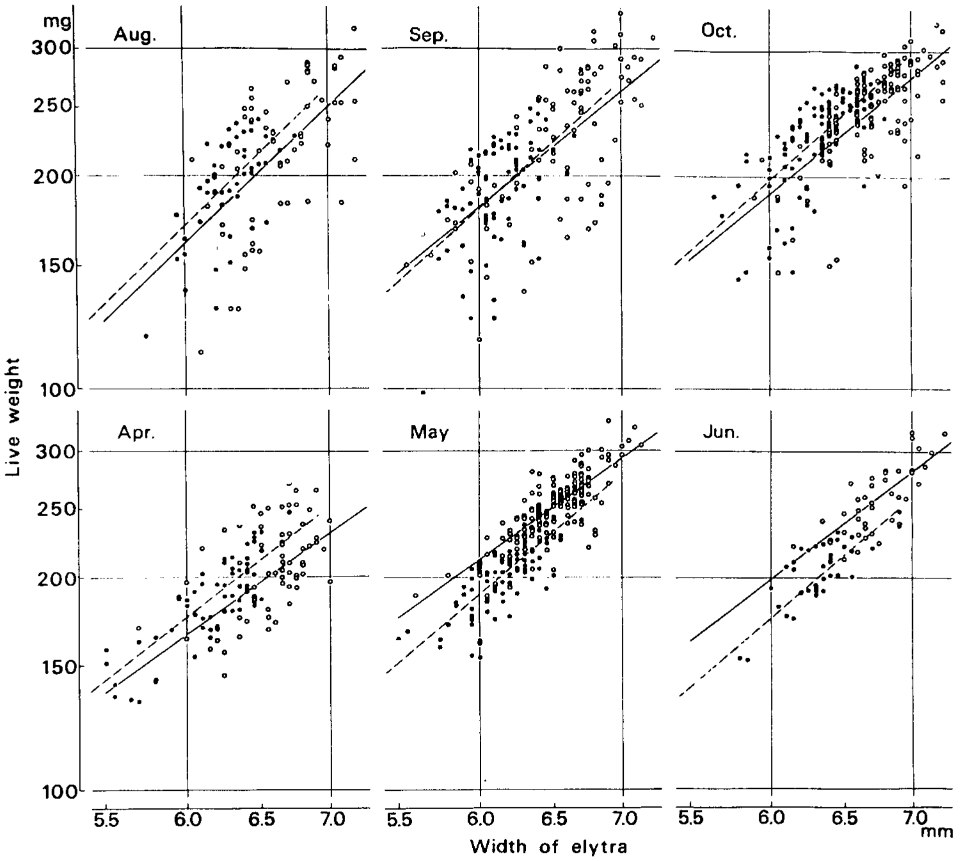


Fig. 38. The relative growth of adults in each month. The regression lines of both sexes are also shown. The open and solid circle denote the female and male respectively.

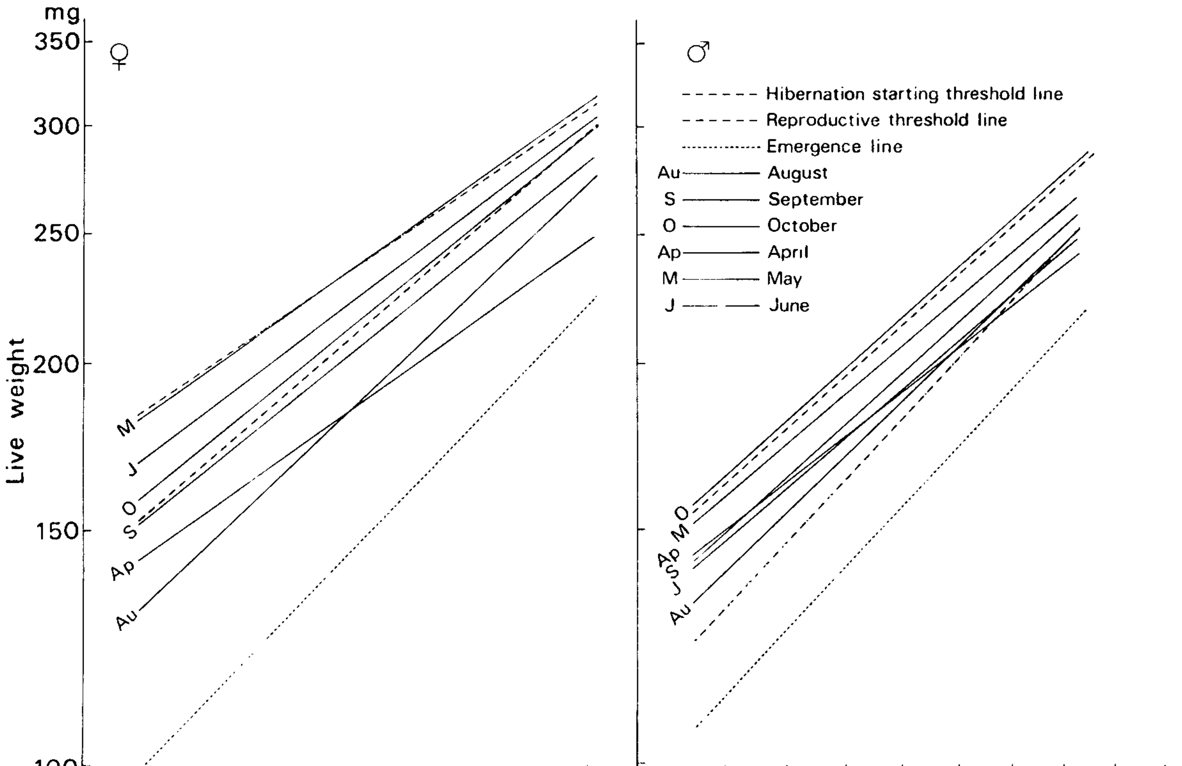


Fig. 39. The seasonal change of regression lines in both sexes. The solid line shows the regression line in each month. For the other lines, see text.

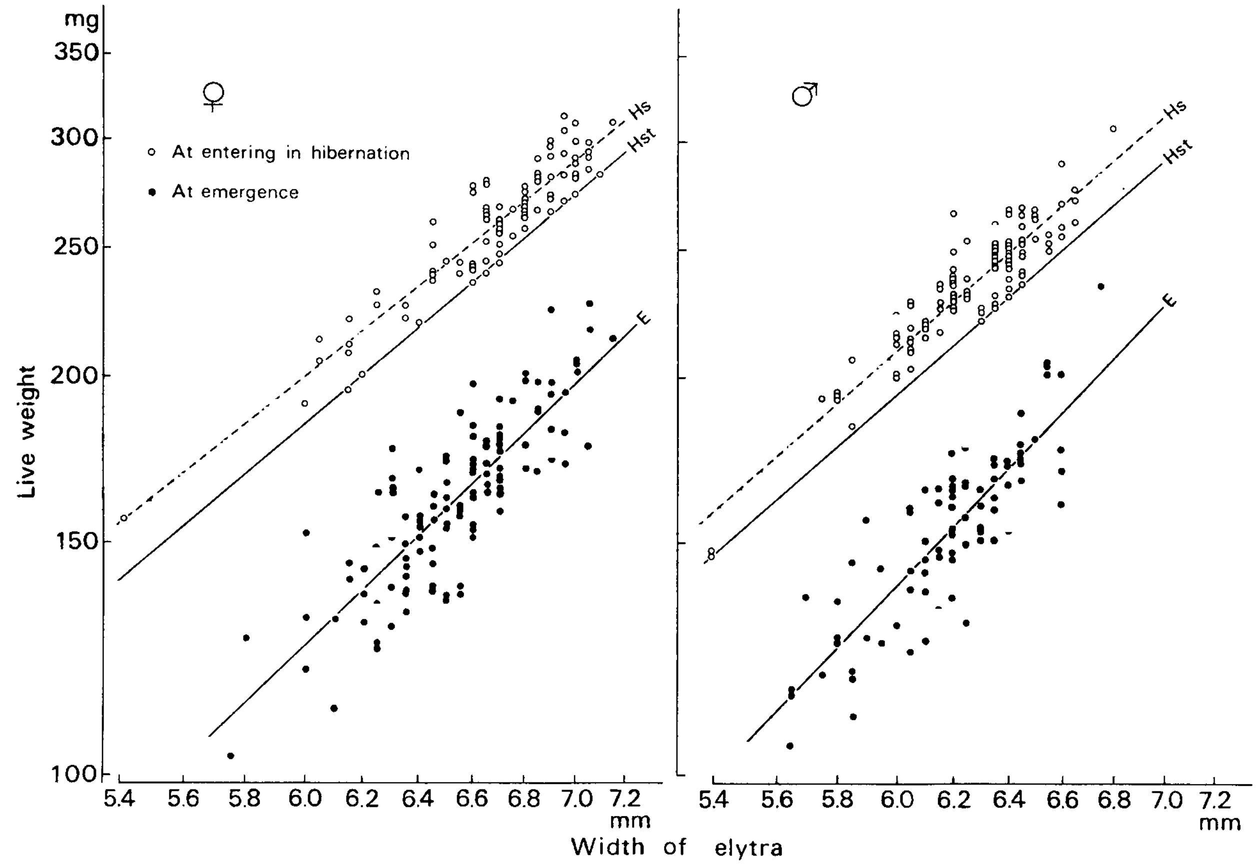


Fig. 40. The relative growth of both sexes at the emergence and the beginning of hibernation. Three regression lines are also drawn in each sex. E, Emergence line; Hs, Hibernation-starting line; Hst, Hibernation-starting threshold line.

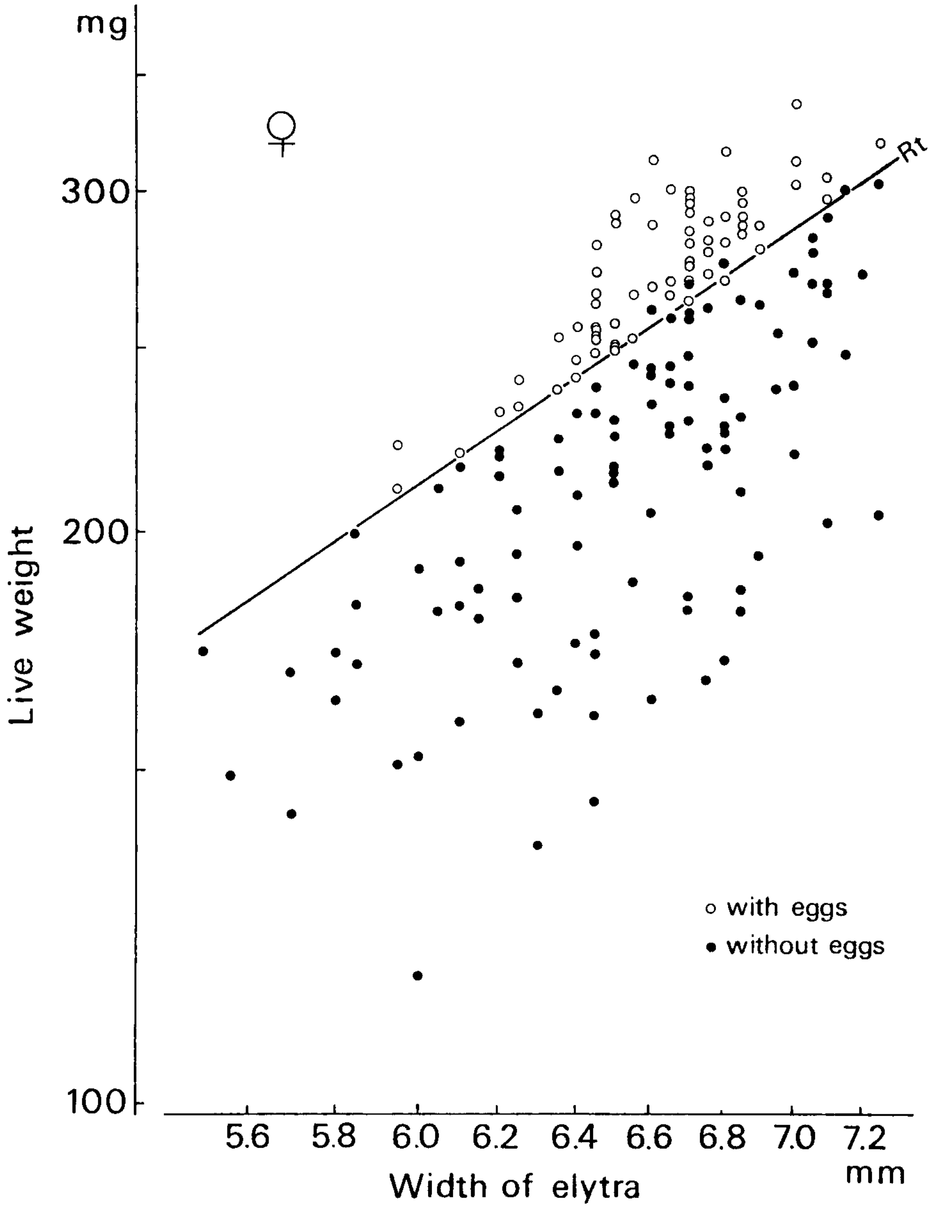


Fig. 41. The relative growth of females in autumn. Whether an individual holds eggs or not is discriminated, and an regression line named as Reproductive threshold line (Rt) is drawn.

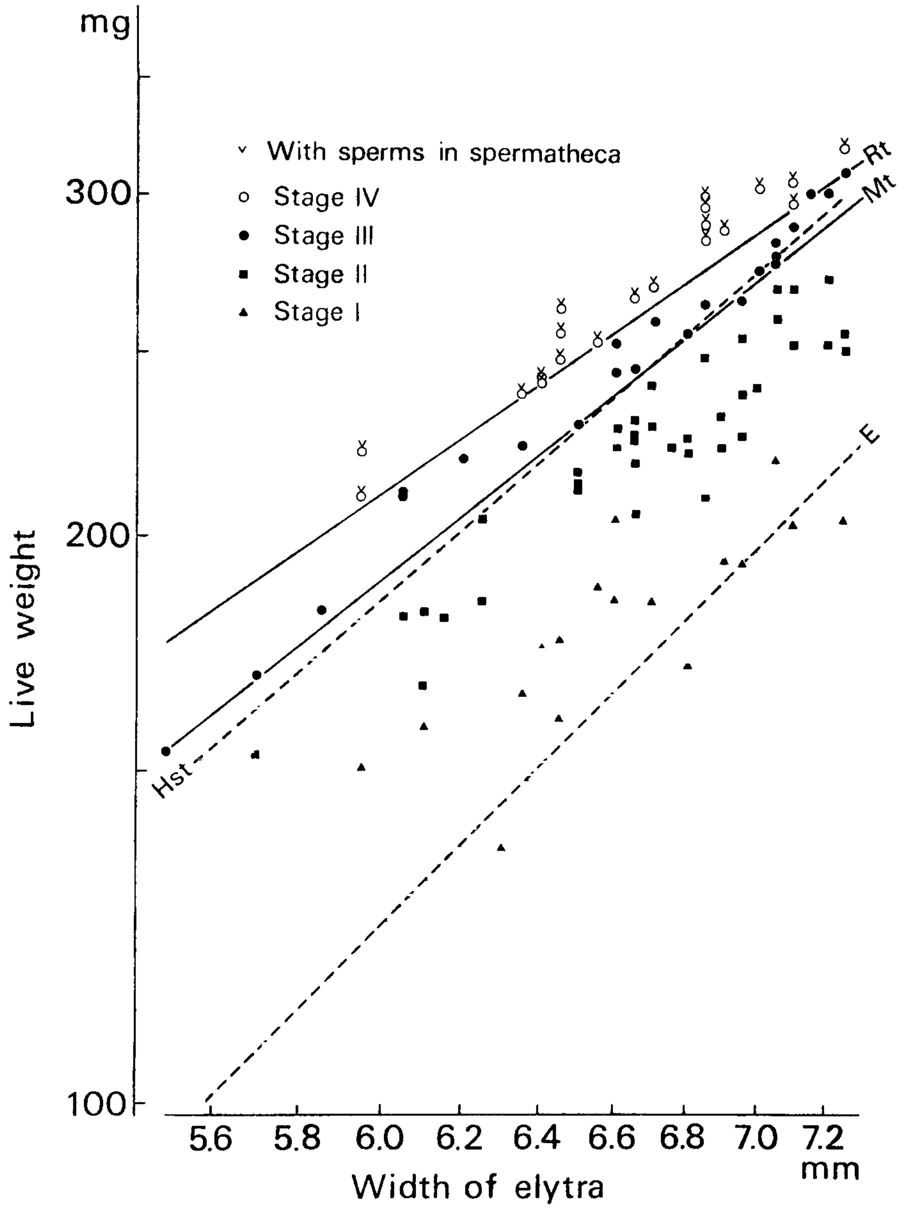


Fig. 42. The relative growth of females during the reproductive period in autumn with distinction among four stages. No individual of Stage V appeared in this period. The inseminated female is also discriminated.

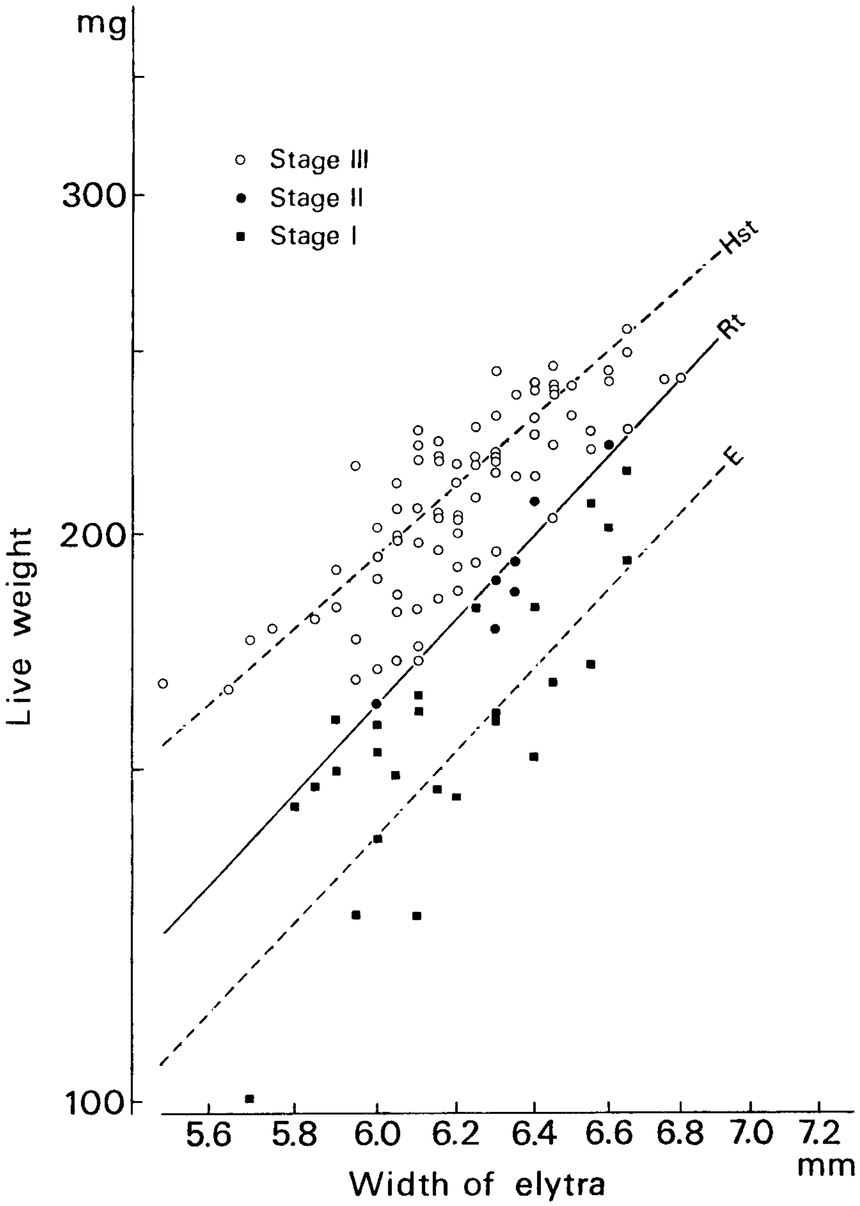


Fig. 43. The relative growth of males during the reproductive period in autumn with distinction among three stages. E- and Hst-lines are also drawn. For Rt line, see text.

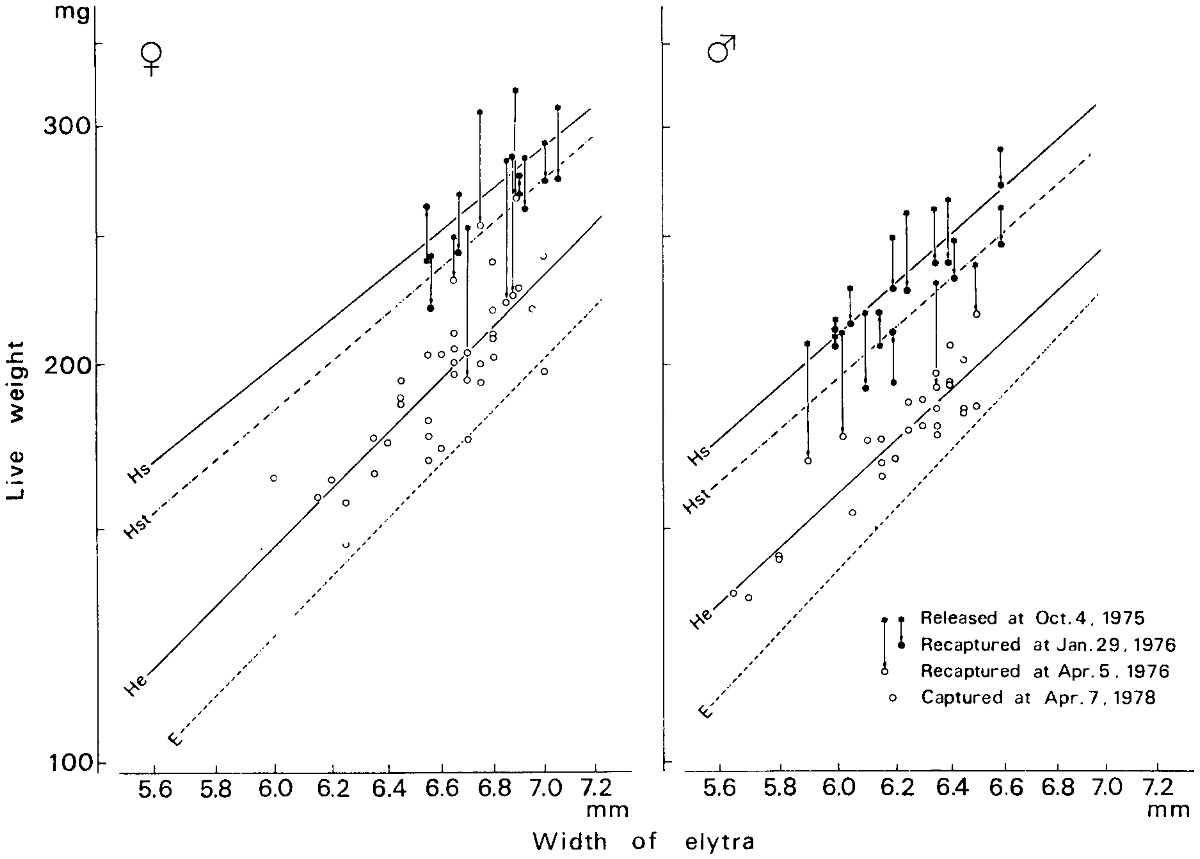


Fig. 44. The relative growth at the ending of hibernation (open circle) and the waste during hibernation in both sexes. The vertical arrow shows the decrease or increase of body weight between two survey times.

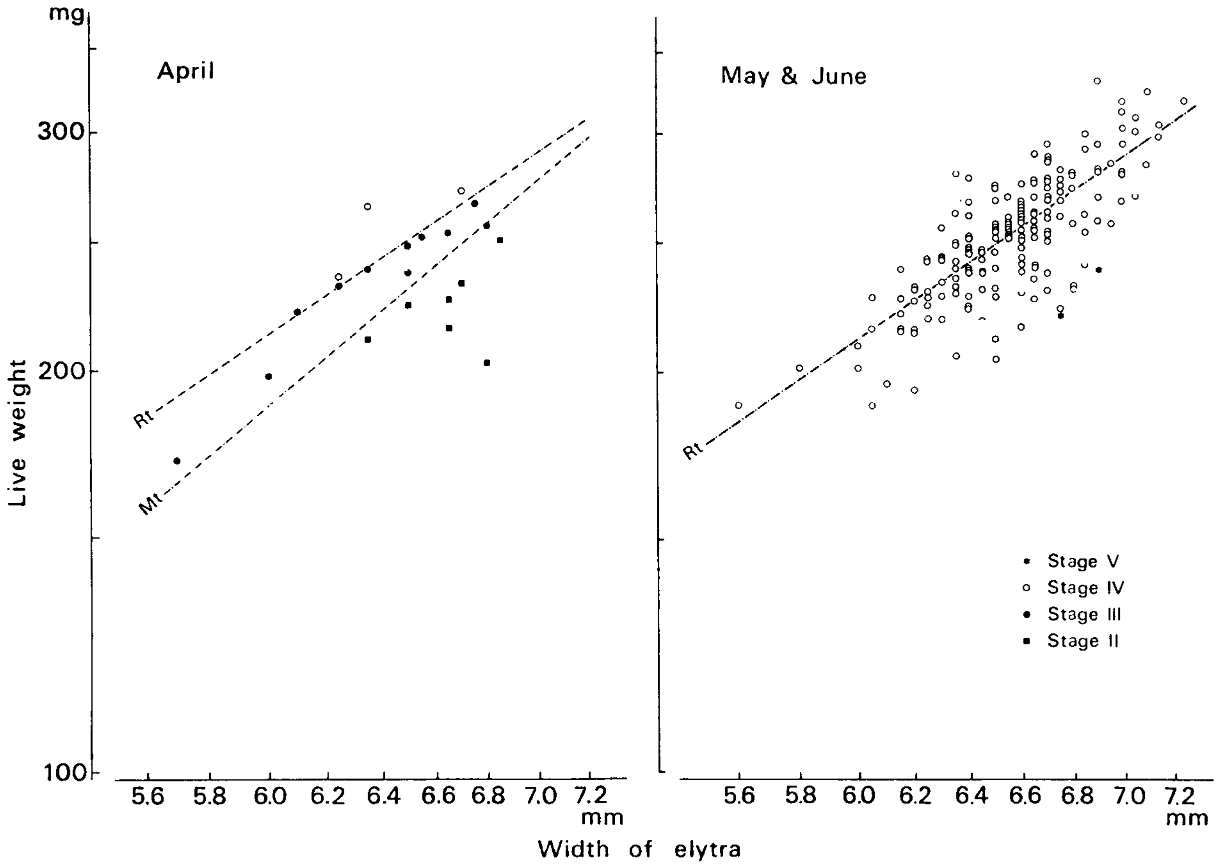


Fig. 45. The relative growth of female before (April) and during (May and June) the reproductive period in early summer. The four stages of ovary are discriminated. No individual in Stage I appeared in this period.

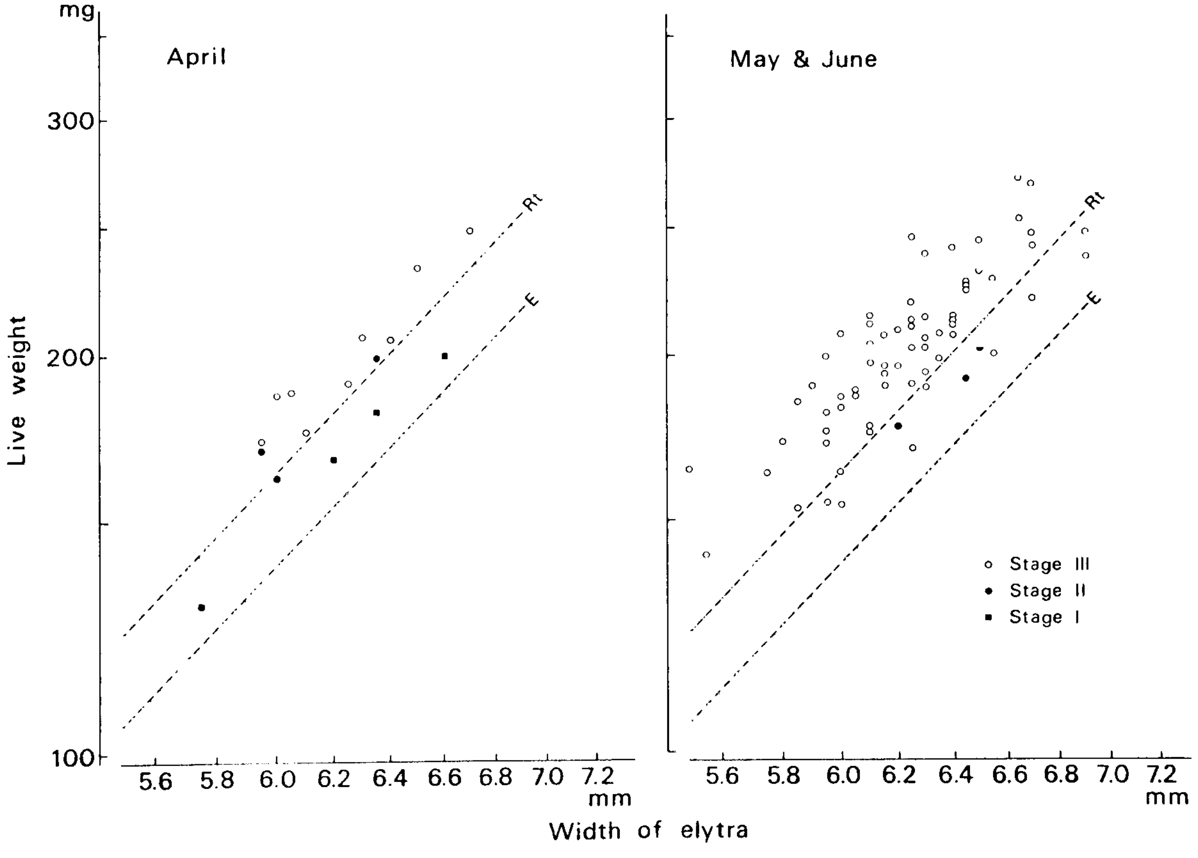


Fig. 46. The relative growth of male before (April) and during (May and June) the reproductive period in early summer. The three stages of spermatogenesis are discriminated.

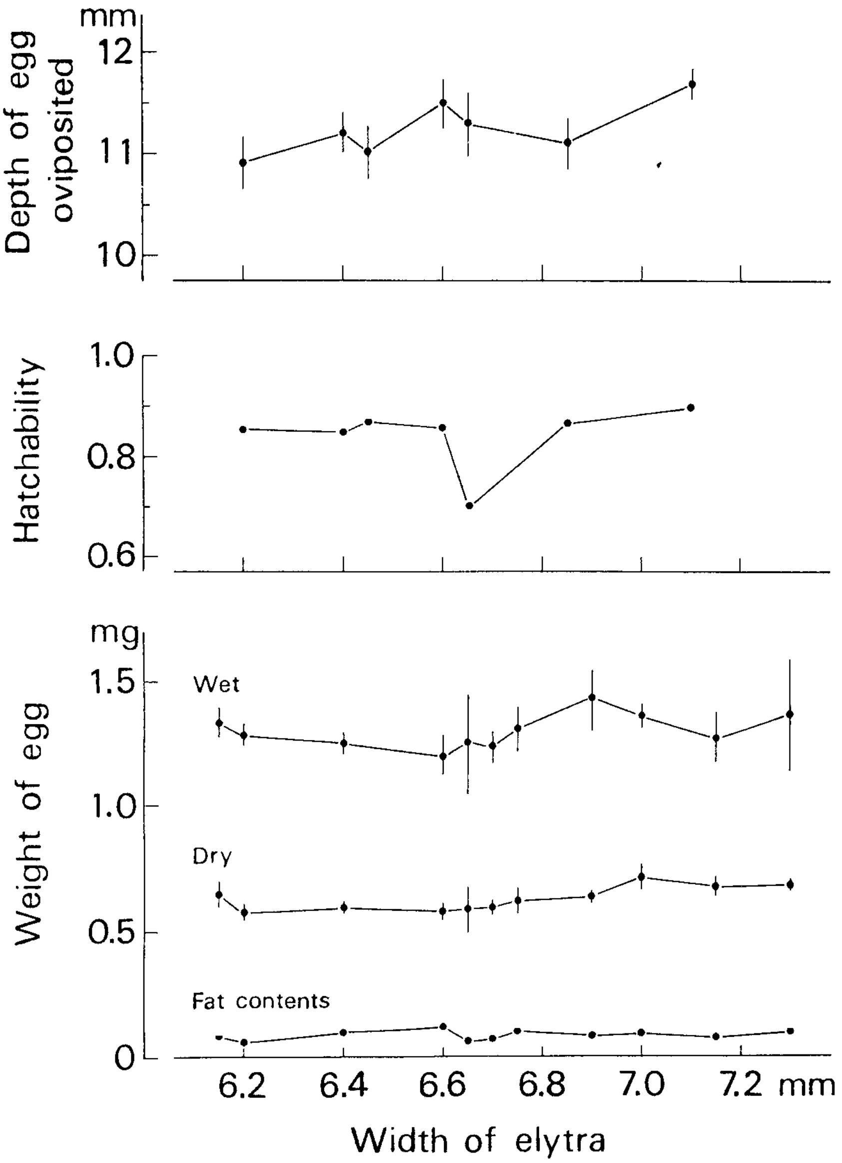


Fig.47. The relation between the size of female and the weight of egg, fat contents, hatchability and the depth from soil surface to bottom of laid egg. The latter two results derived from the rearing of female outdoors. The vertical bar shows the 95 % fiducial limit of mean.

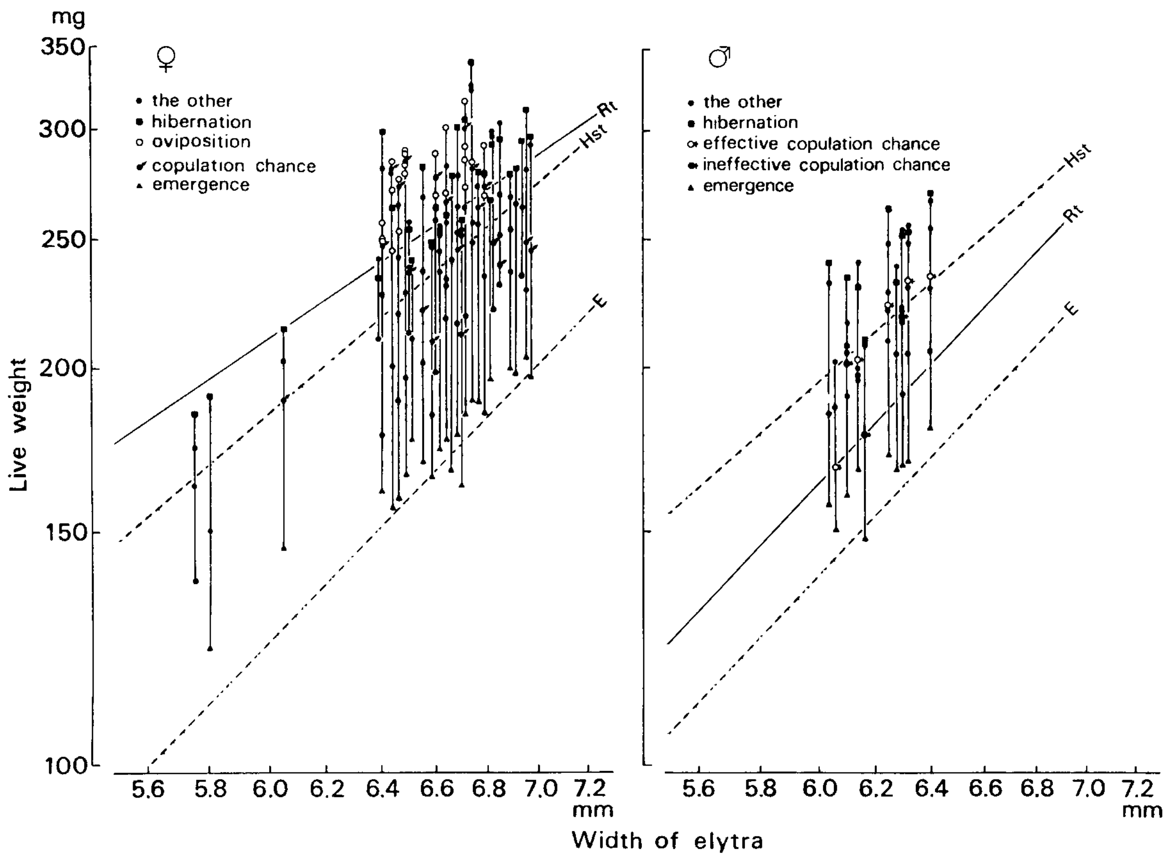


Fig. 48. The growth and development of each adult for each sex in Rearing-I (1974). The marks connected by a vertical line show the body weight and the state of and individual at every measurment. The effective copulation chance means that the male could inseminate a female at that time. The regression lines clarified in the preceding chapter are also drawn.

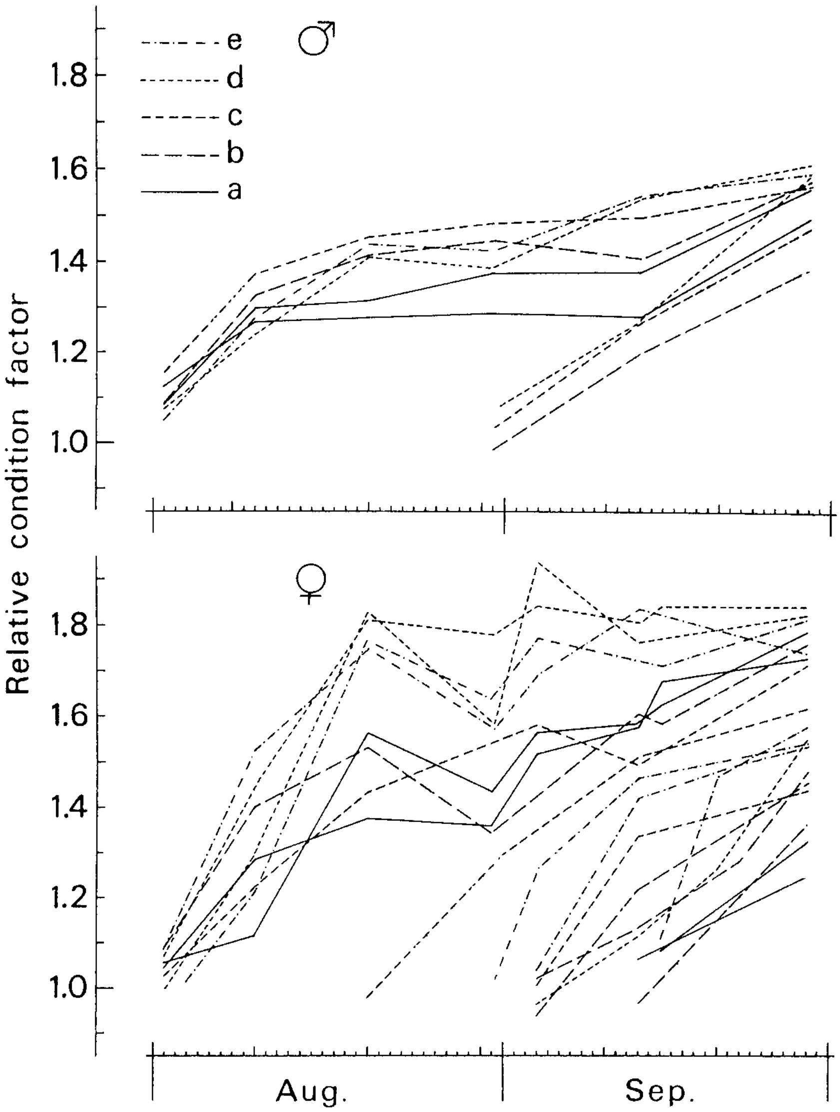


Fig. 49. The change of relative condition factor of each adult from emergence to the end of September for each sex in Rearing-I (1974). Each line shows an adult in each division.

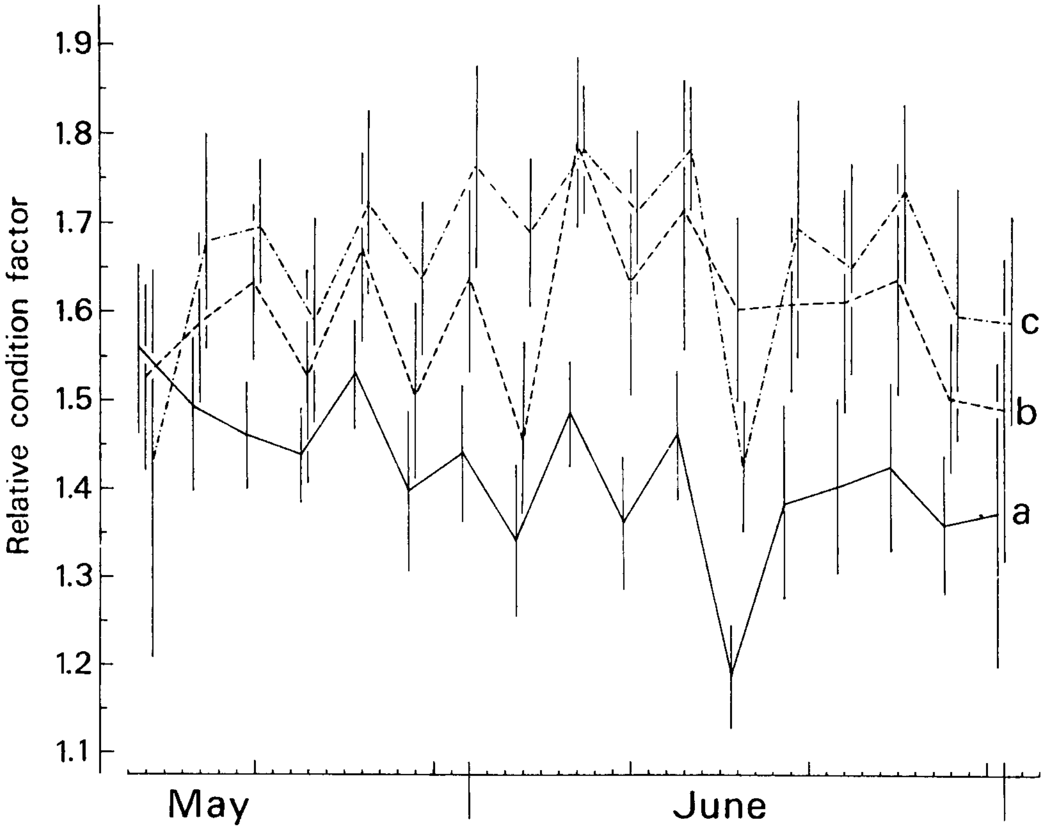


Fig. 50. The change of mean relative condition factor of male in each division in Rearing-III. The vertical bar shows the 95 % fiducial limit of mean.

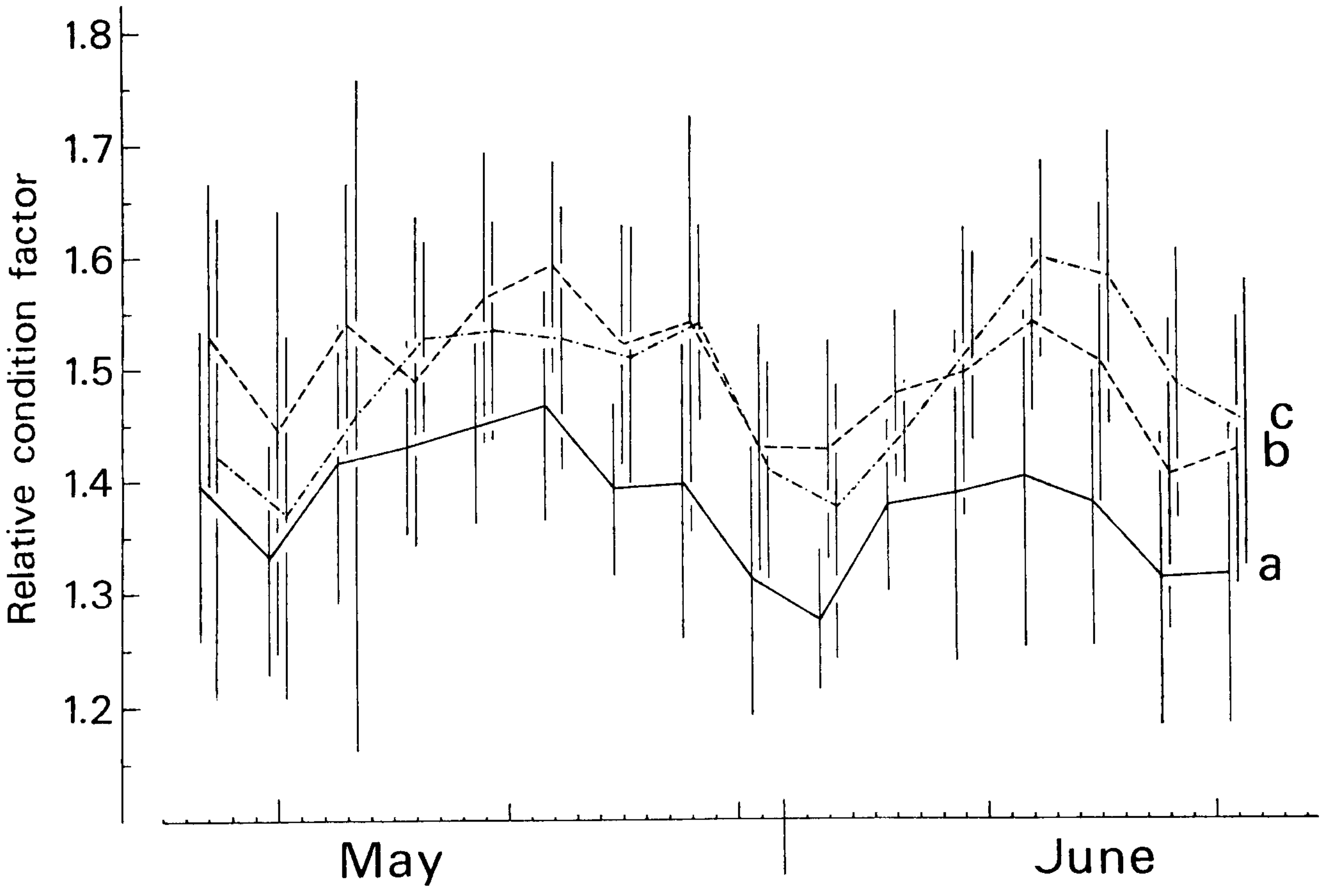


Fig. 51. The change of mean relative condition factor of females in each division in Rearing-II (1975). The vertical bar shows 95 % fiducial limit of mean.

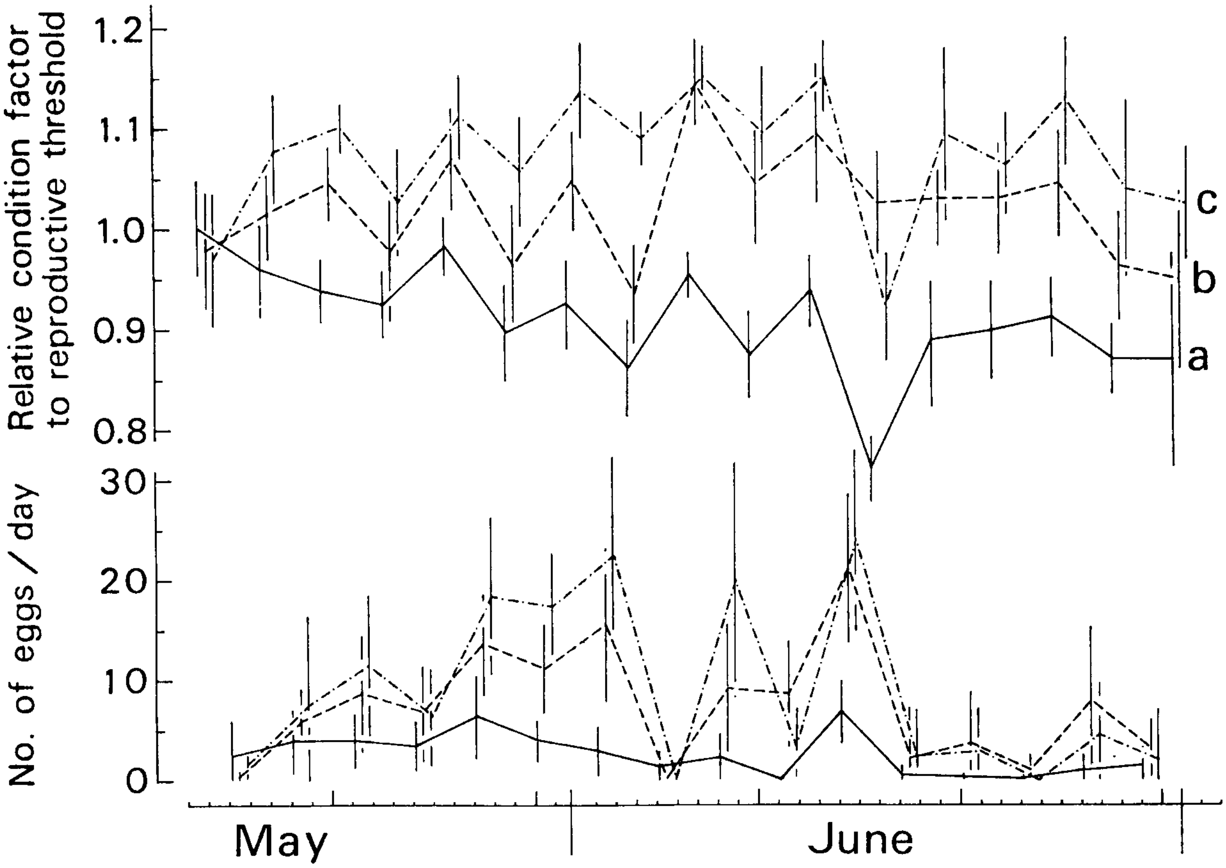


Fig. 52. The change of mean relative condition factor to reproductive threshold of females and that of number of eggs laid every 3 days in each division in Rearing-II (1975). The vertical bar shows the 95 % fiducial limit of mean.

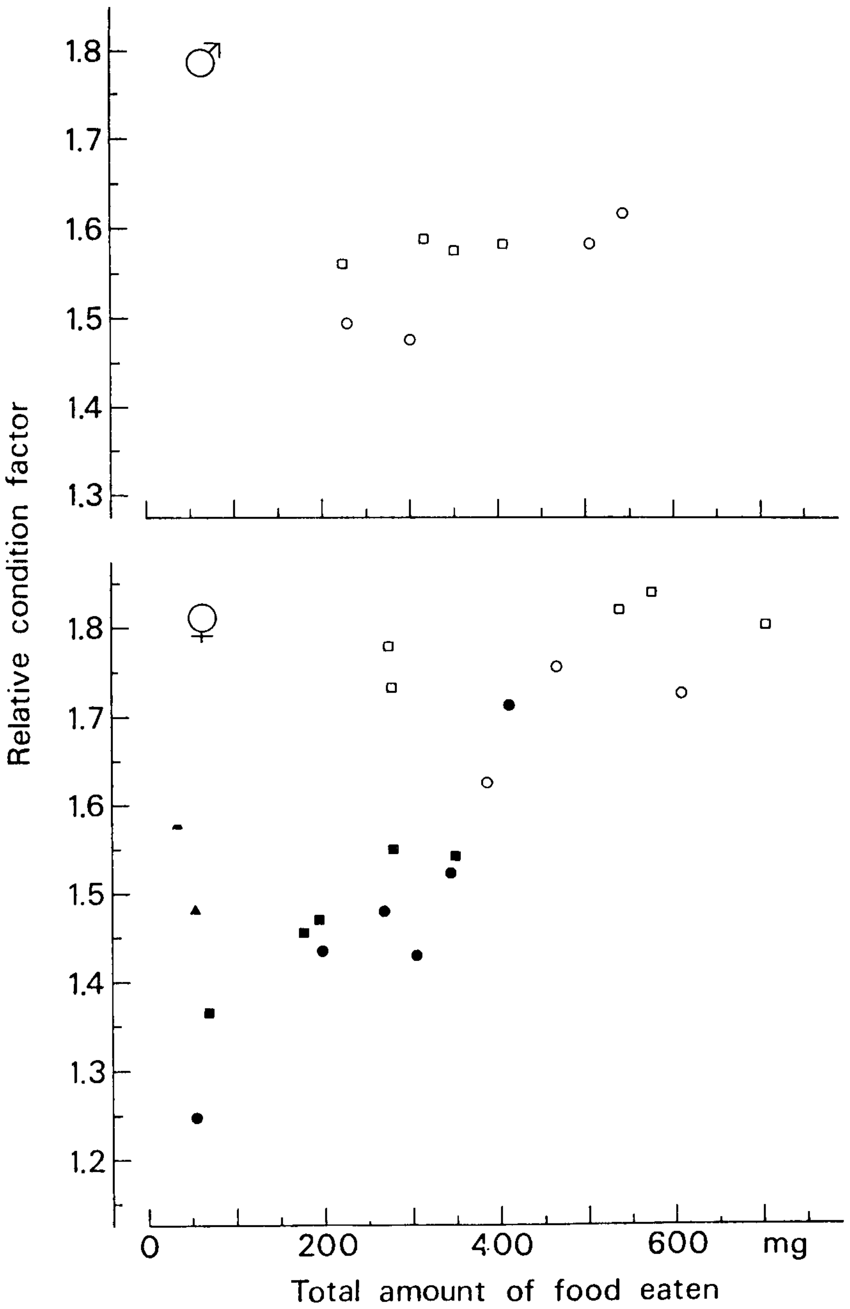


Fig. 53. The relation between total dry weight of food eaten from emergence to late September (28th) and relative condition factor of each adult at the time for each sex in Rearing-I (1974). The size of each individual (width of elytra in mm) was discriminated as follows. Female; triangle ≦ 6.35, 6.40 ≦ square ≦ 6.65, 6.70 ≦ circle. Male; triangle ≦ 5.95, 6.00 ≦ square ≦ 6.25, 6.30 ≦ circle. The open mark denotes the individual which reproduced.

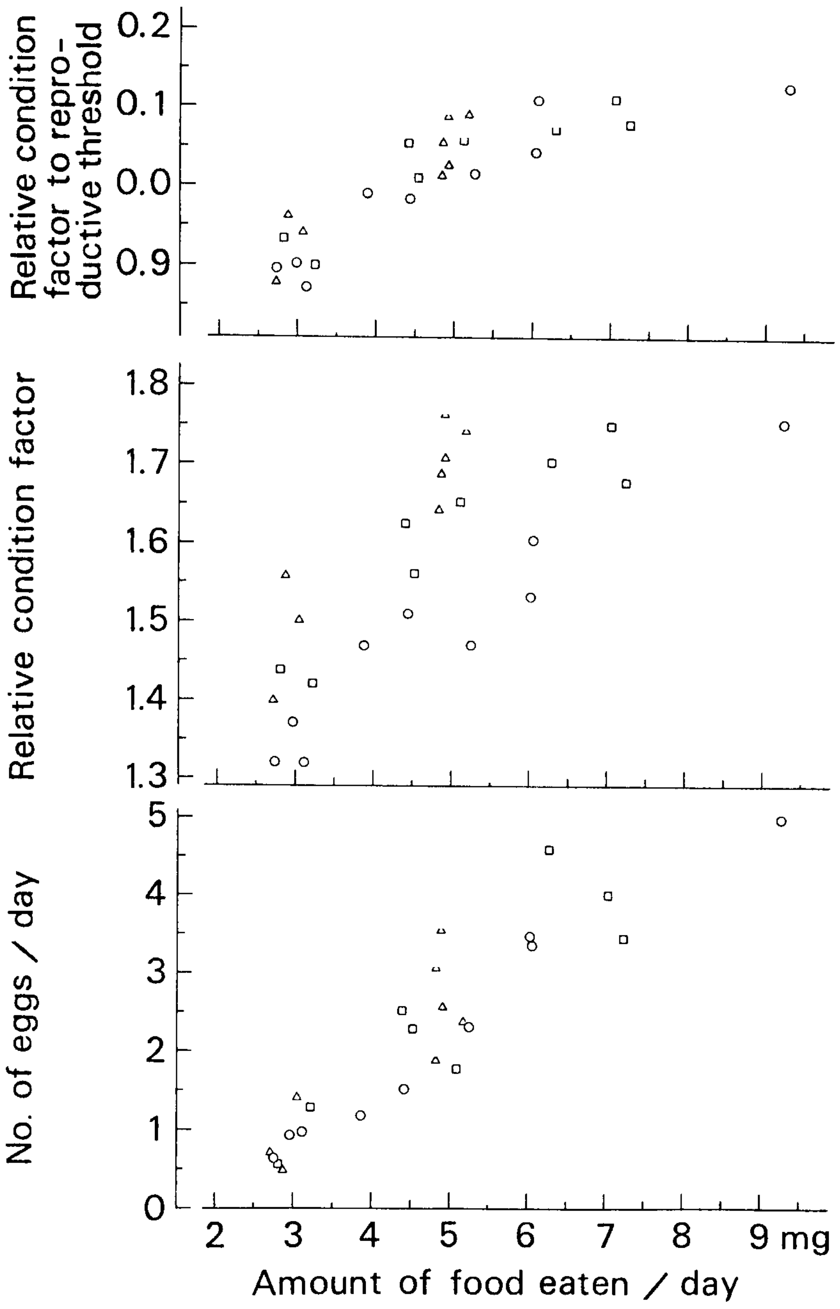


Fig. 54. The relation between dry weight of food eaten per day and the number of eggs laid per day, relative condition factor, or relative condition factor to reproductive threshold for each female in Rearing-II (1975). The data were limited only for those from May 14th to June 30th, in which most female survived and oviposited. The size discrimination with every mark is the same as Fig. 53.

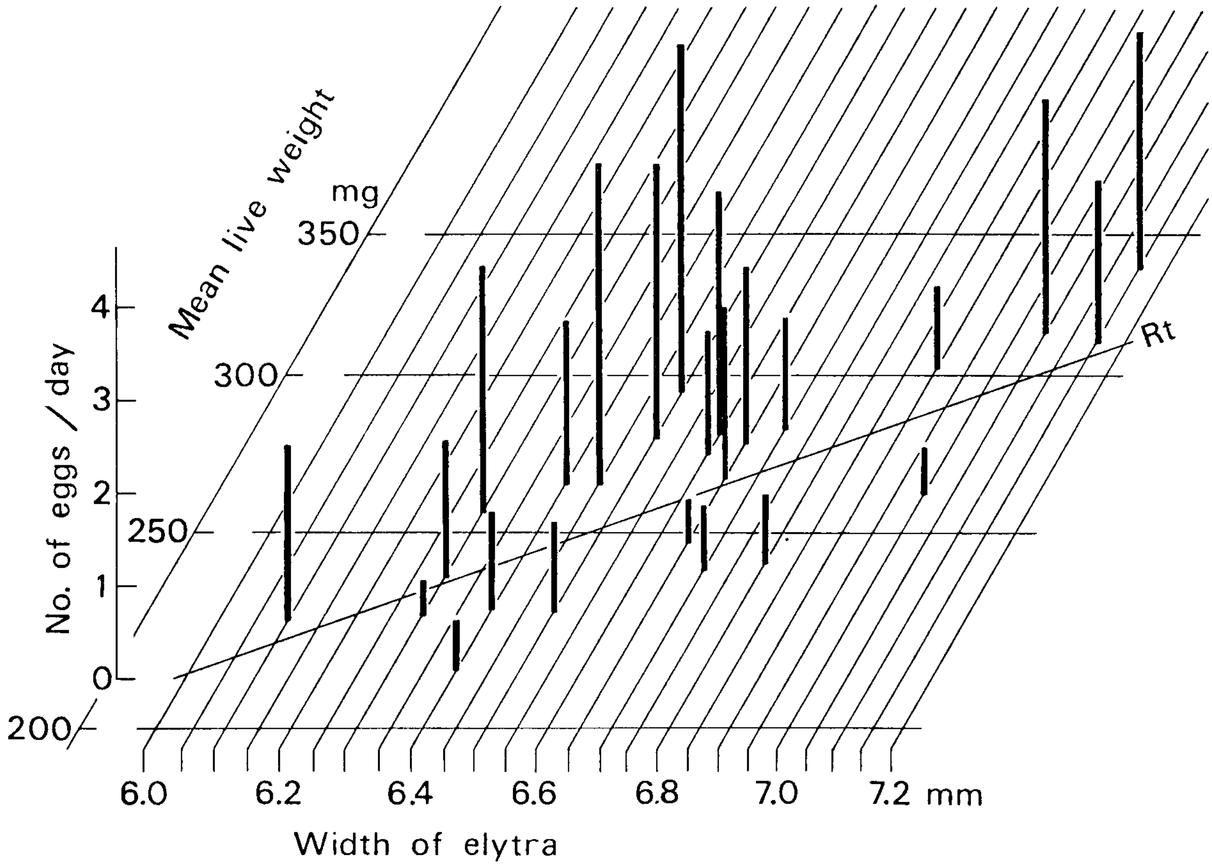


Fig. 55. The number of eggs laid per day by each female from May 14th to June 30th in Rearing-II (1975) in respect to relative growth. The position of each female on relative growth was defined by its size and mean live weight over the period.

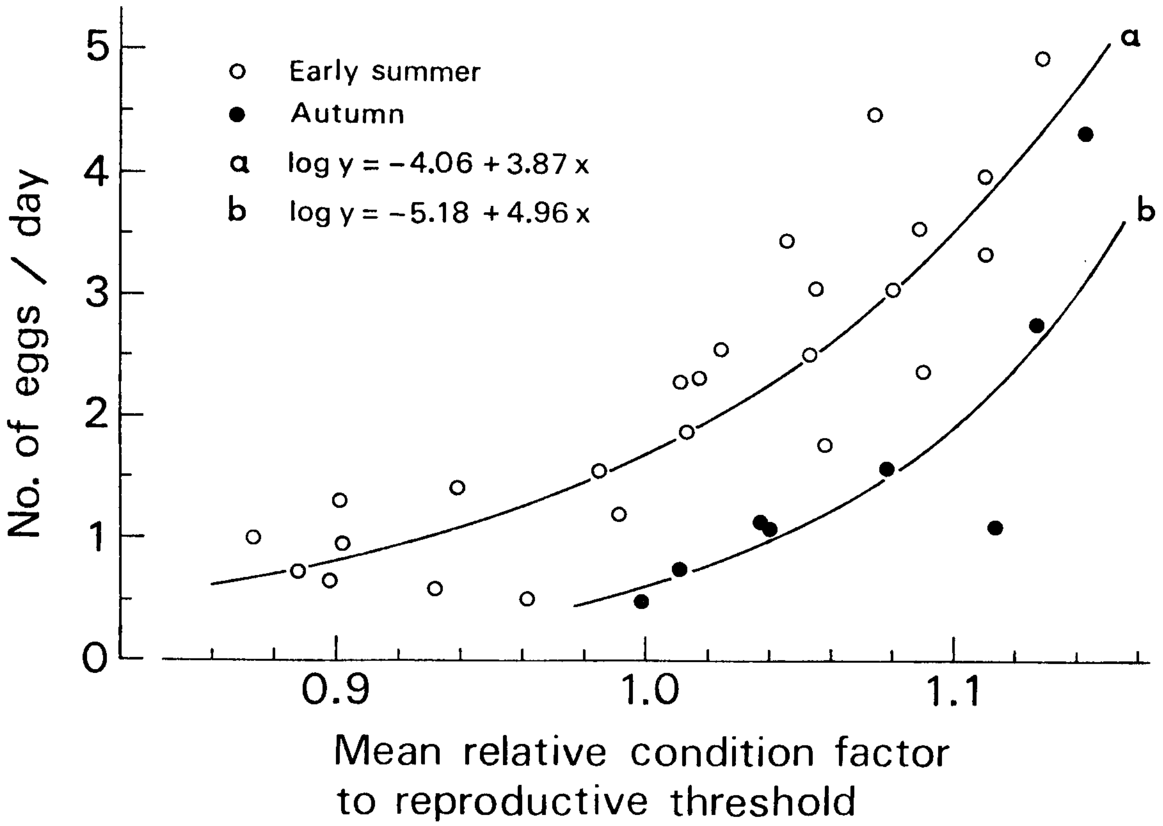


Fig. 56. The relation between mean relative condition factor to reproductive threshold of each female and the mean number of eggs laid per day in Rearing-I (autumn of 1974) and Rearing-II (early summer of 1975). For the former, the data from August 20th to September 15th were only used, in which oviposition was malinly done. Each regression line was calculated by the method of least squares in logarithm.

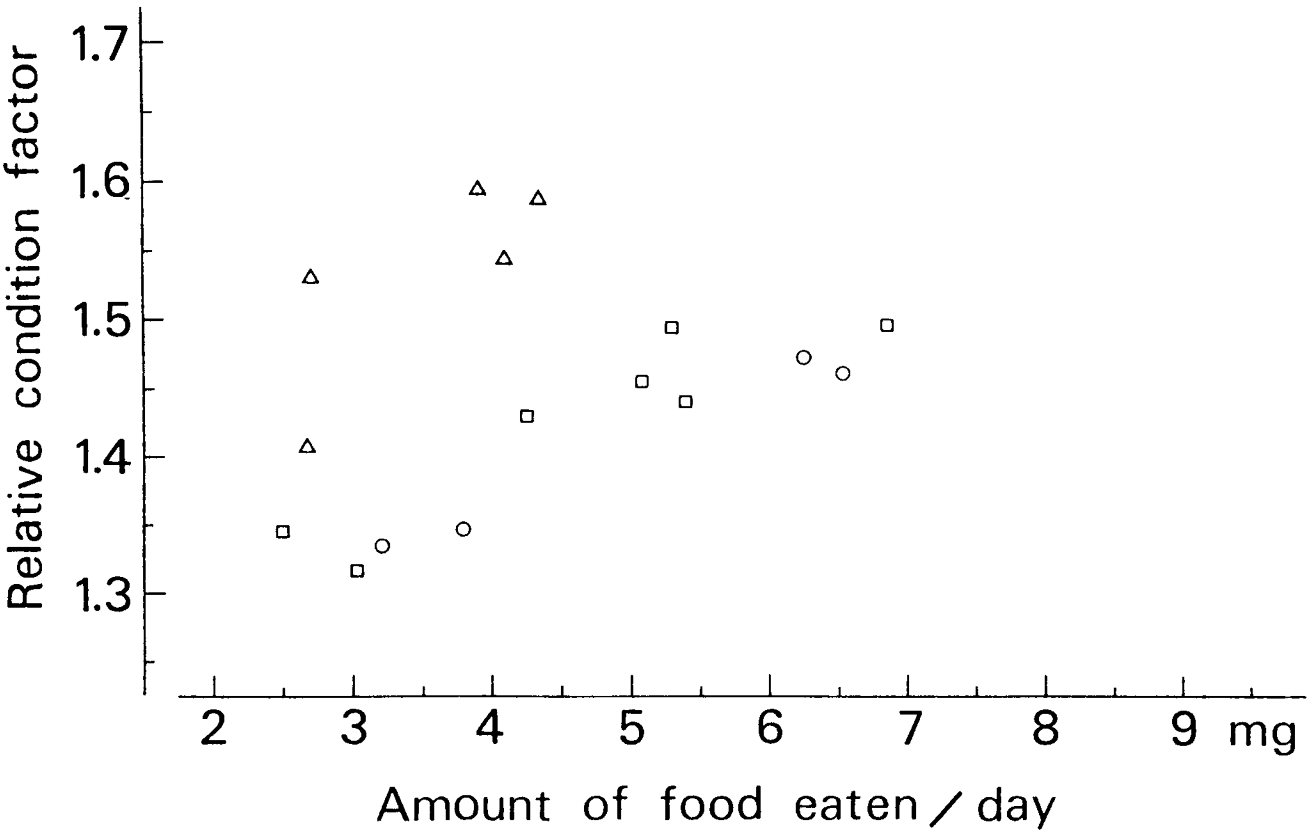


Fig. 57. The relation between the dry weight of food eaten per day and the mean relative condition factor of each male from May 10th to June 23th in Rearing-III (1976). The size discrimination with every mark is the same as Fig. 53.

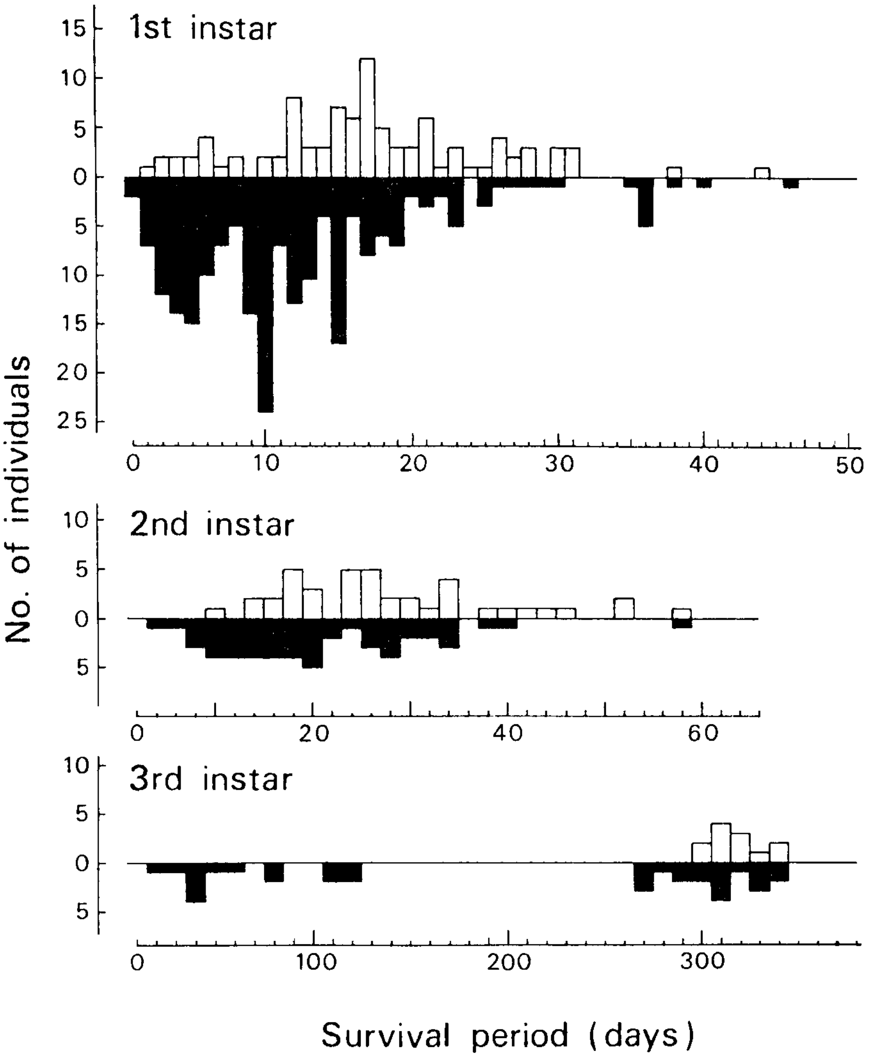


Fig. 58. The frequency distribution of the survival period of the dead (solid column) and the survivor (open column) in each instar for early summer cohort of 1974 in St. A.

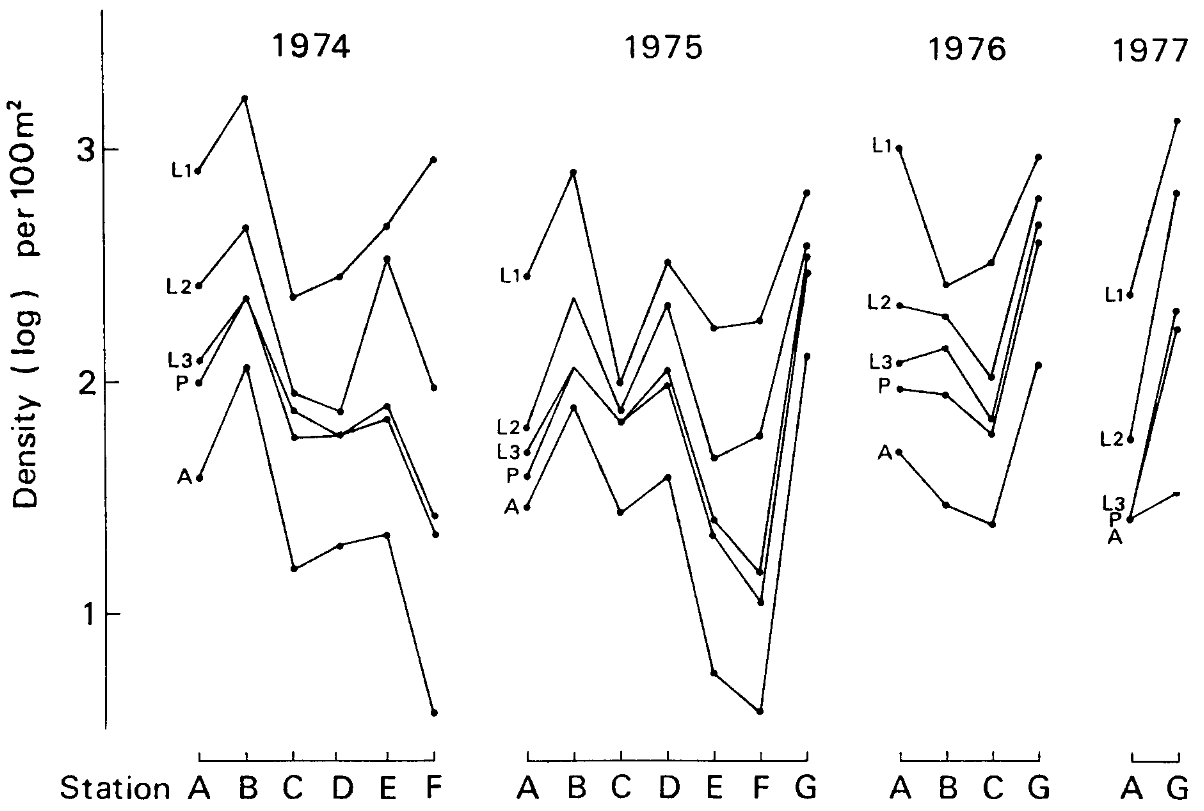


Fig. 59. The change of density of each stage in logarithm among stations for the early summer cohort in every year, 1772-1978.

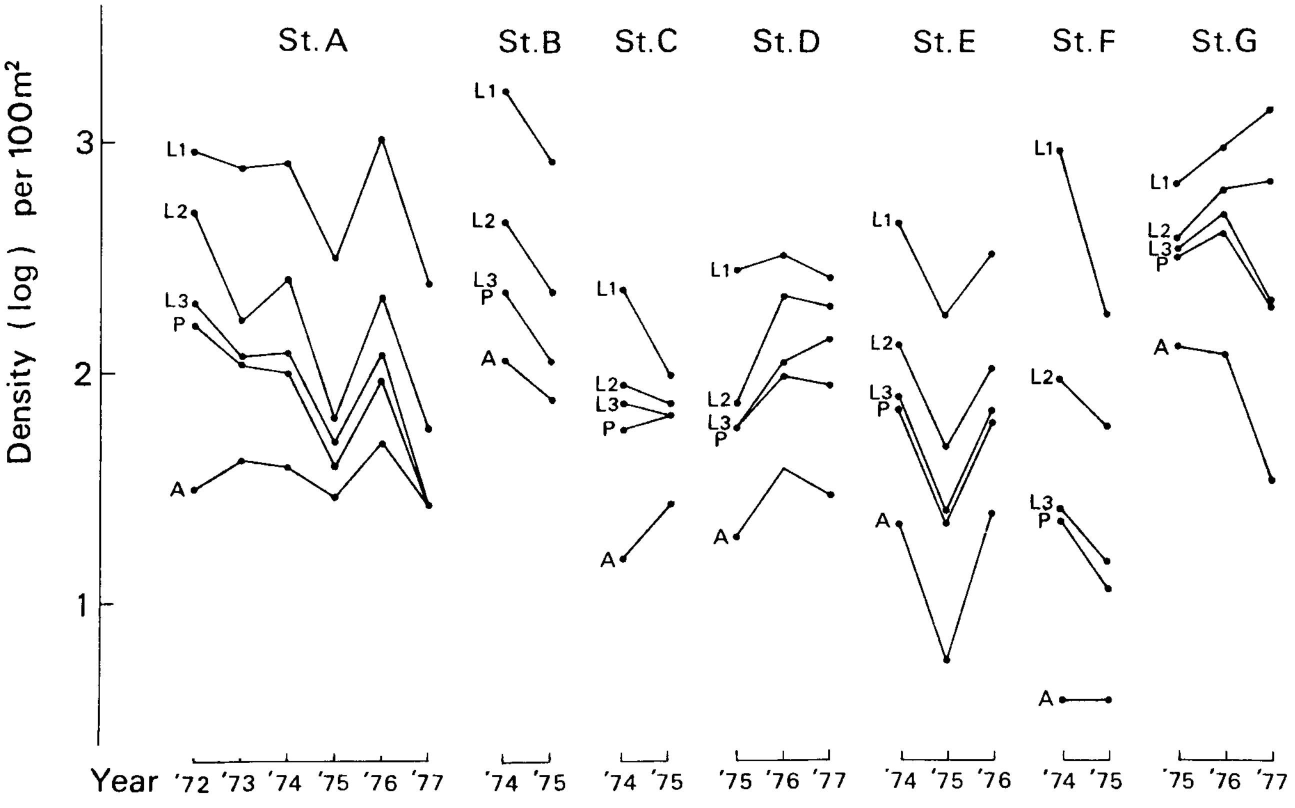


Fig. 60. The change of density of each stage in logarithm among years in every station for the early summer cohort, 1972-1978.

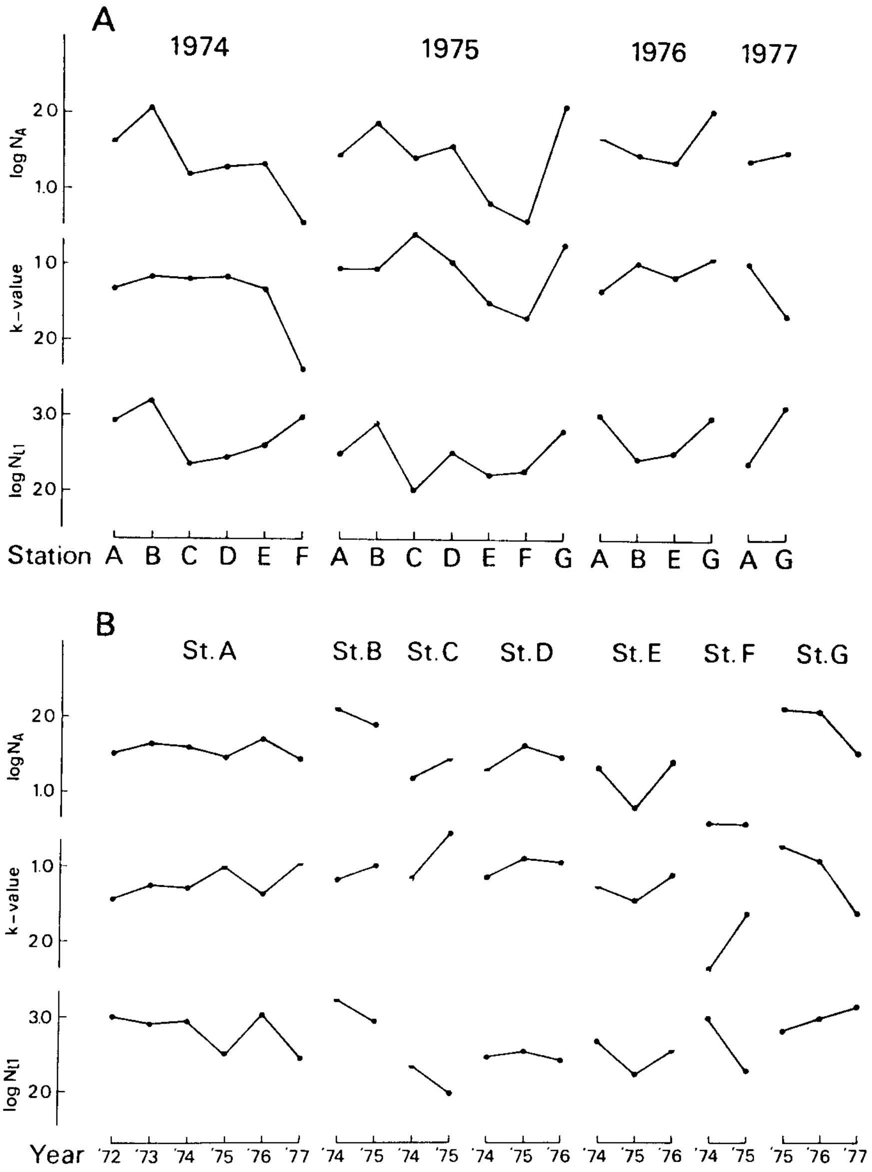


Fig. 61. The change of initial number, mortality in developmental stage, and the number of emerged adults among stations (A) and among years (B), for the early summer cohorts, 1972-1978.

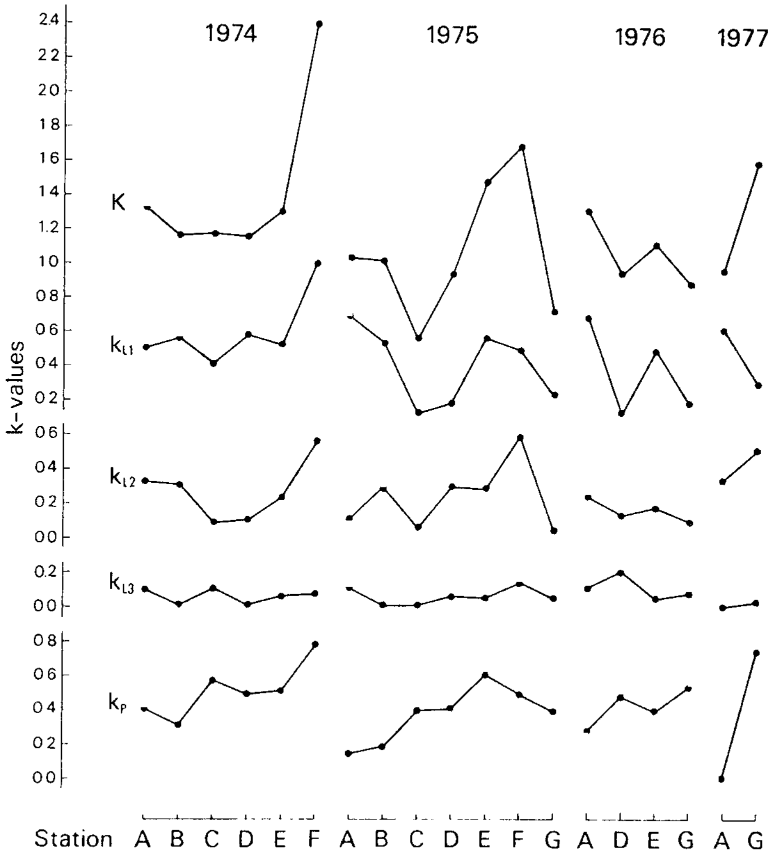


Fig. 62. Key stage analysis among stations in every year, for the early summer cohorts, 1974-1978.

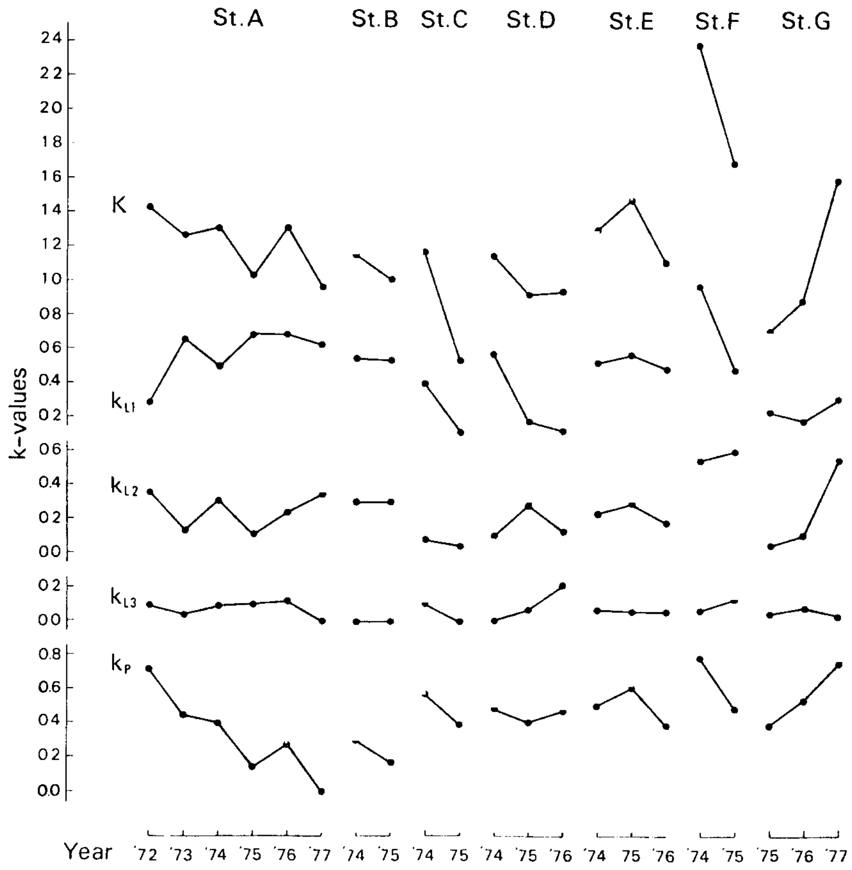


Fig. 63. Key stage analysis among years in every station, for the early summer cohorts, 1972-1978.

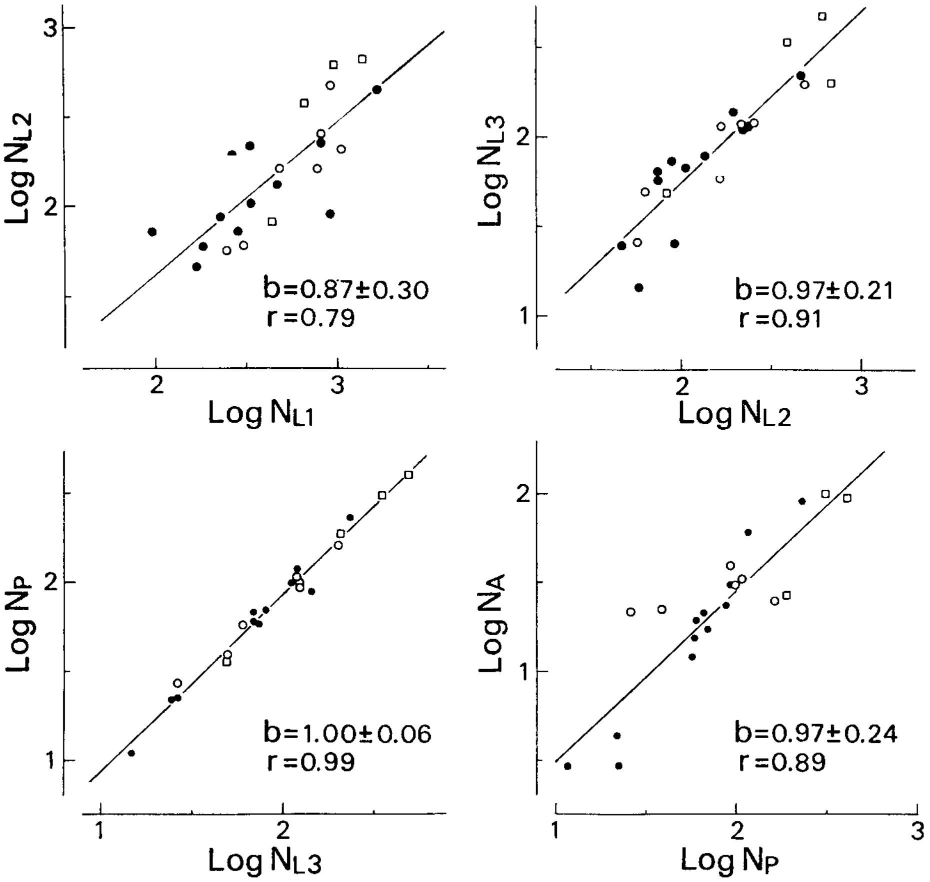


Fig. 64. The relation between the densities of two successive developmental stages in logarithms in 7 stations, 1974-1978. St. A (open circle) and St. G (open square) whose densities were often high are discriminated from the other stations (solid circle). The regression line and the value of its slope with 95 % fiducial limit are also drawn.

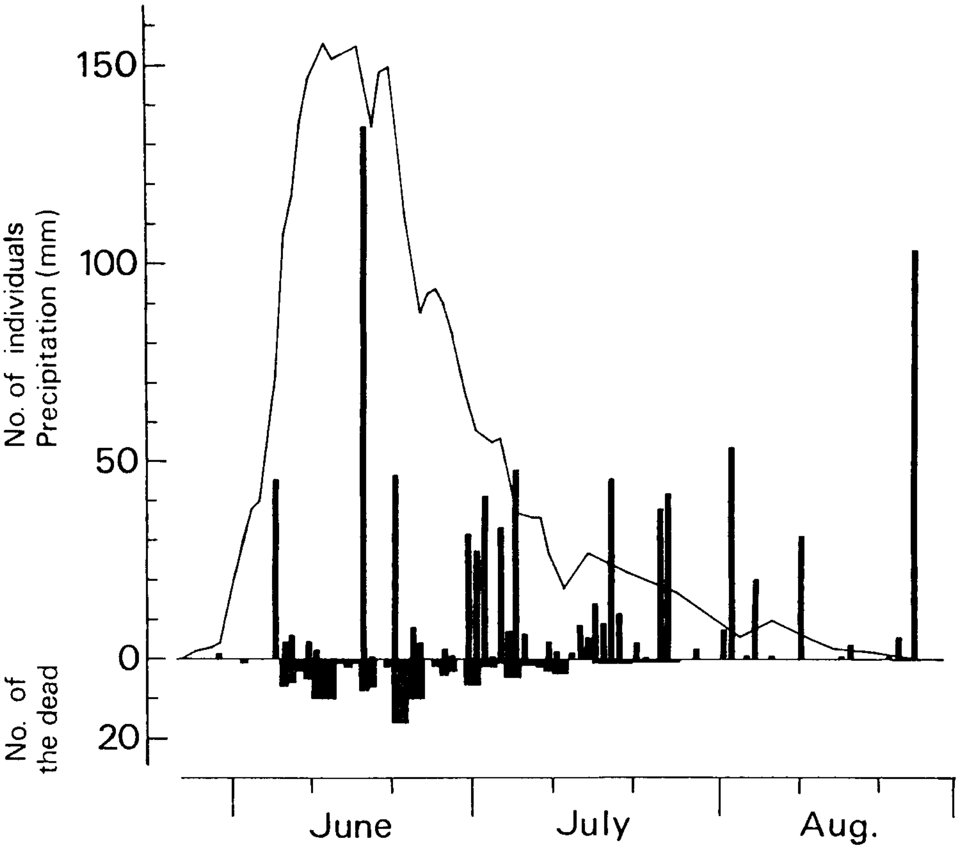


Fig. 65. Daily precipitation (narrow bar) and the number of the dead of the 1st instar (solid column) in early summer cohort of 1974 in St. A. The line shows the change of the number of the 1st instar larvae present.

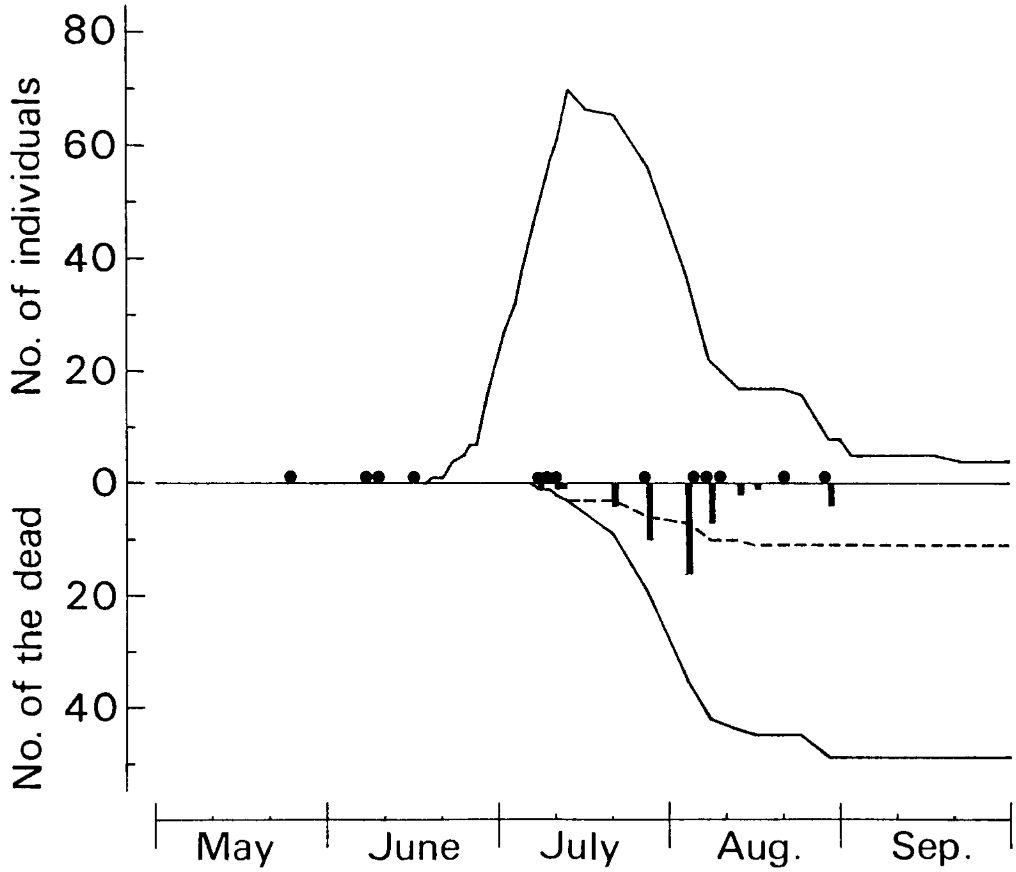


Fig. 66. The number of wasps (Methoca yasumatsui Iwata) observed and the victims of the 2nd instar larva in the early summer cohort of 1974 in St. A. A point denotes one wasp. Solid and broken line for the dead show the cumulative number of all the dead and those killed by the wasp respectively. The hight of bar shows the number of larvae died during each interval of survey.

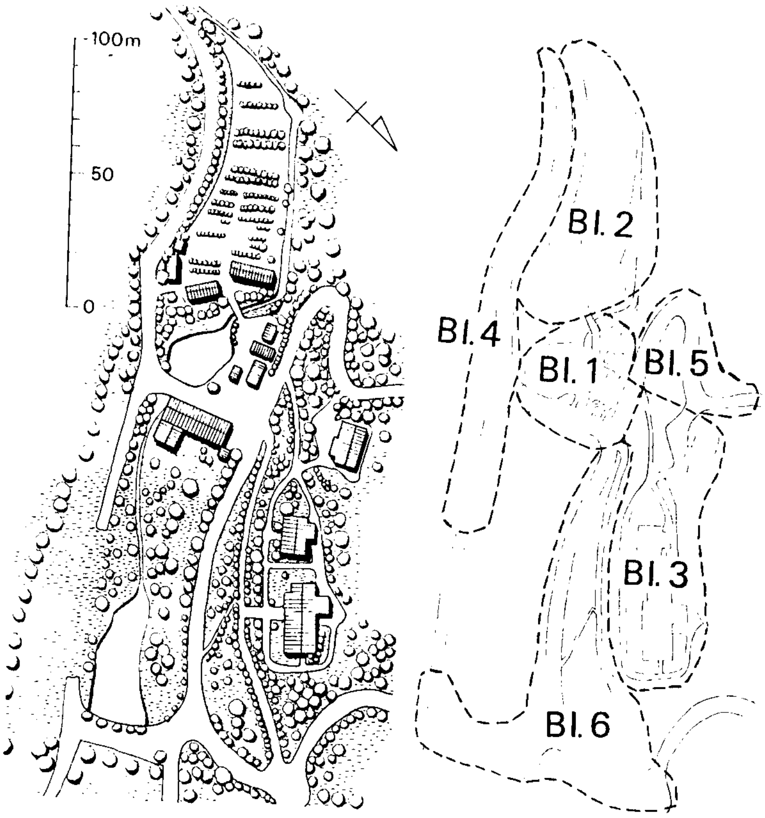


Fig. 67. Map of Field-I and the partition of blocks. The open area of map shows the bare ground. Dashed area and circle show the grassy area and tree or bush respectively. See also Fig. 2.

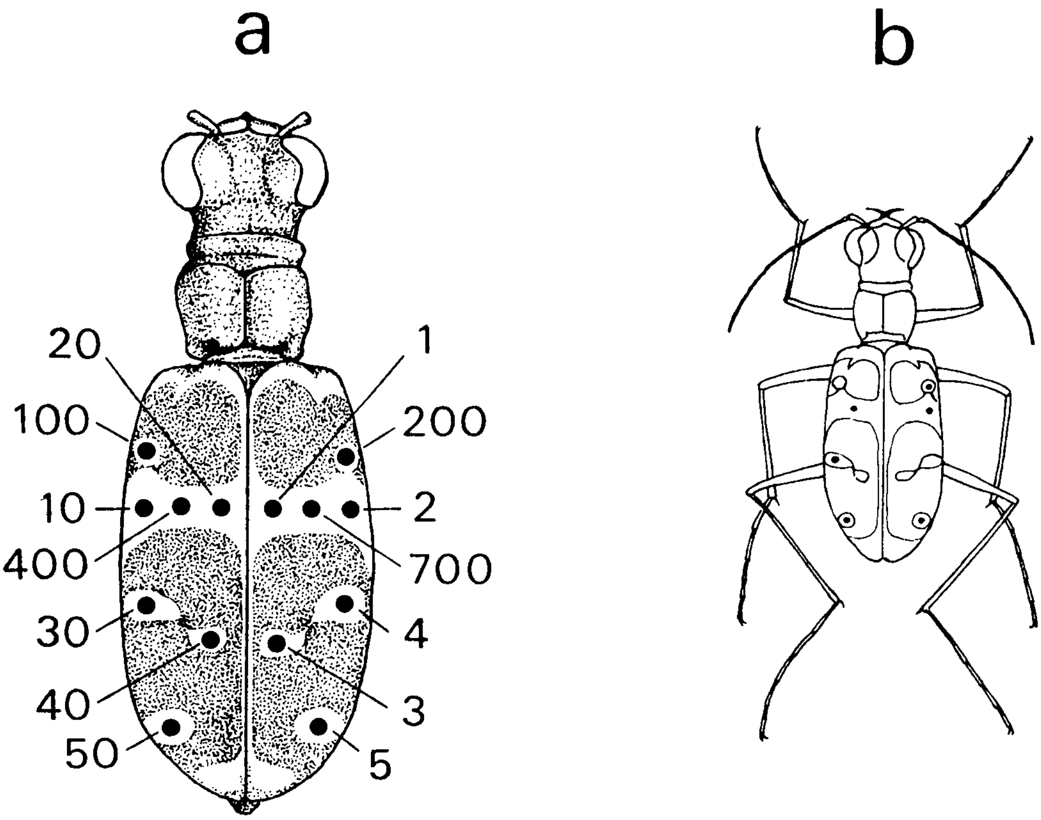


Fig. 68. Code system of individual mark (a) and an example (No. 687) of marked adult (b).

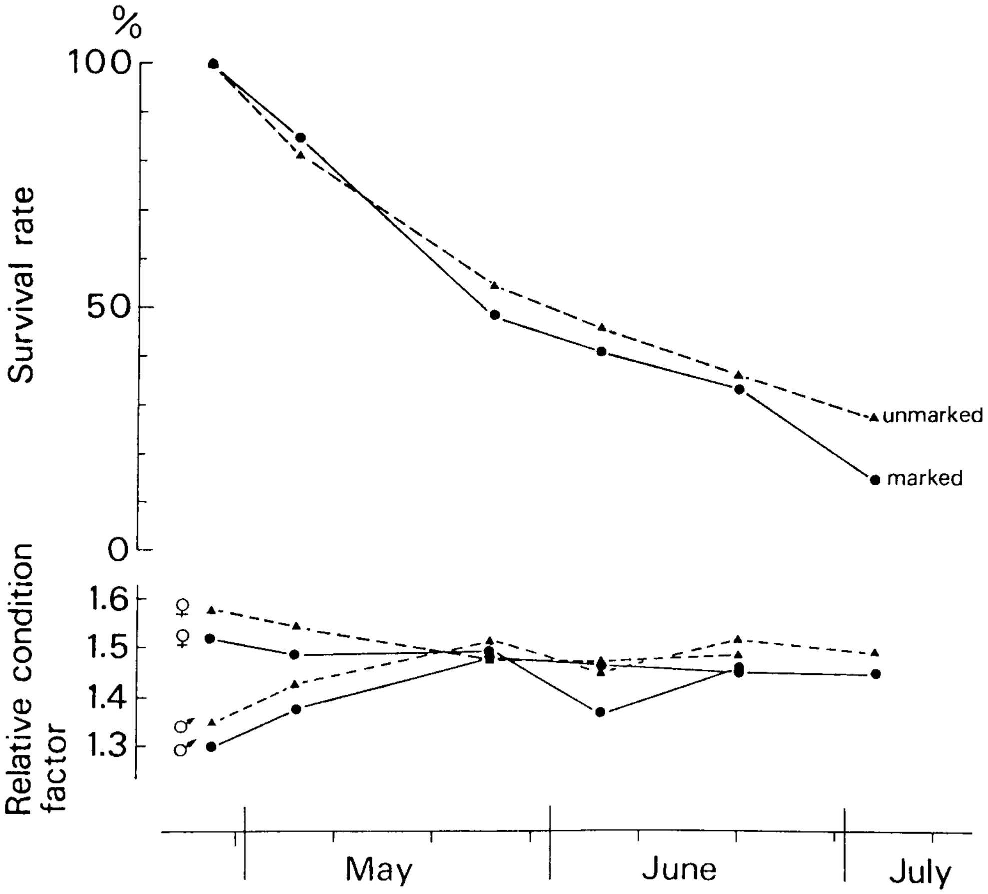


Fig. 69. The survivorship and the change of mean relative condition factor of marked and unmarked adults in outdoor cage in 1976.

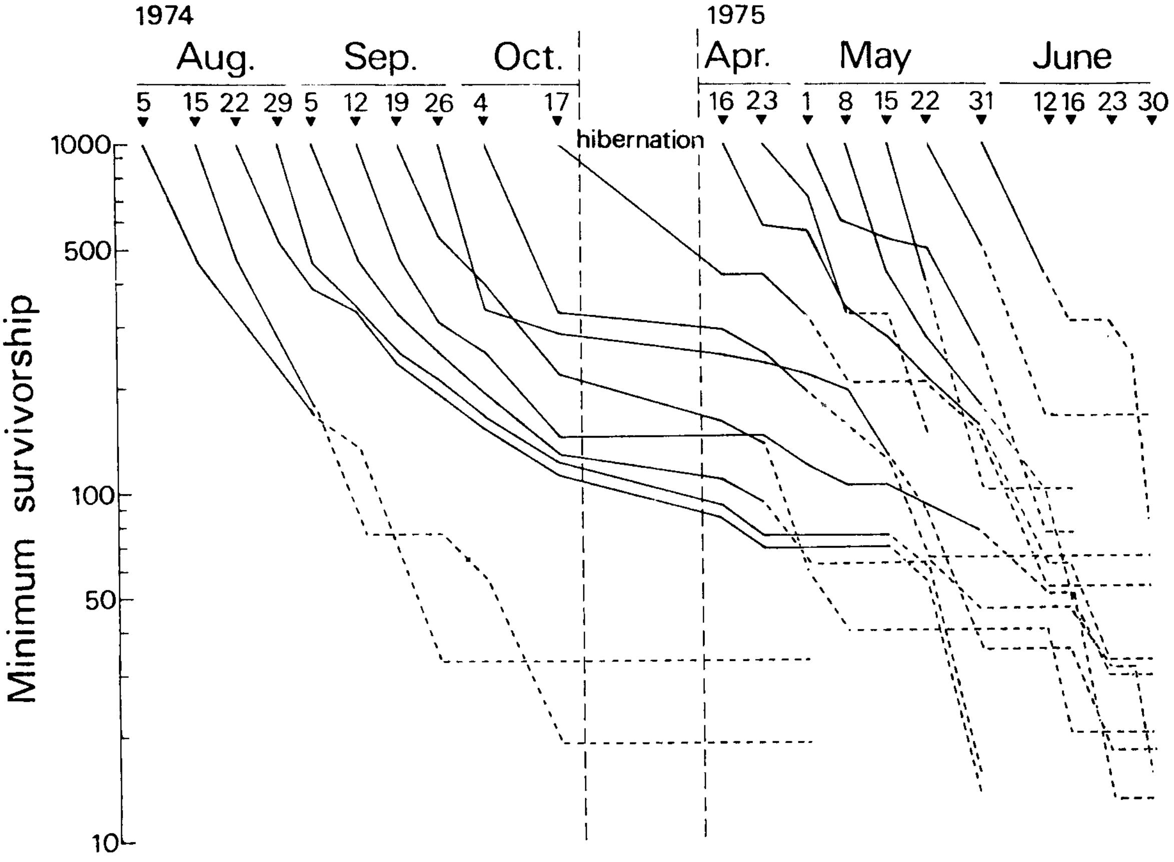


Fig. 70. The minimum survivorship of the newly captured adults at every time for the generation of 1974 in Field-I. It derived from the records of recapture after then, and converted into a ratio to 1,000 as the initial. The broken line shows the survivorship when the actual number of adults was below 5.

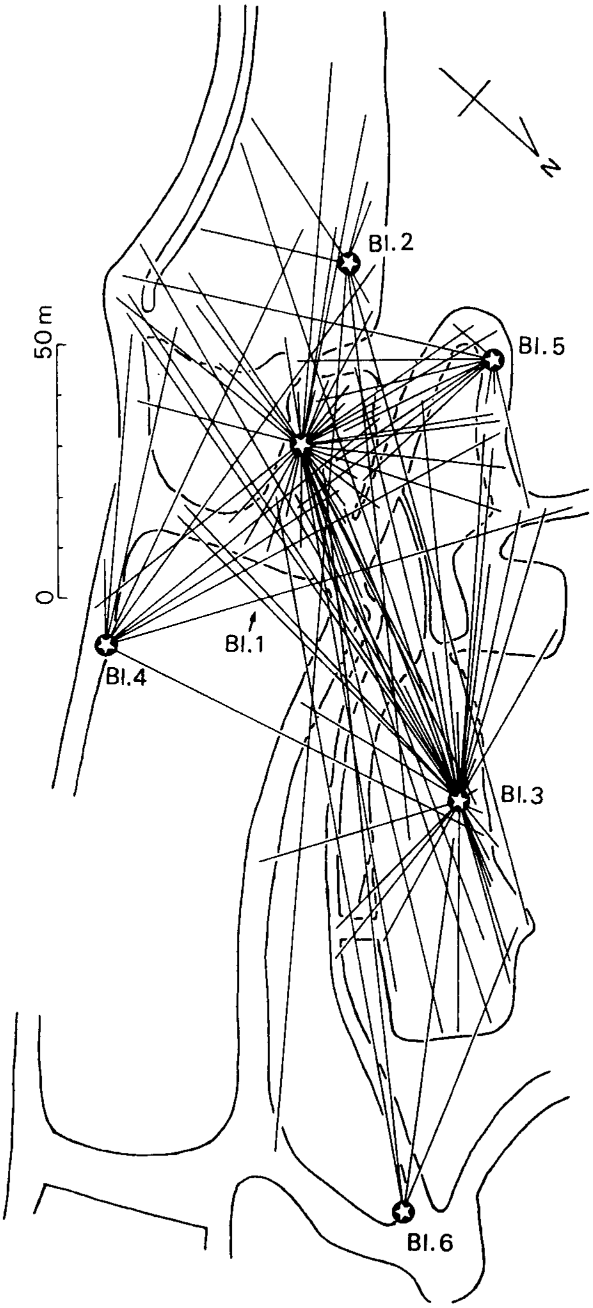


Fig. 71. The records of recature point of each adult in respect to the releasing point during overall period of the generation of 1975 in Field-I. Star shows the fixed releasing point in each block.

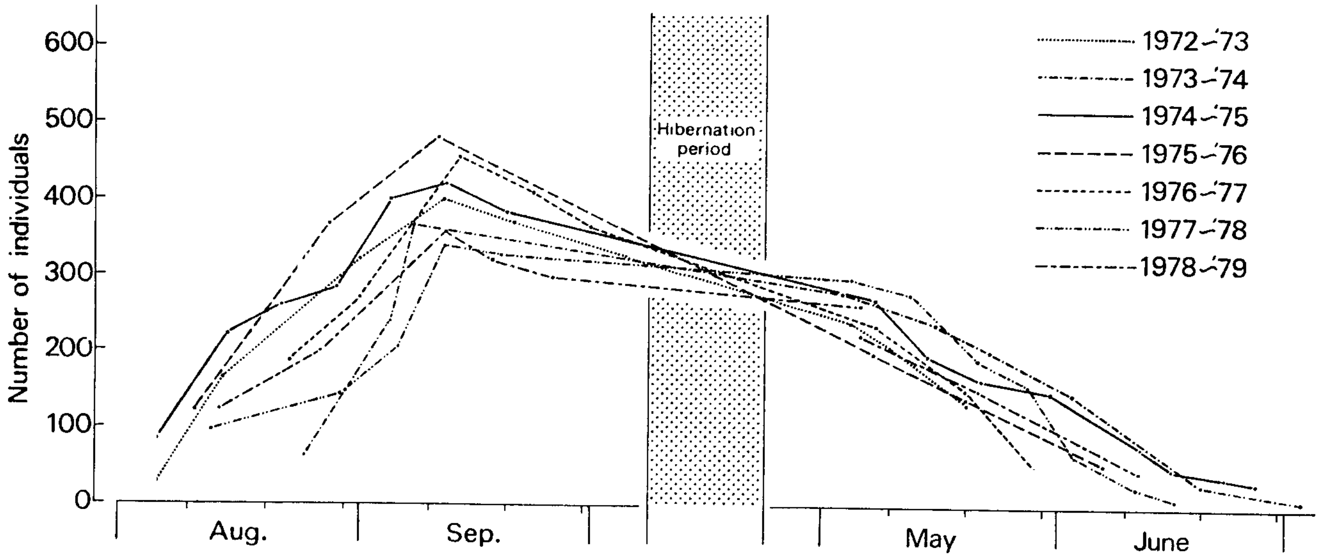


Fig. 72. Seasonal change of adult population size estimated for each generation from 1972 to 1979 in Field-I.

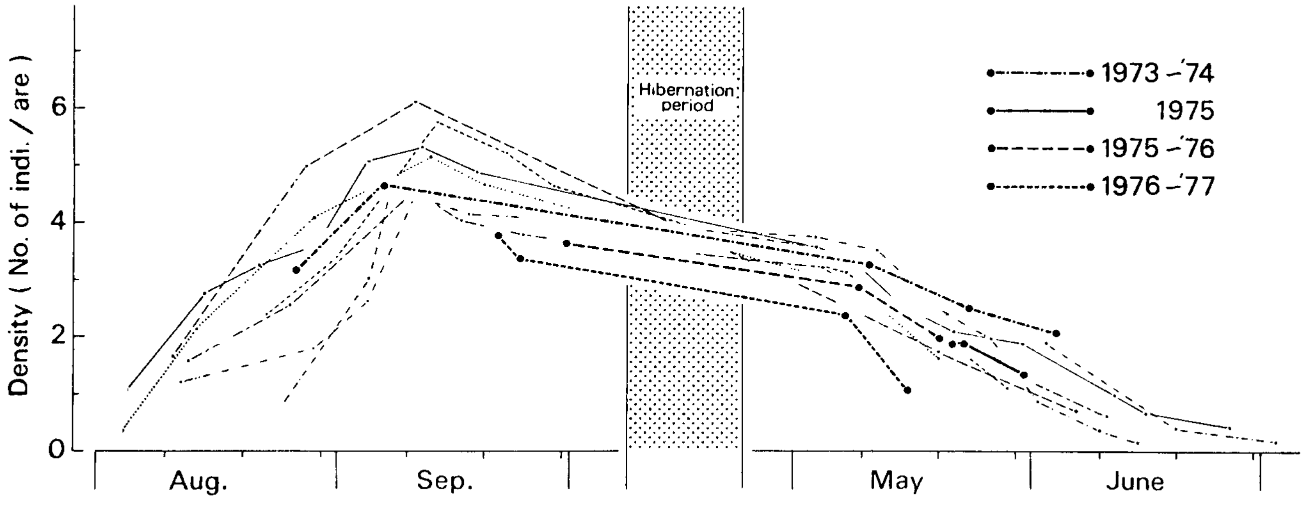


Fig. 73. Seasonal change of adult population density estimated for each generation from 1973 to 1978 in Field-II. The narrow line shows that of each generation in Field-I.

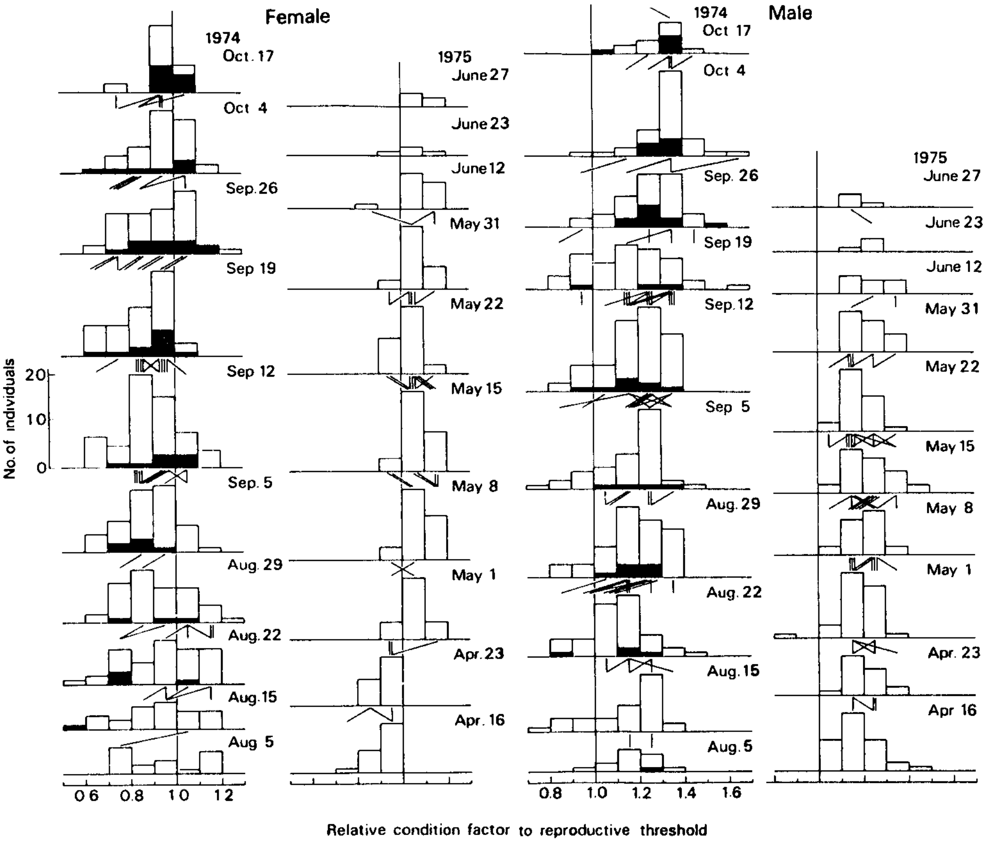


Fig. 74. Seasonal change of the frequency distribution of relative condition factor to reproductive threshold of female (left two rows) and male (right two) in generation of 1974 in Field-I. A line between two successive times shows the change of the value of an individual which was captured in both times. The solid column denotes the individuals recaptured in the following year.

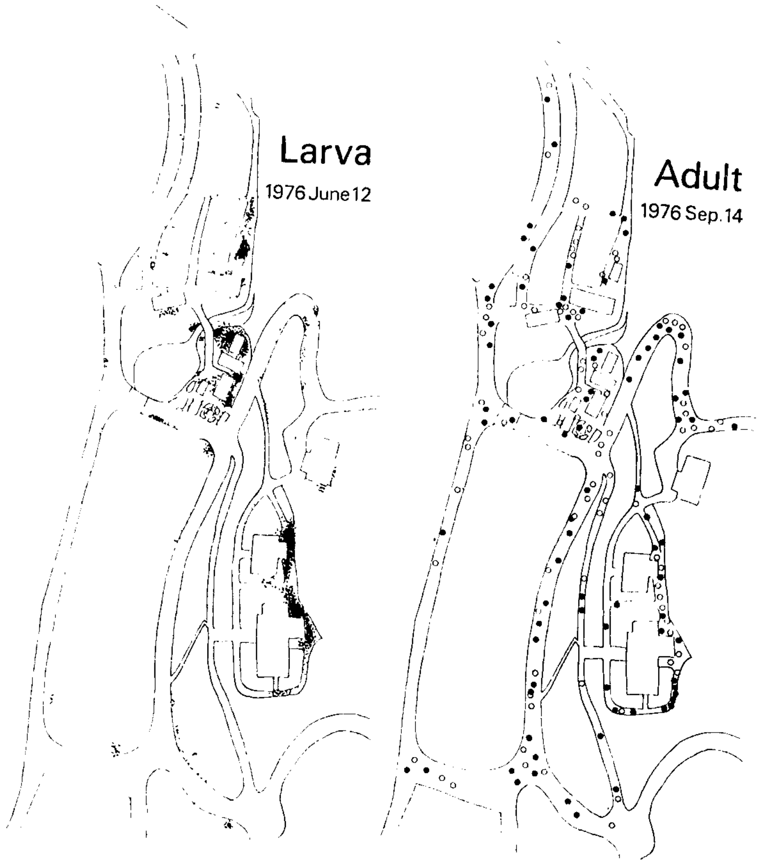


Fig. 75. An example of spatial distribution of adults and larvae in Field-I in the season of each maximum abundance. A dot in the left shows one larva observed, and a open and solid circle denote the captured point of a female and male respectively. The data for larva derived from a census which will be described in the following chapter.

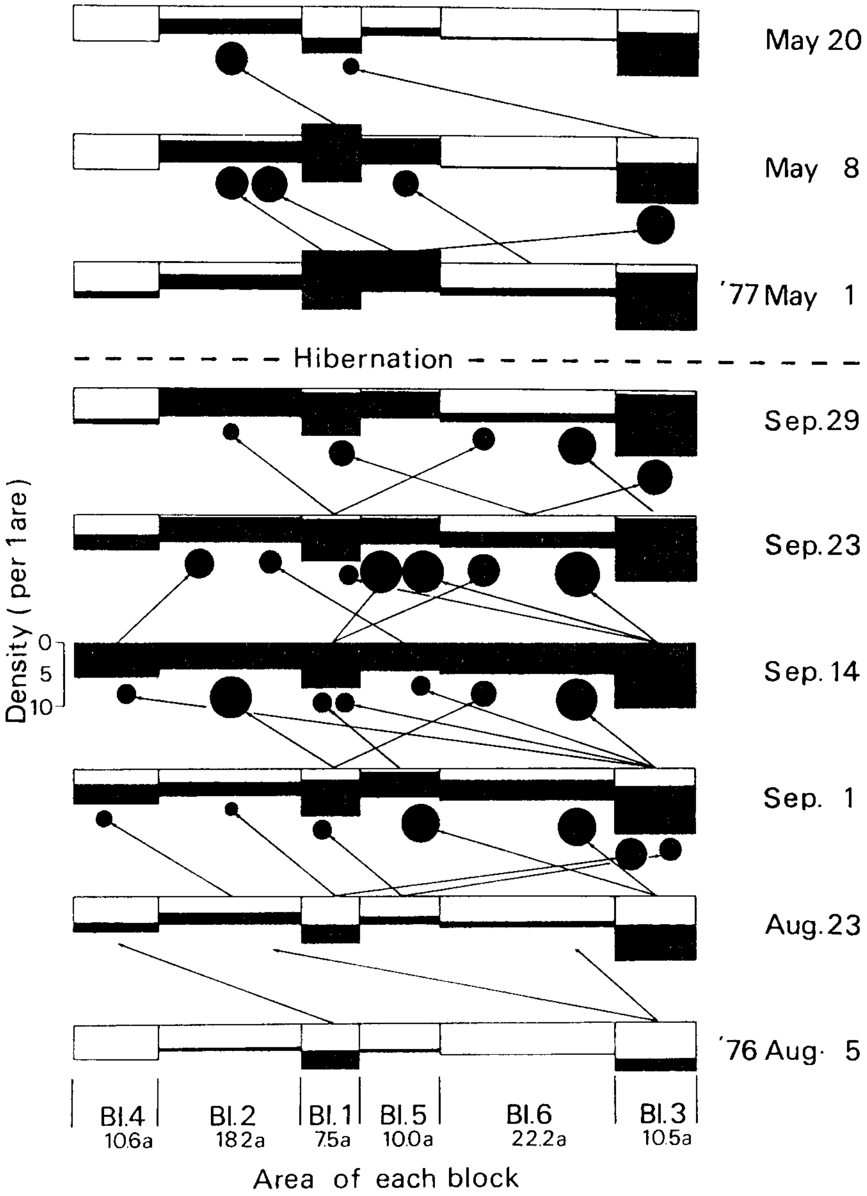


Fig. 76. The seasonal change of density in each block and interchange of adults between blocks in the generation of 1976 in Field-I. The height of solid column shows the actual density in each block at the time and the depth of whole column shows the density at the peak of population size (mid-September). The width of each column is proportional to the area of each block. The area of solid circle shows the estimated number of adults interchanged between the two blocks during the two successive times, and its scale is equivalent to the area of solid column which represents the number of adults in each block.

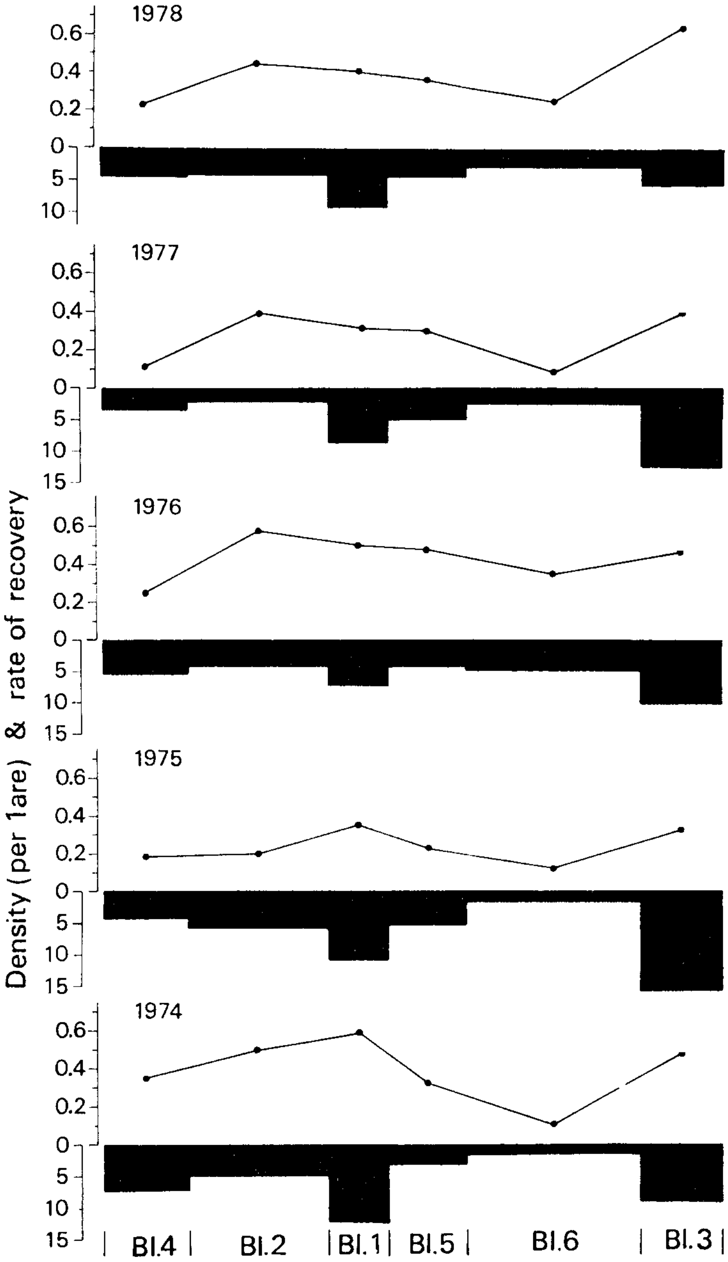


Fig. 77. The density in each block at the peak of population size and the rate of recovery for every generation from 1974 to 1979 in Field-I. The latter derived from the records of recapture after then till extinction of the generation within the overall area regardless of their releasing point.

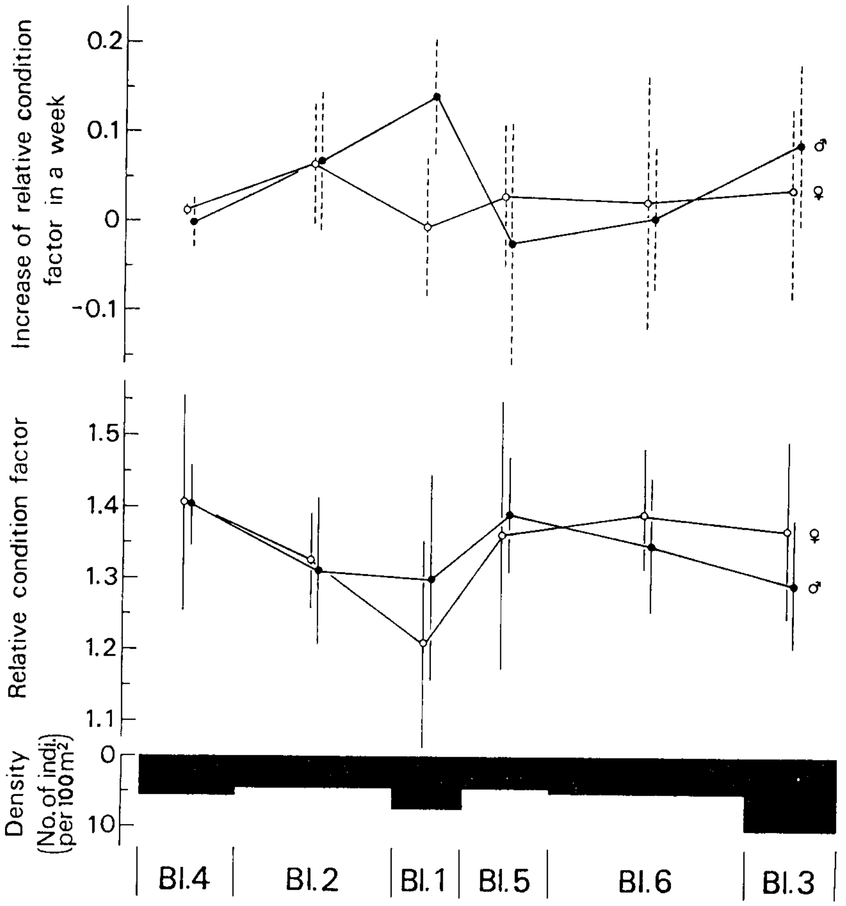


Fig. 78. The density at the peak of population size, the mean relative condition factor and amount of increase of relative condition factor in a week around the period in each block for the generation of 1976 in Field-I. The vertical solid and broken bar denote the 95 % fiducial limit of mean and standard deviation respectively.

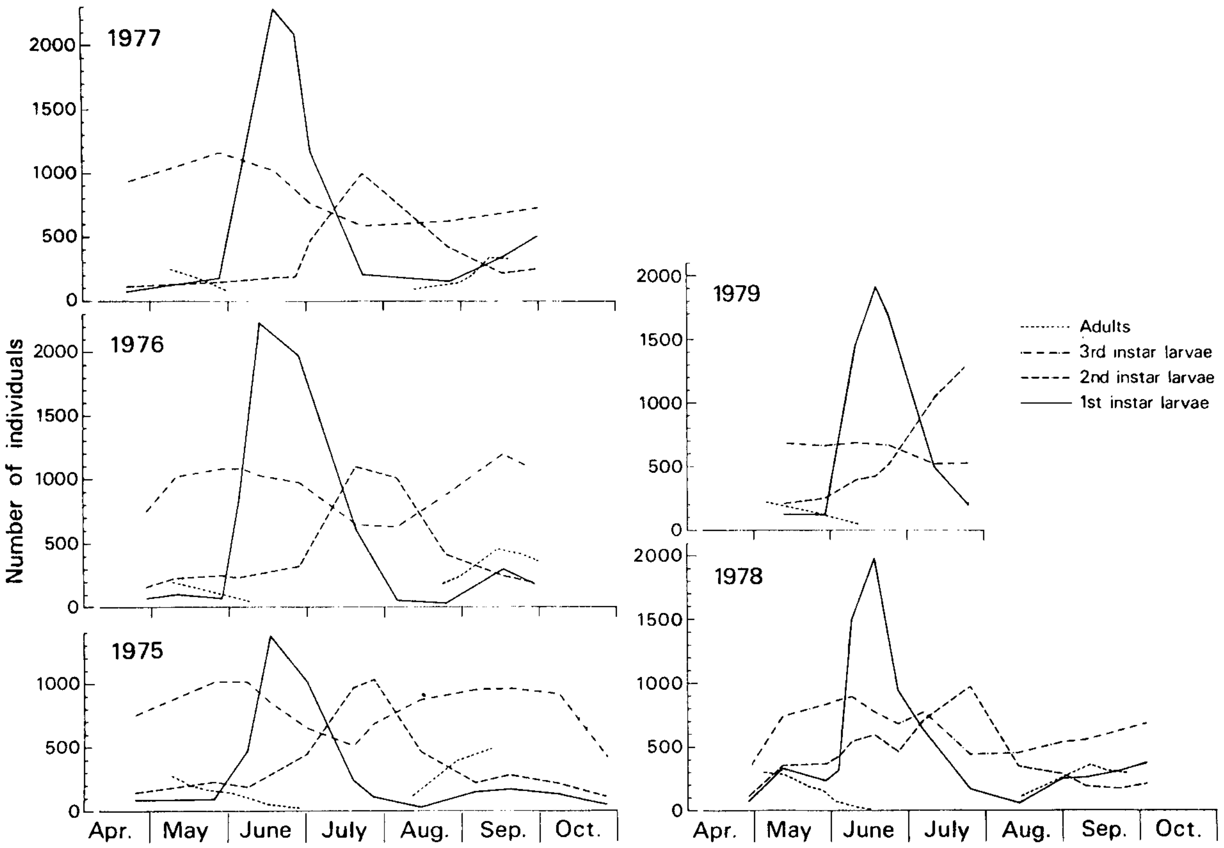


Fig. 79. Seasonal change of larval population size of each instar estimated in Field-I from 1975 to 1979. The seasonal change of adult population size is also drawn.

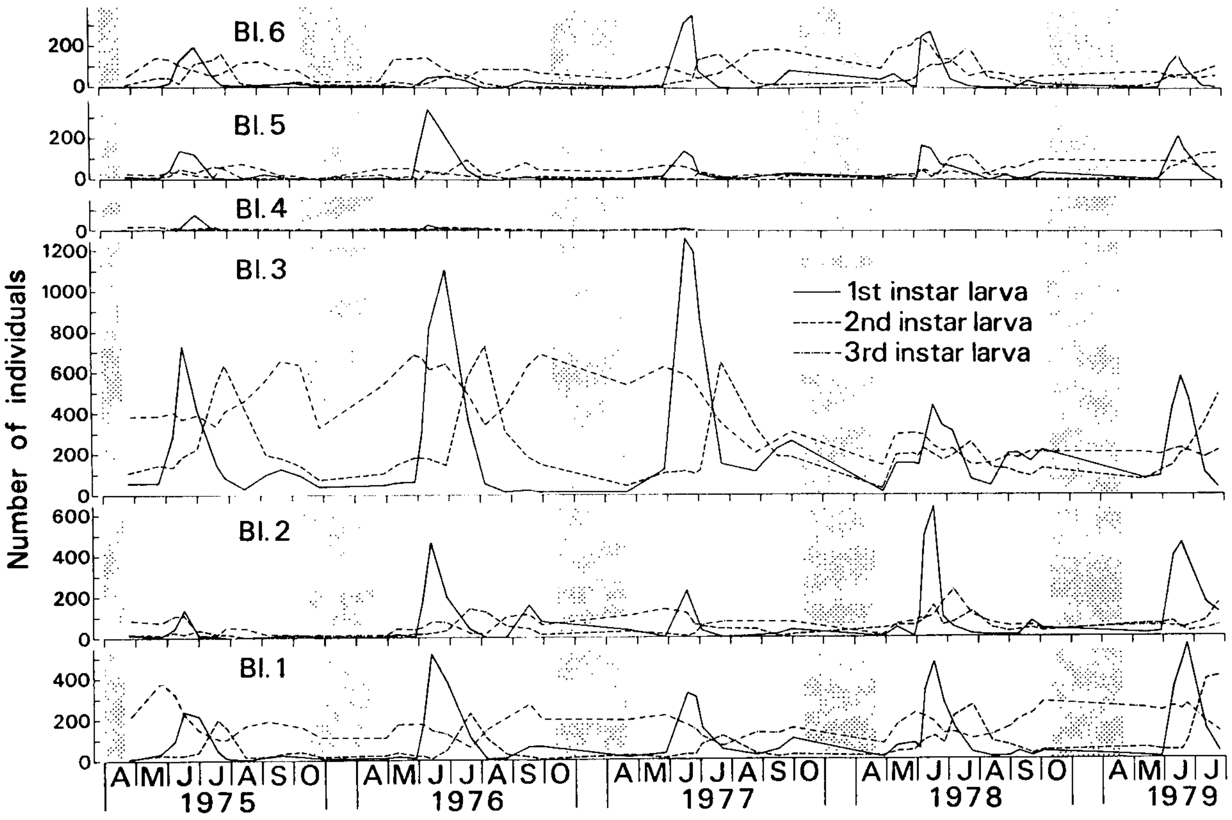


Fig. 80. Seasonal change of larval population size of each instar estimated in each block in Field-I from 1975 to 1979.

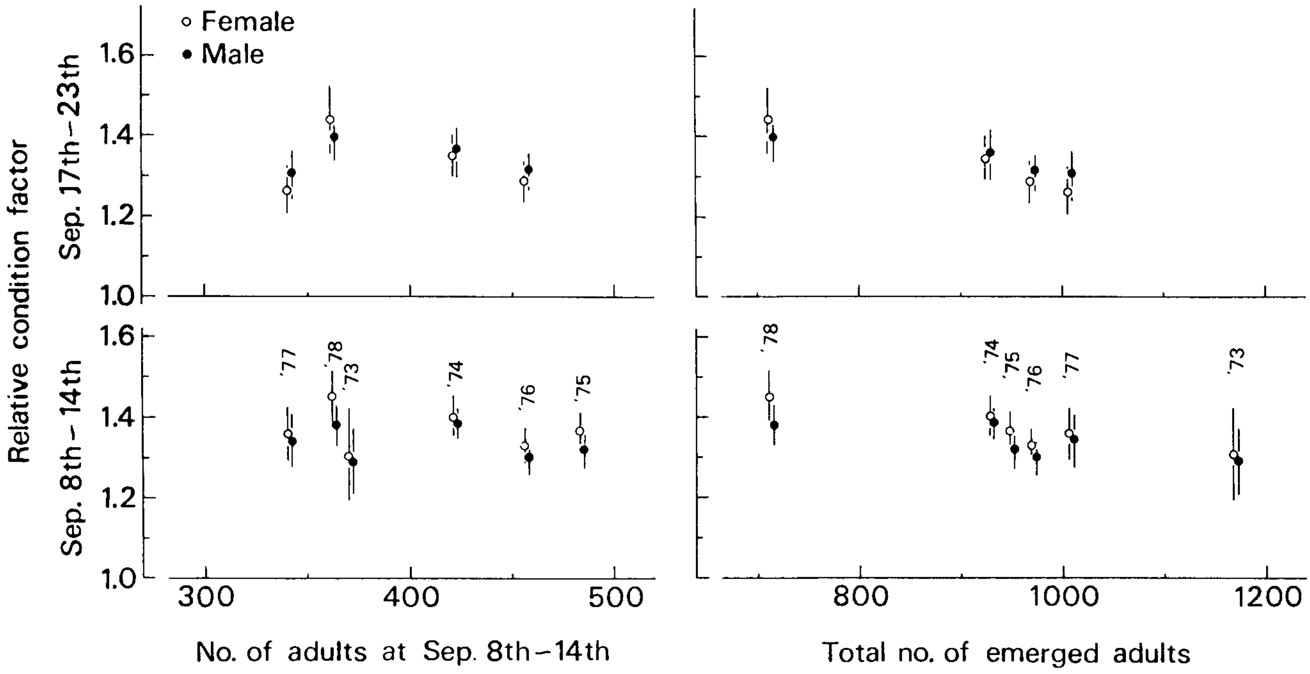


Fig. 81. The relation between maximum population size of adult (left) or total number of emerged adults (right) and the relative condition factor of each sex in two periods in autumn from 1973 to 1978 in Field-I. The vertical bar shows 95 % fiducial limit of mean.

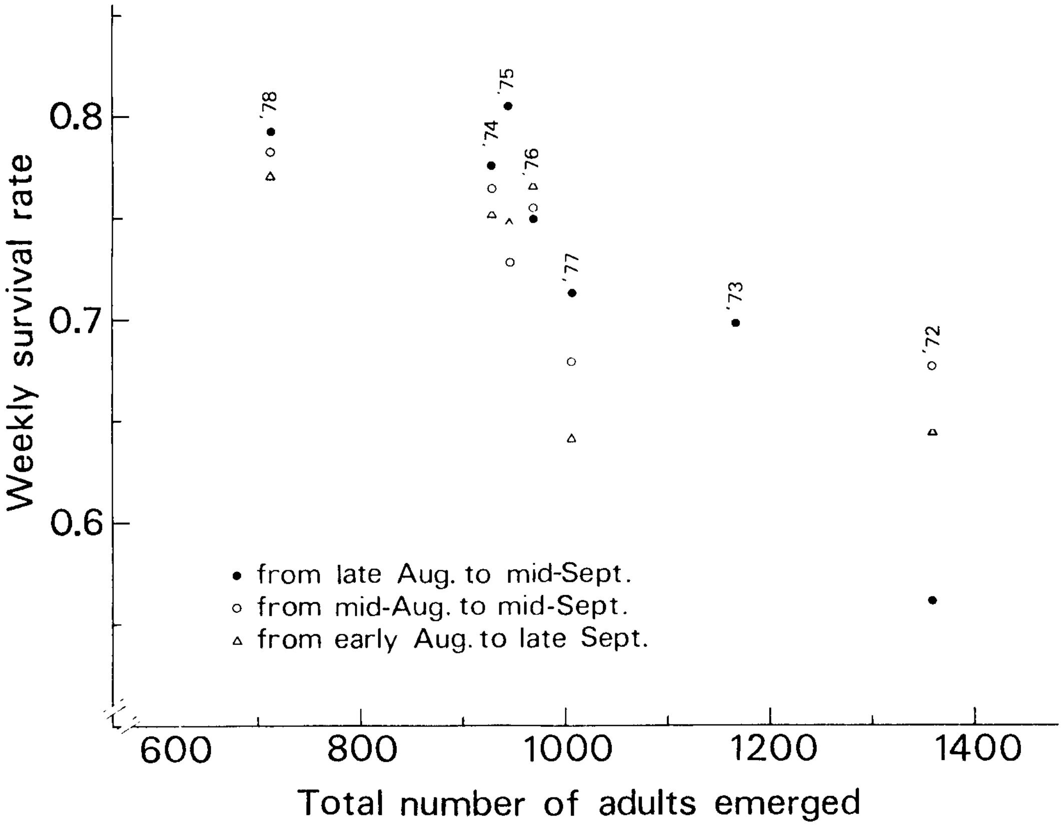


Fig. 82. The relation between total number of adults and weekly survival rate estimated for various periods in autumn from 1972 to 1978 in Field-I.

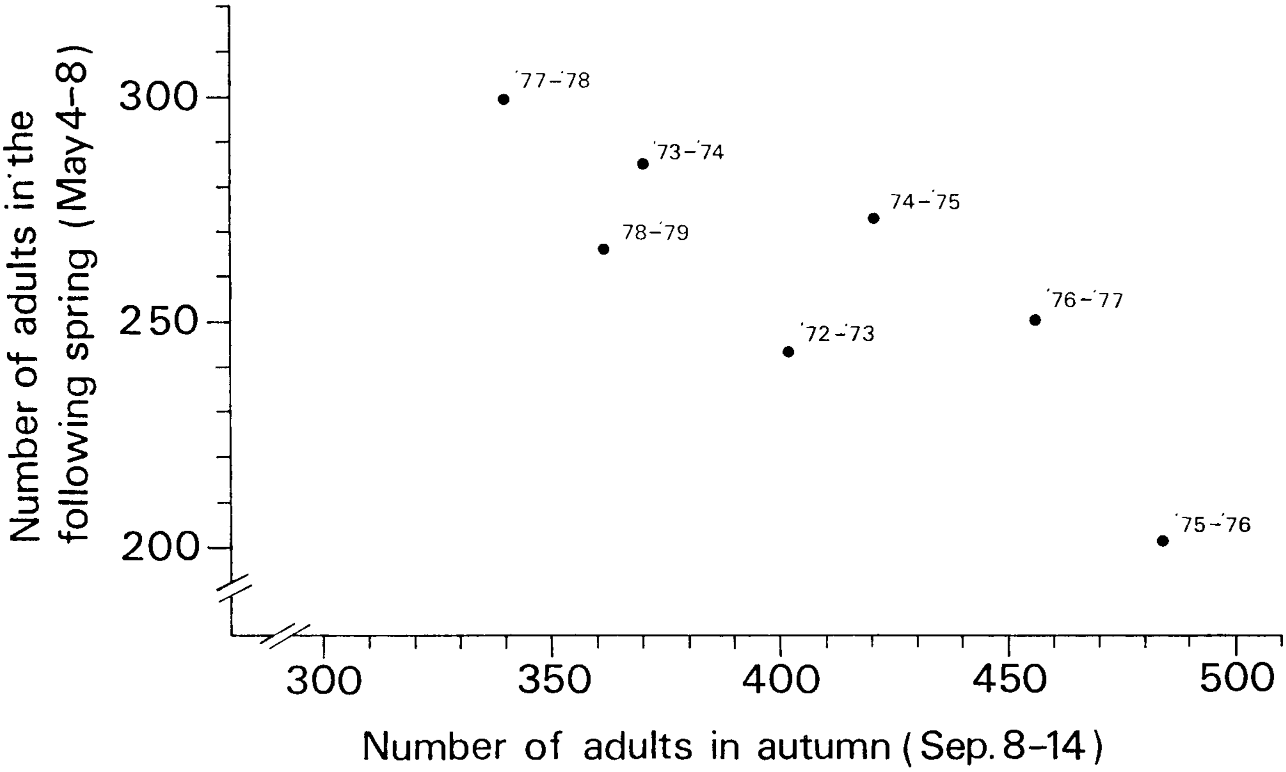


Fig. 83. The relation between adult population size at peak in autumn and that at beginning of reproductive period in the following year from 1972 to 1979 in Field-I.

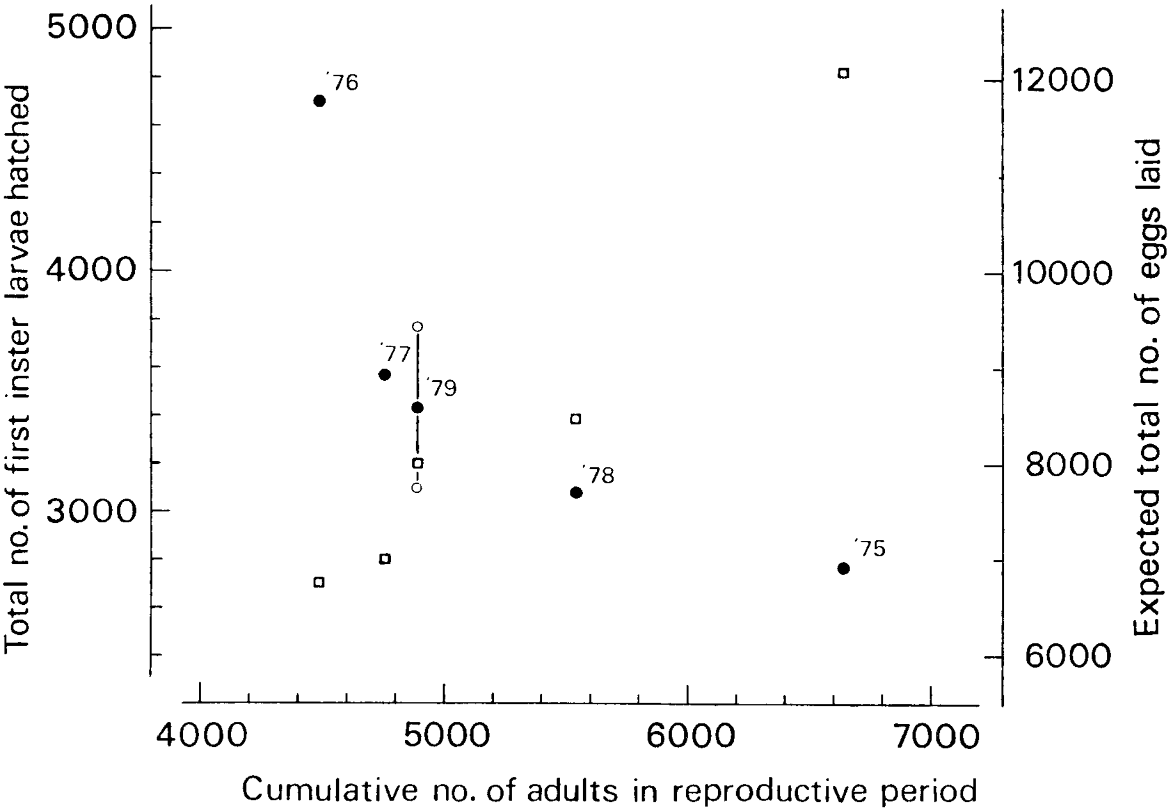


Fig. 84. The relation between cumulative number of adults in reproductive period and total number of larvae hatched (circle) or expected total number of eggs laid (square) during the period in Field-I from 1975 to 1979. In 1979 the total number of hatched larvae was estimated with the survival period of the instar averaged for 4 years (solid circle) or with that of the longest year (1977) and the shortest year (1975) (open circle).

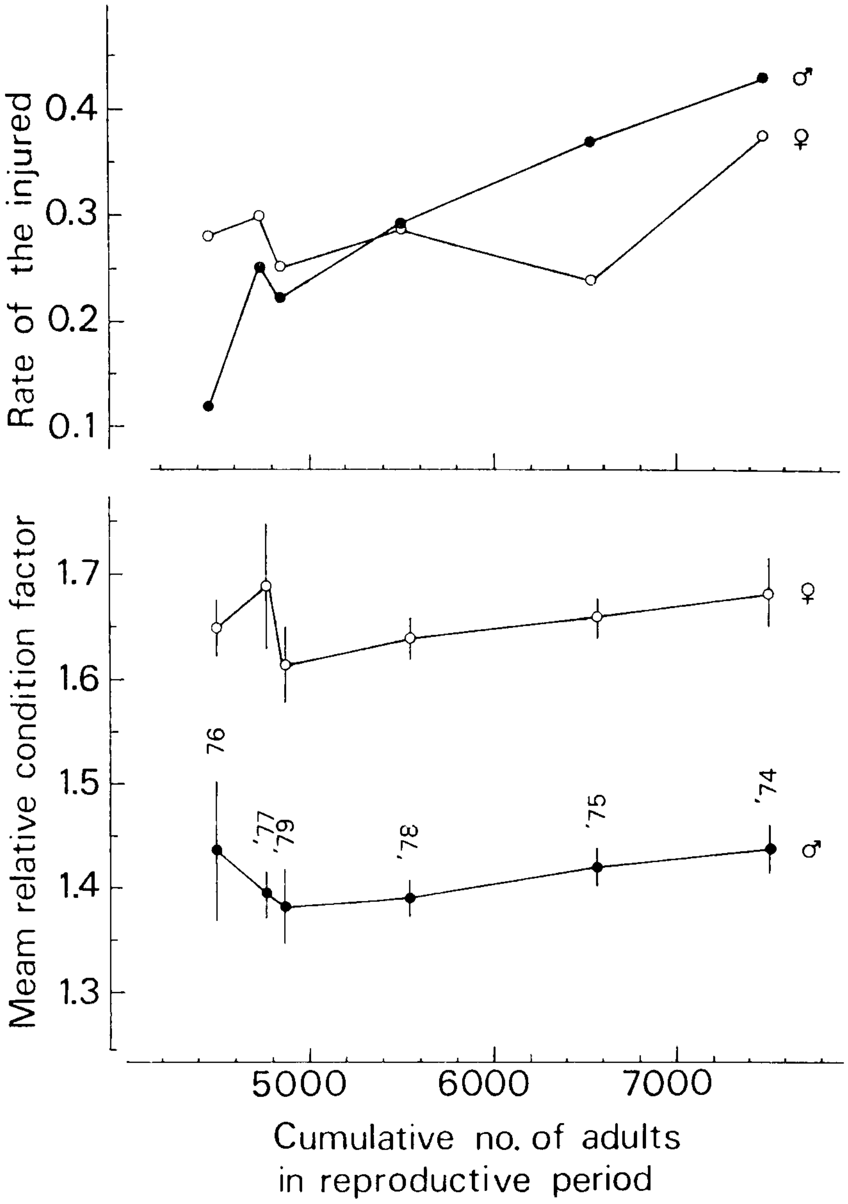


Fig. 85. The relation between cumulative number of adults in reproductive period and mean relative condition factor or rate of the injured in each popultion in early summer in field-I, 1974-1979. The vertical bar shows the 95 % fiducial limit of mean.

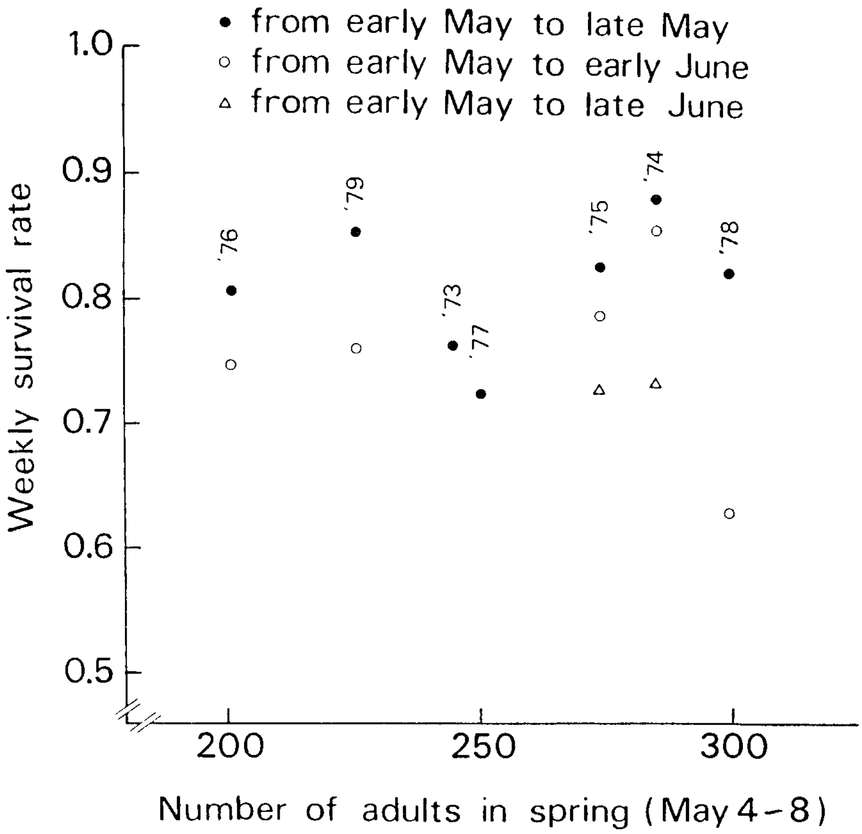


Fig. 86. The relation between number of adults at the beginning of reproductive period and weekly survival rate estimated for various periods in Field-I, 1973-1979.

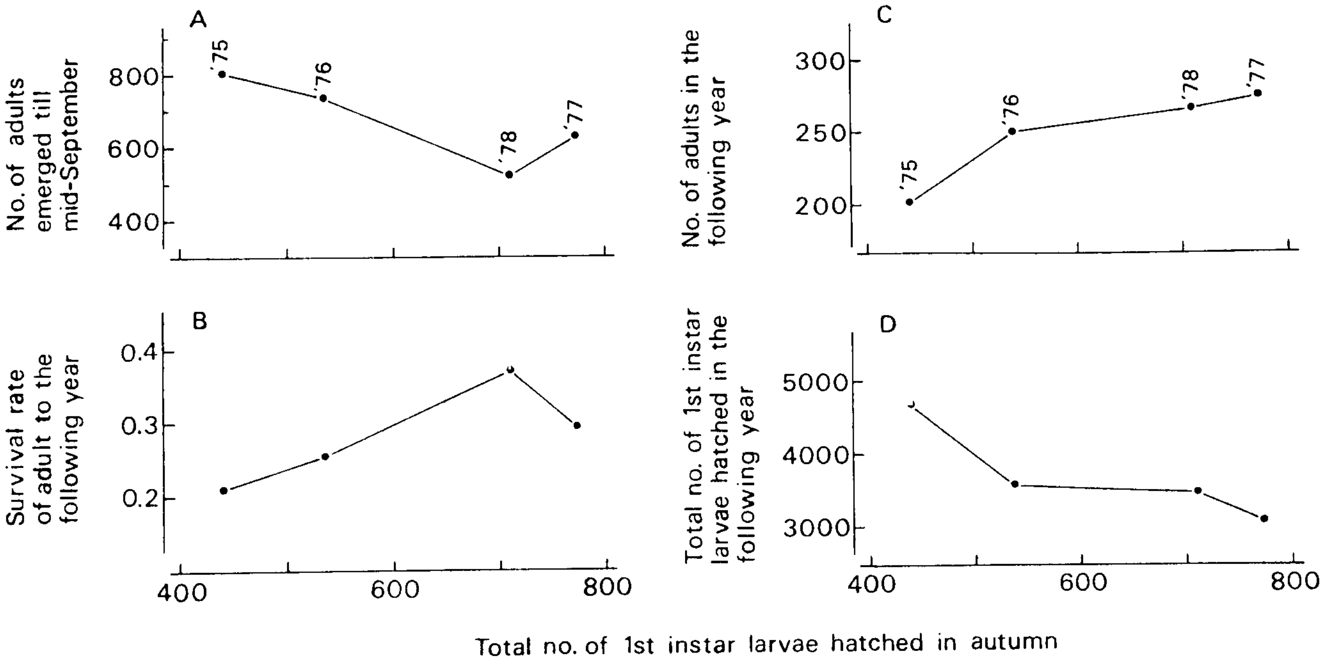


Fig. 87. The relation between total number of larvae hatched in autumn and number of adults emerged till mid-September (A), survivial rate of adult from emergence to the following year (B), number of adults at the beginning of reproductive period in the following year (C), or total number of larvae hatched in the following early summer in Field-I, 1975-1979.

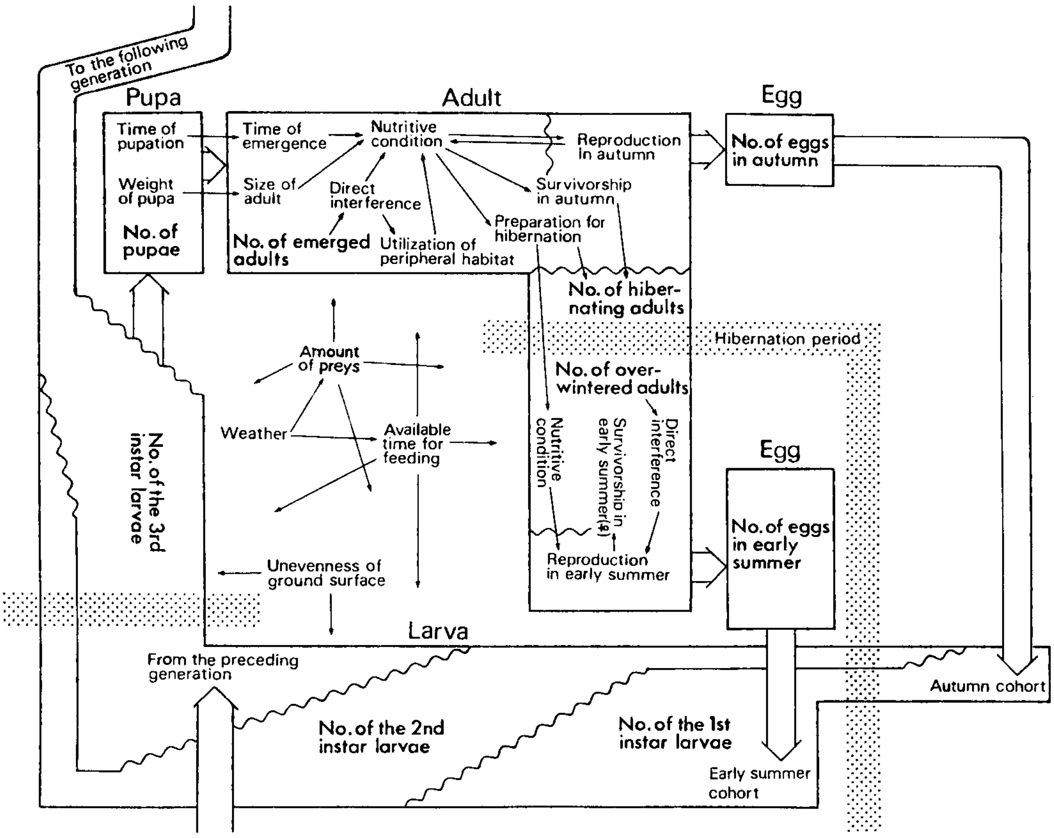


Fig. 88. Schematic diagram showing the relations among population processes and factors in the course of life cycle of *C. japonica*. The arrow means that the process or factor affects another directly of inversely. The wavy line means a threshold present between two successive stages or processes.

Table 1. The conditions of 7 main and 3 subsidiary stations for census of larvae and surveyed period.

Station	Area(m^2)	Vegetation	Wetness	Period of survey
St. A	38.6	bare but partly mossy	dry	1972-'78
B	2.6	slightly grassy	dry	1974-'78
C	25.9	densely grassy	much wet	1974-'78
D	20.4	slightly grassy	wet	1974-'78
E	36.2	bare	much dry	1974-'78
F	27.0	slightly grassy	dry	1974-'78
G	26.5	bare but partly mossy	dry	1975-'78
St. H	28.3	slightly grassy	dry	1975-'77
I	30.5	bare	much dry	1975-'77
J	15.0	lawn	wet	1975-'77

Table 3. The predators on adult tiger beetles observed in Field-I from 1972 to 1978.

	No.	Month
Araneae		
Neoscona scylla	1	May
Nephila clavata	1	Jun.
Therididion tepidariorum	1	Jun.
Argiope bruennichii	1	Sep.
Insecta		
Asilid fly		
Promachus yesonicus	2	Jun., Aug.
other Asilid fly	1	Jul.
Dragonfly		
Anax parthenope	1	Sep.
Mantid		
Paratenodera angustipennis	1	Sep.
Mammalia		
weasel		
Mustela sp. (in droppings)	7	May, Jun., Jul.
Aves		
shrike		
Lanius sp. (in pellet)	2	Sep.

Table 2. Reaction of larva to various-sized dummy of prey.

Reactions of larvae at presentation of dummy (ball of lead) were classified into four categories as follows: i) jumped at dummy and tried to pull it into durrow; ii) repelled dummy with mandibles but did not show any sign of pulling into; iii) retired to bottom quickly; iv) did not react for first severl seconds.

		Size of dummy (diameter in mm)	2.3	3.0	3.8	4.5	5.8	6.4	7.2	8.4	11.2	14.5
1st instar		No. of larvae tested	9	13	16	9	11	10	8	11	12	8
	Reaction	i	6	9	3	2	0	0	0	0	0	0
		(%)	(66.7)	(69.2)	(18.9)	(22.2)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
		ii	0	0	3	5	2	1	1	0	0	0
		iii	2	3	3	1	3	3	3	9	12	8
		iv	1	1	7	1	6	6	4	2	0	0
2nd instar		No. of larvae tested	11	12	14	10	10	14	11	6	6	9
	Reaction	i	11	12	14	10	10	10	4	0	0	0
		(%)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(71.4)	(36.4)	(0.0)	(0.0)	(0.0)
		ii	0	0	0	0	0	1	1	1	1	0
		iii	0	0	0	0	0	2	5	5	5	9
		iv	0	0	0	0	0	1	1	0	0	0
3rd instar		No. of larvae tested	11	10	10	10	13	13	18	13	9	10
	Reaction	i	11	10	9	10	12	12	16	1	1	0
		(%)	(100.0)	(100.0)	(90.0)	(100.0)	(92.3)	(92.3)	(88.8)	(7.7)	(11.1)	(0.0)
		ii	0	0	0	0	0	0	0	4	0	0
		iii	0	0	1	0	1	1	2	8	8	10
		iv	0	0	0	0	0	0	0	0	0	0

Table 4. The number of carcases of adult collected in Field-I from 1972 to 1978.

		Aug.	Sep.	Oct.	Apr.	May	June	July
Category	I	2	4	13	3	6	6	
	II	3	9	4	8	13	23	4
	III		1		2	2	1	
A) Total		5	14	17	13	21	30	4
B) No. of working times		20	20	11	8	22	16	4
A/B		0.25	0.70	1.55	1.63	0.95	1.88	1.00

- Category I; fresh carcase with no wound, II; carcase separated into several parts or with some wound, III; crushed carcase probably by accident.

Table 5. The number of female wasps, Methoca yasumatsui, observed in Field-I from 1973 to 1978.

		Apr.			May			June			July			Aug.			Sep.			Oct.	
		E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M
Size	Small									2	3	3	3	1	4						
	Middle						1	19	8	6	4	3	4	2	5	7	1	1	1		
	Large						1	3	3	5	2	2	1	5	5	1	1		2		
A)	Total						2	22	11	13	9	8	8	8	14	8	2	1	3		
B)	No. of working times	2	5	7	9	12	19	27	20	17	15	14	11	11	12	17	13	11	10	7	5
	A/B x 100						11	81	55	76	60	57	73	73	117	47	15	9	30		

Table 6. Summary for the methods of larval rearings in laboratory

Summer-I rearing (three series in different periods)

Period: June, 1973- Aug., 1975

Prey: Drosophila (for the 1st instar of Series A)
Tribolium (for the others)

Frequency of prey supply: twice / a week

Series A

Start of rearing: the 1st instar larvae just after hatched, at 7th, 17th, and 27th of June, 1973, derived from rearing of adult.

Division	a	b	c	d	e	f	g	h	i	
No. of preys	1	2	3	4	5	6	7*	8*	10*	
No. of indi. reared	7	7	7	4	4	4	4	4	8	total: 49

* In Division g, h, and i, after the 3rd instar, the half of larvae were supplied with about twice as many preys as in the 1st and 2nd instar.

Series B

Start of rearing: the 2nd instar, 10th of Aug., 1973, derived from the rearing of adult, but grown outdoors till the time.

Division	j	k	l	m	
No. of preys	1	5	10	20	
No. of indi. reared	6	6	6	6	total: 24

Series C

Start of rearing: the 2nd and 3rd instar, 25th of Apr., 1975, derived from the rearing of adult, but grown outdoors till the time.

Division	n	o	p	q	r	s	t	u	v	w	
Instar	2nd						3rd				
No. of preys	1	2	5	10	15	20	1	5	10	20	
No. of indi. reared	4	2	4	4	2	2	2	2	1	1	total: 24

Table 6. (Continued)

Summer-II rearing

Period: July, 1976-Nov., 1977

Prey: <u>Tribolium</u>

Frequency of prey supply: once / 4 to 7 days (average 5.5 days)

Start of rearing: the 1st instar larvae just after hatched, at 14th of July, derived from rearing of one pair of adults.

Division		a	a′	a″	b	b′	b″	c	c′	c″	
No. of preys	for 1st inst.	1	1	1	3	3	3	6	6	6	
	for 2nd inst.	1	2	2	3	6	6	6	12	12	
	for 3rd inst.	1	2	4	3	6	12	6	12	24	
No. of indi. reared		5	5	10	5	5	10	5	5	10	total: 60

Autumn rearing

Period: Sep., 1974- Aug., 1975

Prey: <u>Tribolium</u>

Frequency of prey supplied: once / 3 to 7 days (average 4.9 days)

Start of rearing: the 1st instar larvae just hatched, at 9th of Sep., derived from rearing of one pair of adult.

Division	a	b	c	d	
No. of preys	1	5	10	20	
No. of indi. reared	10	10	8	5	total: 33

Table 7. The results of Outdoor experiment-I.

Division	Instar at start	No. of individuals				Weight of pupa (mg)	Increase of weight by pupa (mg)	Weight of adult (mg)	Increase of weight by adult (mg)	Width of elytra		Date of emergence	
		At start of rearing	Survivors to matured larva	Survivors to pupate	Survivors to emerge					female (mm)	male (mm)	female	male
a	2nd inst.	8	7	7	7	241.3 (289.1 200.5	204.6 (240.0 166.8	203.1 (245.3 179.6	166.4 (213.7 138.5	6.45 (6.70 6.35	6.06 (6.10 6.00	Sep.02 (Aug.26 Sep.08	Aug.25 (Aug.14 Sep.04
	3rd inst.	8	7	5	5	-	-	218.9 (249.0 189.8	98.5 (146.5 64.0	6.45 (6.60 6.30	6.15 (6.20 6.05	July28 (July23 Aug.01	July26 (July25 July29
b	2nd inst.	8	6	6	4	242.1 (257.1 221.1	202.7 (224.6 187.5	200.3 (239.8 176.5	160.9 (188.3 136.5	6.45 (6.40 6.50	6.00	Aug.26 (Aug.24 Aug.28	Aug.18 (Aug.16 Aug.19
	3rd inst.	8	6	4	4	-	-	218.0 (231.0 201.1	59.3 (66.5 49.8	6.50	6.13 (6.20 6.10	July25	July24 (July23 July25
c	2nd inst.	8	7	7	7	290.0 (294.7 285.3	246.5 (252.2 240.7	228.0 (260.1 185.6	191.6 (223.6 146.4	6.60 (6.70 6.45	6.30 (6.40 6.25	Aug.16 (Aug.10 Aug.26	Aug.17 (Aug.12 Aug.26
	3rd inst.	8	7	4	4	-	-	271.5 (290.9 255.1	116.9 (141.4 88.7	6.78 (6.85 6.70	6.45	July22 (July21 July23	July19 (July15 July23

Table 8. The number of days druing the entrance of burrow is closed, and that of the divided three stages.

The data derive from the laboratory and outdoor rearing.

Sex	Number of individuals observed	Total period of entrance closed		Period of matured larva		Period of pupa		Period of emerged adult	
		mean	range	mean	range	mean	range	mean	range
female	10	32.6	26.0 41.5	12.3	9.0 27.5	15.4	12.0 19.5	4.4	2.5 5.5
male	8	36.9	29.5 46.0	13.9	12.0 17.5	17.0	12.0 21.5	6.0	4.0 9.5

Table 9. The frequency of width of ovary in each Stage judged

Stage	Width of ovary (mm)																									
	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8
IV																				1			1	1	1	3
III							2	3	2	5	1	1		1		1		1								
II				2	5	10	4																			
I		4	4	3	1																					

Table 10. Summary of adult rearings

Rearing-I (for both sexes, from August to October)

Food supply; every 2 days.

Measurment of weight and sorting of egg; every about 10 days.

Derivation of adults; larval rearing, emergence trap in field, and collection from field.

	Female					Male				
Division	a	b	c	d	e	a	b	c	d	e
No. of preys supplied	1	2	3	5	10	1	2	3	5	10
No. of adults reared	5	5	5	7	7	2	2	2	2	2
			Total 29					Total 10		

Rearing-II (for female, from May to July 1975) &

Rearing-III (for male, from May to July 1976)

Food supply; every 3 days.

Measurment of weight and sorting of egg; every 3 days.

Derivation of adults; collection from field.

	Rearing-II (Female)			Rearing-III (Male)		
Division	a	b	c	a	b	c
No. of preys supplied	1	3	6	1	3	6
No. of adults reared	9	9	9	6	5	5
	Total 27			Total 16		

Rearing-IV (for female, from August, 1975 to July, 1976)

Indoors; Augst 1975 - October 1975.

Outdoors; October 1975 - April 1976.

Indoors; April 1976 - July 1976.

Food supply; every 3 days.

Measurment of weight and sorting of egg; every 3 days.

Derivation of adult; larval rearing and emergence trap in field.

Table 10. (continued)

	Female	
Division	a	b
No. of preys supplied	1	3
No. of adults reared	17	7
	Total 24	

Rearing-V (for female, from September 1976 to April 1977)

Indoors; September 1976 - October 1976.

Outdoors; October 1976 - April 1977.

Food supply; every 3 days.

Measurment of weight and sorting of egg; every 3 days.

Derivation of adults; emergence trap and collection from field.

	Female		
Division	a	b	c
No. of preys supplied	1	3	6
No. of adults reared	11	11	11
	Total 33		

Table 11. Summary of results from the rearing of females (Rearing-IV & -V).

A) Relationship between Rcf to Hst and the survival to the following year.

		Till the following year		
		survived	dead	
In autumn	Rcf to Hst $\geqq 1$	31(13+18)	8(4+4)	39
	Rcf to Hst < 1	2(1+1)	11(2+9)	13
		33	19	52

B) Relationship between the oviposition in autumn and the survival to the following year.

		Till the following year		
		survived	dead	
In autumn	Oviposit	6(2+4)	4(1+4)	10
	Not oviposit	27(12+15)	15(5+10)	42
		33	19	52

C) Relationship between the oviposition in two seasons (Rearing-V).

		In the following year		
		oviposit	not oviposit	
In autumn	Oviposit	2	0	2
	Not oviposit	8	3	11
		10	3	13

* The two numerals in parentheses show the number of individuals concerned in Rearing-IV and -V respectively.

Table 12. Relationship between number of preys taken and survival of 2nd and 1st instar larvae.

	2nd instar			1st instar			
No. of preys taken	0	1-2	3-4	0	1-2	3-4	5≦
No. of larvae in the instar observed	201	38	7	136	38	17	3
No. of the dead in the instar	84	12	2	94	24	6	1
(%)	(41.8)	(31.6)	(28.6)	(69.1)	(63.2)	(35.3)	(33.3)
No. of the larvae prolonged the stage to the next year	8	3	0	0	0	0	0
(%)	(4.0)	(7.9)					
No. of the larvae grew up into the next stage	109	23	5	42	14	11	2
(%)	(54.2)	(60.5)	(71.4)	(30.9)	(36.8)	(64.7)	(66.7)

Table 13. Relationship between number of preys taken and the fate of 3rd instar larvae after then.

No. of preys taken			0	1-2	3-4	5-6	7-8	9≤
No. of 3rd instar larvae observed			24	50	33	17	17	15
Fate	plolonged the stage (%)		8 (33.3)	5 (10.0)	3 (9.1)	0	0	0
	died in pupa (%)		10 (41.7)	19 (38.0)	12 (36.4)	5 (29.4)	5 (29.4)	5 (33.3)
	emerged in adult (%)		6 (25.0)	26 (52.0)	18 (54.5)	12 (70.6)	12 (70.6)	10 (66.7)
Rate of emergence (adults/pupae)			.375	.578	.600	.706	.706	.667
Mean emergence time (no. of days from 1st of August)		♀	39.6	29.7	31.2	33.3	27.4	27.2
		♂	38.9	38.3	35.5	23.8	24.3	14.7
Mean size of adult (width of elytra in mm)		♀	6.31	6.41	6.58	6.56	6.72	6.52
		♂	6.20	6.10	6.28	6.29	6.13	6.32

Table 14. The number of preys taken by a larva of the 3rd instar at each density and the survival to the adult stage in St. G in September 1975.

The density was evaluated with the number of other larvae of the instar within a radius of 10, 20 and 30 cm around each individual on September 1st, which had been maintained almost the same during the month. n; no. of larvae observed, $\bar{x}$; average no. of preys taken, ± 95 %; 95 % fiducial limit of mean, R.E.; no. of emerged adults in the following year / n.

No. of other larvae	0	1	2	3	4	5	6	7	8≦
n	67	29	10						
$\bar{x}$	1.46	1.17	1.30						
Range	0 - 8	0 - 7	0 - 3						
± 95 %	1.93 0.99	1.85 0.50	2.13 0.47						
R.E.	0.582	0.552	0.400						
n	26	29	24	10	8	8			
$\bar{x}$	1.38	1.17	1.63	0.30	2.50	1.25			
Range	0 - 7	0 - 5	0 - 8	0 - 2	0 - 8	0 - 3			
± 95 %	2.13 0.63	1.76 0.59	2.53 0.72	0.78 -0.18	4.64 0.36	2.32 0.18			
R.E.	0.615	0.483	0.458	0.600	0.750	0.750			
n	11	18	18	19	7	6	7	9	9
$\bar{x}$	1.36	1.61	1.06	1.84	0.29	1.17	1.29	1.00	1.00
Range	0 - 7	0 - 5	0 - 7	0 - 8	0 - 1	0 - 3	0 - 3	0 - 3	0 - 8
± 95 %	2.78 0.05	2.58 0.64	1.93 0.18	2.82 0.86	0.73 -0.17	2.71 -0.38	2.31 0.26	1.94 0.06	3.58 0.02
R.E.	0.636	0.444	0.333	0.579	0.429	0.500	0.714	0.889	0.778

Table 15. Total number of the dead of 2nd instar larvae and of the victims of Methoca yasumatsui in each station, 1972-'78.

n; total number of 2nd instar larvae appeared.

d; total number of the dead in the instar.

m; total number of the dead ascertained to be killed by the wasp, (%); m/(m+o) × 100

o; total number of the dead ascertained to die by the other causes.

Year	St. A				St. B				St. C				St. D				St. E				St. F				St. G			
	n	d	m	o	n	d	m	o	n	d	m	o	n	d	m	o	n	d	m	o	n	d	m	o	n	d	m	o
1972	186	78	4 (5.3)	71																								
1973	64	34	2 (7.1)	26																								
1974	98	49	11 (23.9)	35	9	5	0	4	12	3	0	2	5	1	0	1	24	15	2 (20.0)	8	28	18	3 (20.0)	12				
1975	25	5	0	3	2	1	0	0	16	2	0	1	25	14	2 (16.6)	10	7	4	0	2	11	8	1 (14.3)	6	102	6	1 (20.0)	4
1976	82	33	5 (21.7)	18									40	11	1 (12.5)	7	38	13	2 (22.2)	7					166	33	3 (10.0)	27
1977	22	6	1 (20.0)	4																					179	111	6 (6.0)	94
1978	63	38	6 (22.2)	21																					23	8	1 (16.7)	5

Table 16. Summary of methods applied in the marking and recapture in Field-I and -II, 1972-'79.

Generation	Mark	Record	Subsidiary object	Usage of Field-I	Area of bare ground (are)	
					Field-I	Field-II
1972	paint and cut	sex	examination into detatchment of mark	as a whole	79.13	unknown
1973	brand	sex, size, weight, injure, and captured point	assessment of interchange	ditto	ditto	85.39
1974	ditto	ditto	survey with the same interval	divided into 6 blocks	ditto	82.89
1975	ditto	ditto		ditto	ditto	72.37
1976	ditto	ditto	survey with large sample size	ditto	ditto	66.19
1977	ditto	ditto		ditto	ditto	unknown
1978	ditto	ditto		ditto	ditto	unknown

Table 17. Number of adults released, recaptured, and migrated in Field-I and -II, 1973-'76.

N; total no. of adults released

R; total no. of adults recaptured in the field

M; total no. of adults recaptured in the other field

	Field-I			Field-II		
Generation	N	R (%)	M (%)	N	R (%)	M (%)
1973	428	123 (28.7)	2 (0.5)	483	102 (21.1)	2 (0.4)
1974	1,195	532 (44.5)	3 (0.3)	131	32 (24.4)	0 (0.0)
1975	544	121 (22.2)	4 (0.7)	463	132 (28.5)	0 (0.0)
1976	948	323 (34.1)	0 (0.0)	356	92 (25.8)	3 (0.8)

Table 18. Weekly survival rate of adult averaged for various lenght of period in autumn or early summer in Field-I, 1972-'79.

	Autumn			Early summer		
Generation	Whole in autumn	Mid-Aug. - mid-Sep.	Late Aug. - mid-Sep.	Early May - late May	Early May - early June	Whole in early summer
1972-'73	.678	.645	.562	.764	....	....
1973-'74	....	....	.699	.880	.860	.735
1974-'75	.752	.764	.776	.826	.788	.728
1975-'76	.747	.728	.805	.806	.748	....
1976-'77	.766	....	.750	.703	....	....
1977-'78	.641	.680	.713	.822	.629	....
1978-'79	.770	.784	.793	.854	.761	....

Table 19. Relative condition factor to reproductive threshold (Rcf to Rt) in autumn and the recapture rate in the next year in Field-I, 1973-'78.

R; total no. of adults released in autumn (from August to mid-September)
r; total no. of adults recaptured in the next year.

Female

Generation	Rcf to Rt		0.6		0.7		0.8		0.9		1.0		1.1		1.2	
1973	R			5		5		9		11		18		7		
	r			1		1		2		3		2		0		
	(%)			(20.0)		(20.0)		(22.2)		(27.3)		(11.1)		(0.0)		
1974	R	3		24		43		69		76		39		25		1
	r	1		2		9		7		9		6		0		0
	(%)	(33,3)		(8.3)		(20.9)		(10.1)		(11.8)		(15.4)		(0.0)		(0.0)
1975	R			18		23		37		45		20		5		
	r			2		1		4		3		1		0		
	(%)			(11.1)		(4.3)		(10.8)		(6.7)		(5.0)		(0.0)		
1976	R	24		67		70		77		99		33		1		
	r	0		5		9		16		17		5		0		
	(%)	(0.0)		(7.5)		(12.9)		(20.8)		(17.2)		(15.2)		(0.0)		
1977	R	10		23		21		37		45		38		11		
	r	0		2		4		9		14		5		1		
	(%)	(0.0)		(8.7)		(19.0)		(24.3)		(31.1)		(13.2)		(9.1)		
1978	R	1		8		13		19		48		54		5		
	r	1		1		2		4		5		3		1		
		(100)		(12.5)		(15.4)		(21.1)		(10.4)		(5.6)		(20.0)		

Male

Generation	Rcf to Rt		0.8		0.9		1.0		1.1		1.2		1.3		1.4		1.5	
1973	R			1		5		26		18		16		9				
	r			0		1		1		2		0		0				
	(%)			(0.0)		(20.0)		(3.8)		(11.1)		(0.0)		(0.0)				
1974	R	1		19		29		40		71		86		38		4		1
	r	0		1		2		3		9		9		2		0		0
	(%)	(0.0)		(5.3)		(6.9)		(7.5)		(12.7)		(10.5)		(5.3)		(0.0)		(0.0)
1975	R	1		11		16		16		46		30		12				
	r	0		4		2		2		2		2		2				
	(%)	(0.0)		(36.4)		(12.5)		(12.5)		(4.3)		(6.7)		(16.7)				
1976	R	14		50		52		62		83		80		16		2		
	r	0		4		7		9		14		7		2		0		
	(%)	(0.0)		(8.0)		(13.5)		(14.5)		(16.9)		(8.8)		(12.5)		(0.0)		
1977	R	3		12		17		18		50		36		16		2		
	r	0		0		1		3		5		5		3		0		
	(%)	(0.0)		(0.0)		(5.9)		(16.7)		(10.0)		(13.9)		(18.8)		(0.0)		
1978	R	2		7		15		24		50		41		23				
	r	0		3		3		5		5		8		2				
		(0.0)		(42.9)		(20.0)		(20.8)		(10.0)		(19.5)		(8.7)				

Table 20. Relative condition factor to hibernation-starting threshold (Rcf to Hst) in late autumn and the recapture rate in the next year in Field-I, 1973-′78.

R; total no. of adults released in late autumn (from late September to early October).

r; total no. of adults recaptured in the next year.

Female

Rcf to Hst Generation		0.7	0.8	0.9	1.0	1.1	1.2	1.3	
1973	R				3	2	12	5	
	r				0	0	2	1	
	%				(0.0)	(0.0)	(16.7)	(20.0)	
1974	R		4	2	8	23	24	2	
	r		2	0	0	6	10	0	
	(%)		(50.0)	(0.0)	(0.0)	(26.1)	(41.7)	(0.0)	
1975	R			1	7	8	24	8	
	r			0	0	1	4	1	
	(%)			(0.0)	(0.0)	(12.5)	(16.7)	(12.5)	
1976	R	3	5	3	2	9	1		
	r	0	0	0	0	3	0		
	(%)	(0.0)	(0.0)	(0.0)	(0.0)	(33.3)	(0.0)		
1977	R	1	0	3	6	16	13	3	1
	r	0		0	1	4	5	1	1
	(%)	(0.0)		(0.0)	(16.7)	(25.0)	(38.5)	(33.3)	(100)
1978	R		1	3	12	15	16	2	
	r		0	0	1	2	1	1	
	(%)		(0.0)	(0.0)	(8.3)	(13.3)	(6.3)	(50.0)	

Male

Rcf to Hst Generation		0.7	0.8	0.9	1.0	1.1	1.2	1.3	
1973	R		1	0	1	7	11	7	
	r		0		0	1	2	2	
	%		(0.0)		(00.0)	(14.3)	(18.2)	(28.6)	
1974	R		1	1	4	10	29	2	1
	r		1	0	0	3	7	1	0
	(%)		(100)	(0.0)	(0.0)	(30.0)	(24.1)	(50.0)	(0.0)
1975	R				8	21	23		
	r				0	3	4		
	(%)				(0.0)	(14.4)	(17.4)		
1976	R		1	3	7	8	3		
	r		0	0	1	2	1		
	(%)		(0.0)	(0.0)	(14.3)	(25.0)	(33.3)		
1977	R			1	4	19	15		
	r			0	0	3	2		
	(%)			(0.0)	(0.0)	(15.8)	(13.3)		
1978	R	2	3	9	13	18	8		
	r	0	0	1	1	5	2		
	(%)	(0.0)	(0.0)	(11.1)	(7.7)	(27.8)	(25.0)		

Table 21. Number of adults emerged in each time and number of the survivors to the next year.

E; no. of adults emerged

R; no. of adults recaptured in the next year

Generation	Sex		August			September			October
			early	mid-	late	early	mid-	late	early
1975	♂	E		6	4	8	7	2	
		R		1	1	2	1	0	
		(%)		(16.7)	(25.0)	(25.0)	(14.3)	(0.0)	
	♀	E		2	3	12	9	4	
		R		0	0	3	1	0	
		(%)		(0.0)	(0.0)	(25.0)	(11.1)	(0.0)	
1976	♂	E	1	4	20	13	15	8	
		R	0	1	6	3	1	0	
		(%)	(0.0)	(25.0)	(30.0)	(23.1)	(6.7)	(0.0)	
	♀	E	1	4	26	13	9	7	4
		R	0	0	5	3	3	0	0
		(%)	(0.0)	(0.0)	(19.2)	(23.1)	(33.3)	(0.0)	(0.0)

Table 22. Efficiency of discovery for larval burrows in 4 category of bare ground.

		Categoty i		Category ii		Category iii		Category iv	
Instar	3rd	40/40	1.000	40.42	0.952	70/84	0.833	66/74	0.892
	2nd	124/141	0.885	98/124	0.790	38/46	0.828	58/79	0.734
	1st	70/80	0.855	46/67	0.687	24/32	0.750	31/56	0.554

* The numerator and denominator of the fraction denote the observed and actual number of individual respectively.

** The condition of each category of bare ground is shown in text.

Legend of plates

Plate 1. General view of Field-I showing an area called as Block 1.

Plate 2. A view of the central area of Field-II.

Plate 3. The labelling of the burrows of larvae with plastic tapes nailed, on which the numbers were carved. The 3rd instar (left) and 2nd instar (right) of larva are seen.

Plate 4. The scene of rearing of females outdoors.

Plate 5.

1) The cylinder of out door rearing
   a) The opaque cylinder of 11 cm long made of vinyl chroride with 4 cm inside diameter. On its wall, 54 small hales with 5 mm diameter were made and covered over with plaster for moisture control.
   b) The stopper; It is made of cork, and the central part is hollowed out and put the plaster into for moisture control. This part is the same as part " d " in Fig. VI-1-1.
2) A view of Outdoor experiment-I. a, settling a cover on the larval burrow (Division a); b, standing a screen (Division b); c, control (Division c).
3) A view of Outdoor experiment-II. an, the ant's nest; c, the buried cylinder of outdoor rearing.

Plate 6. The microscopic photographs of spermatheca in female (1, 2), and testis (3, 4) or vas deferens (5) in male.

1) spermatheca (sm) with no sperm contained, 2) spermatheca with sperms (sp) contained, 3) spermatocyte in testis, 4) spermatid in testis, 5) sperms in vas deferens.

1) and 2), paraffin section method with hematoxylin-eosin staining, ×100; 3),4) and 5), smear method with Giemsa staining, ×280.

Plate 7. The rearing cage for adult. The inside volume is 26 x 17 x 12 cm^3. The bottom made of plaster is detachable, on which a layer of fine soil is piled 2cm deep. The vessel is filled with water falf-full every 2 days.

Plate 8. The rearing cage for adult in outdoor. The sizes of frame are 1.8 (L), 1.8 (W) and 1.2 (H) m. The inside have a depth of 30 cm from the ground and is wetted moderately by a siphon.

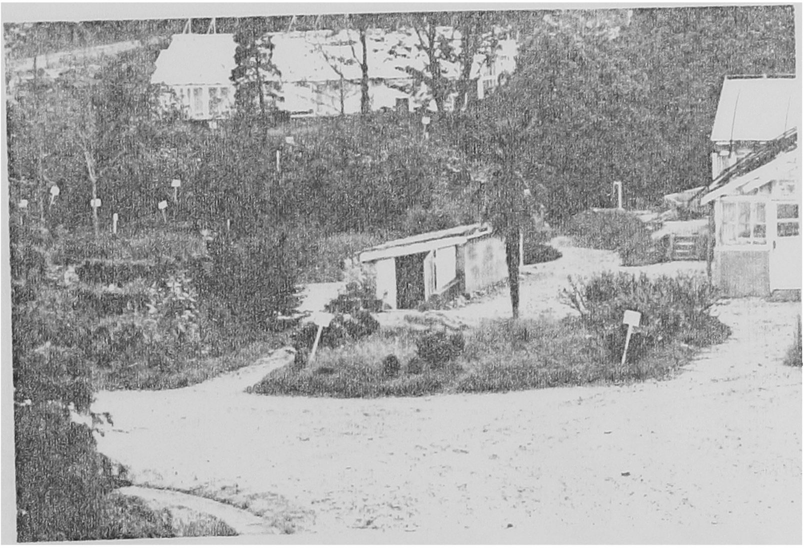
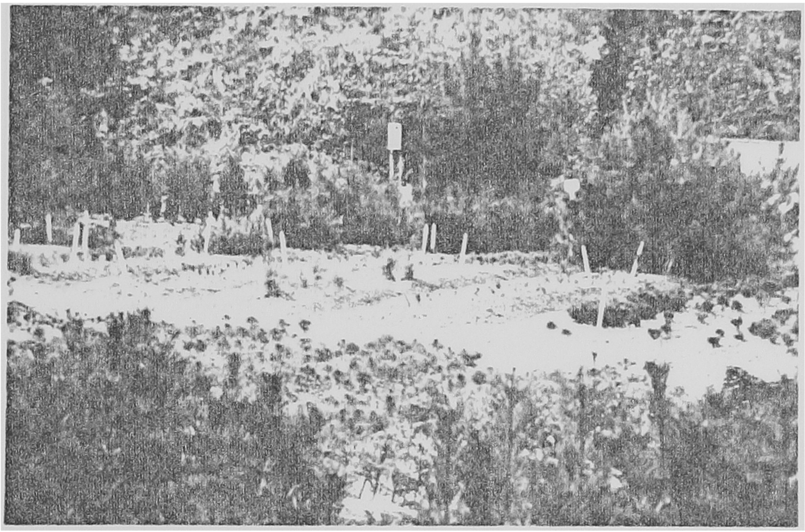


Plate 1.



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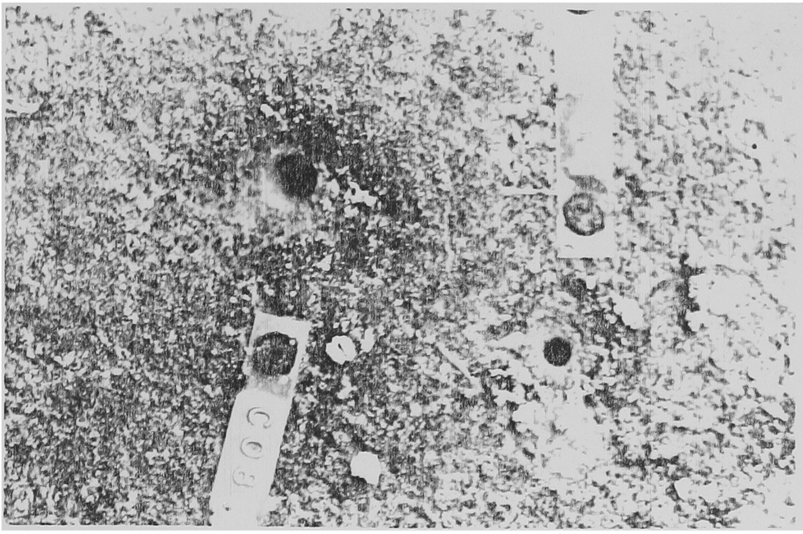


Plate 3.

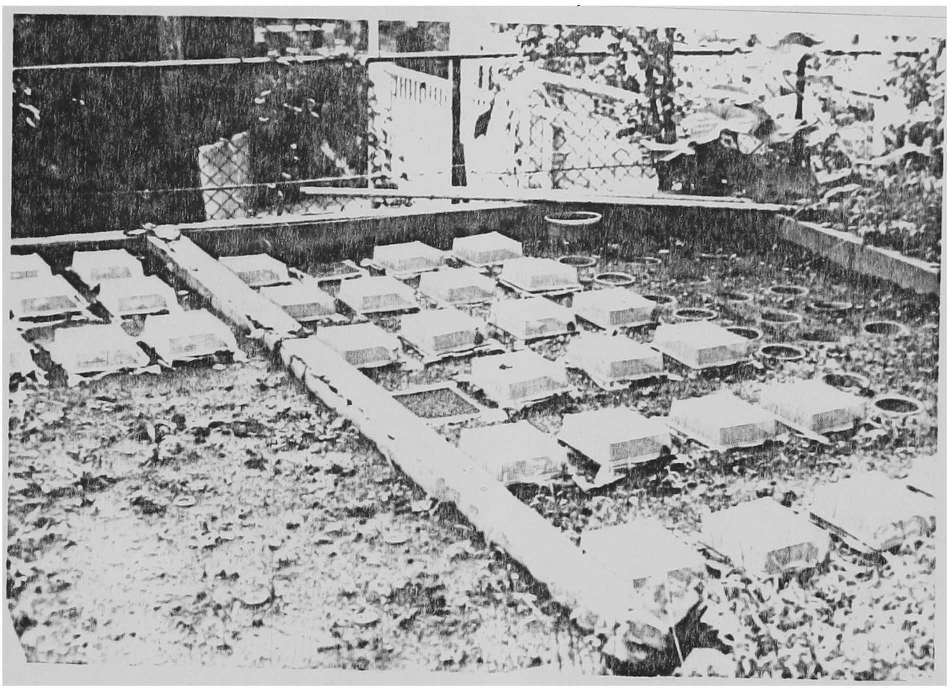
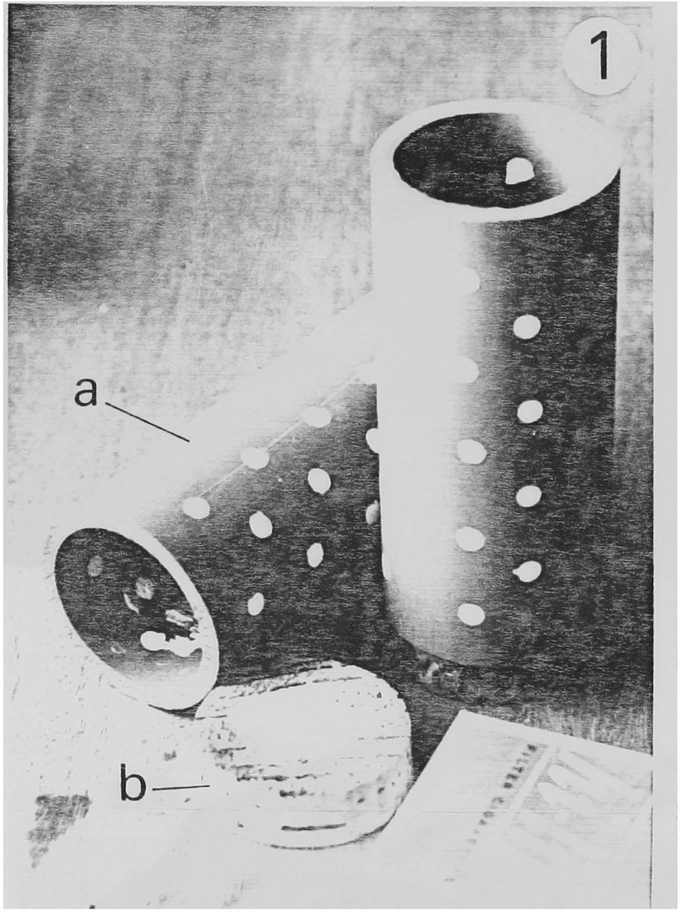
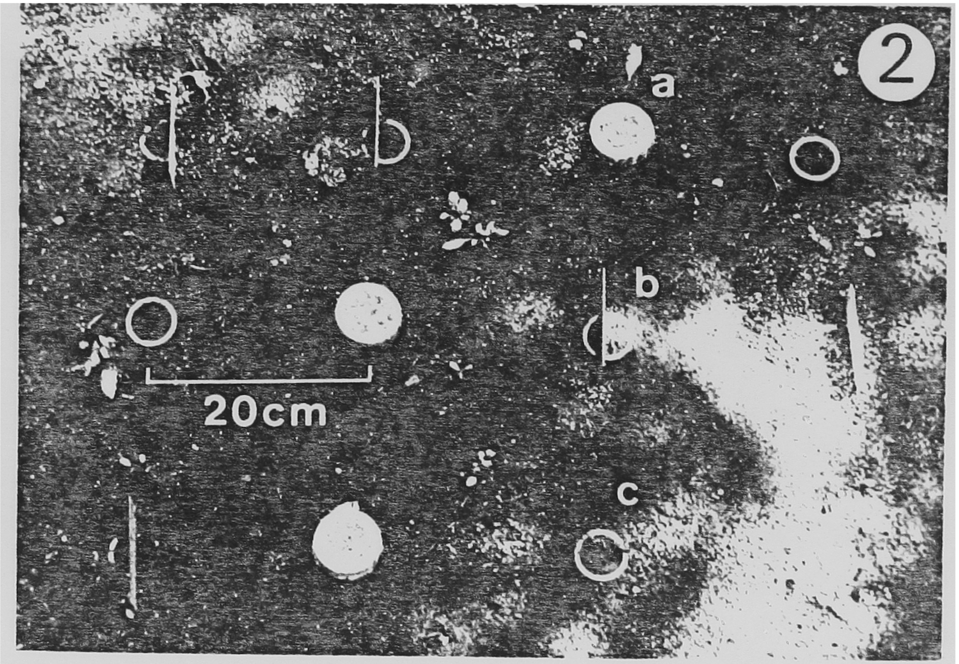
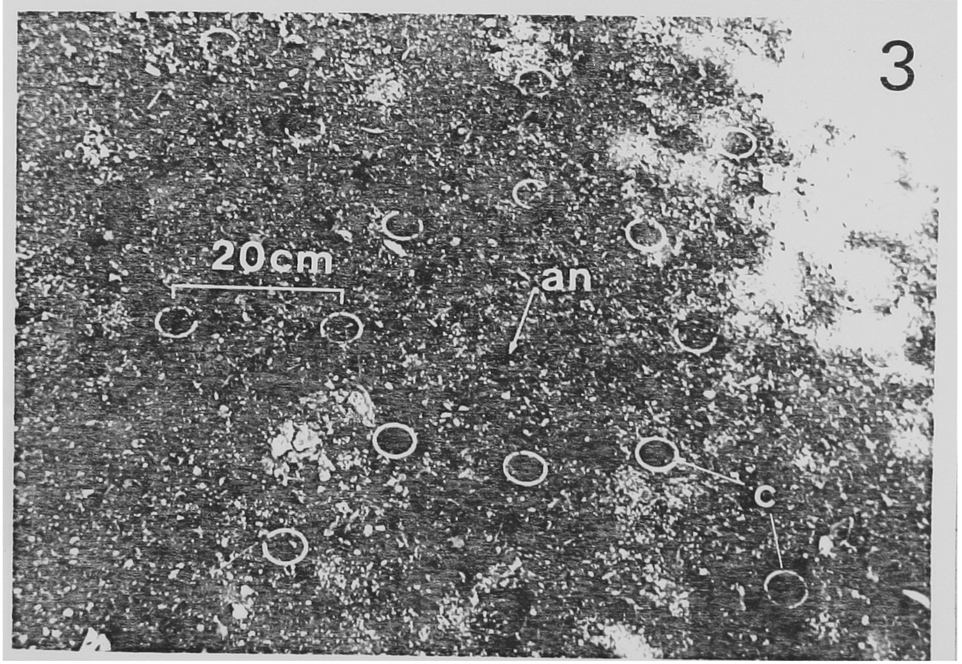


Plate 4.







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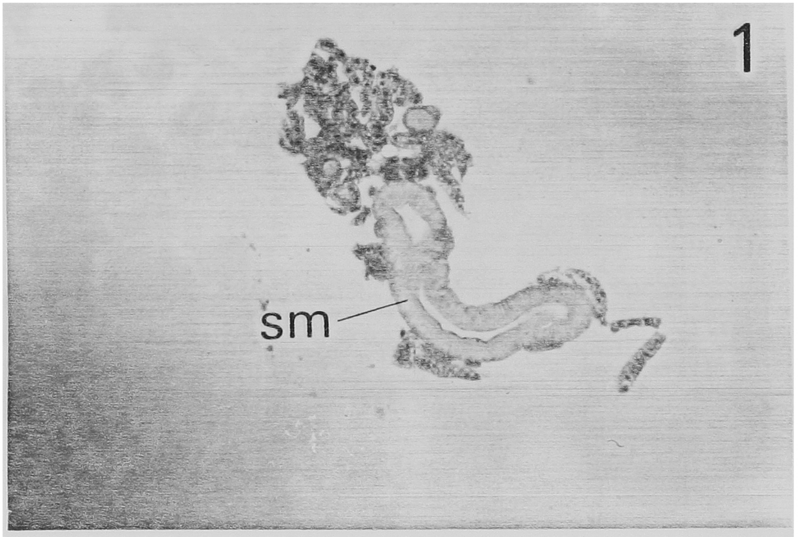

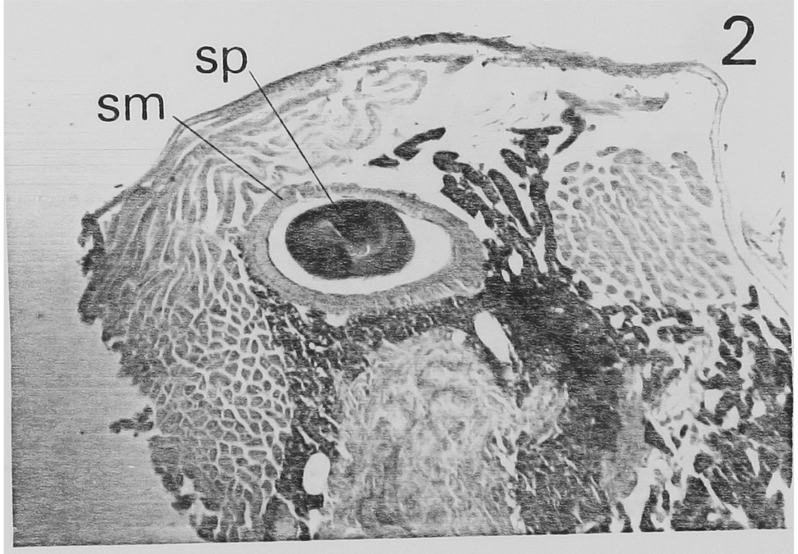

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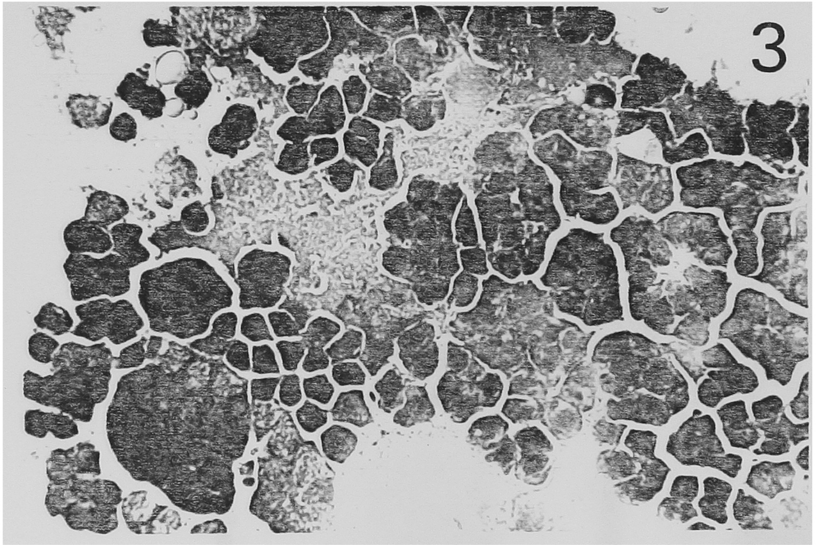
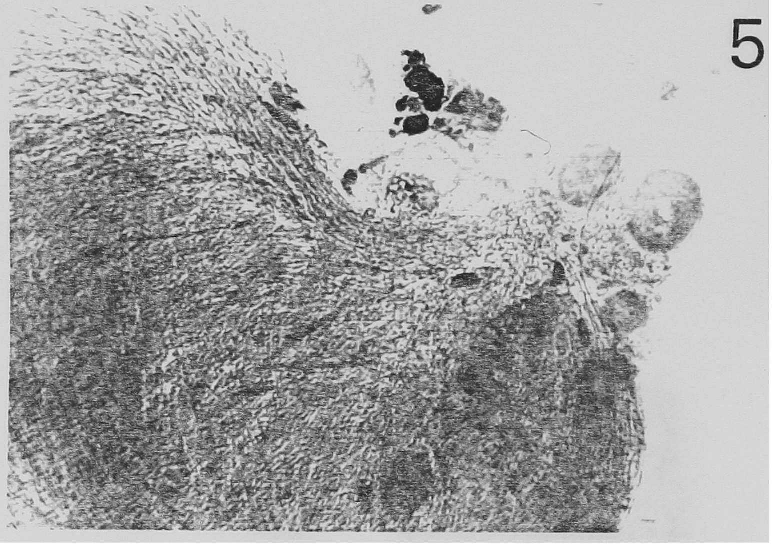




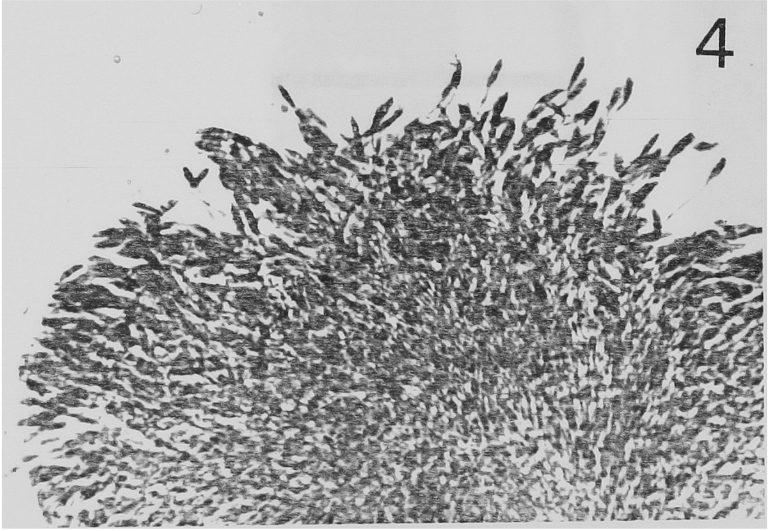
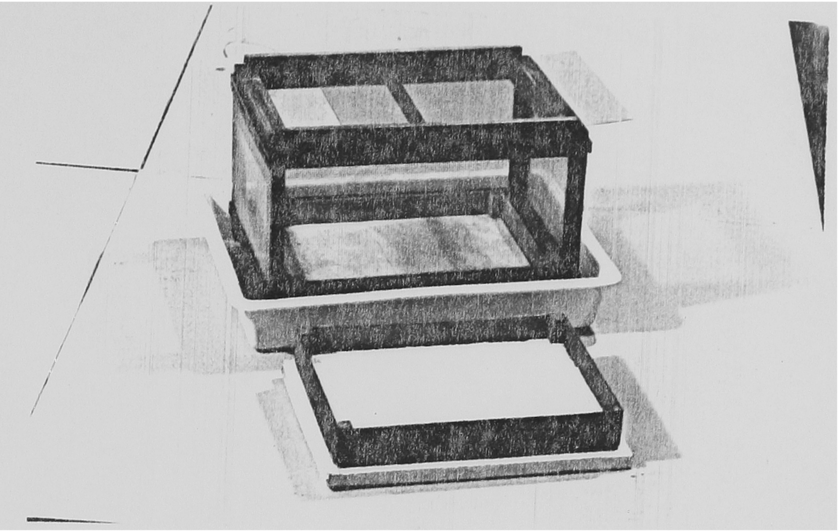


Plate 6. (continued)



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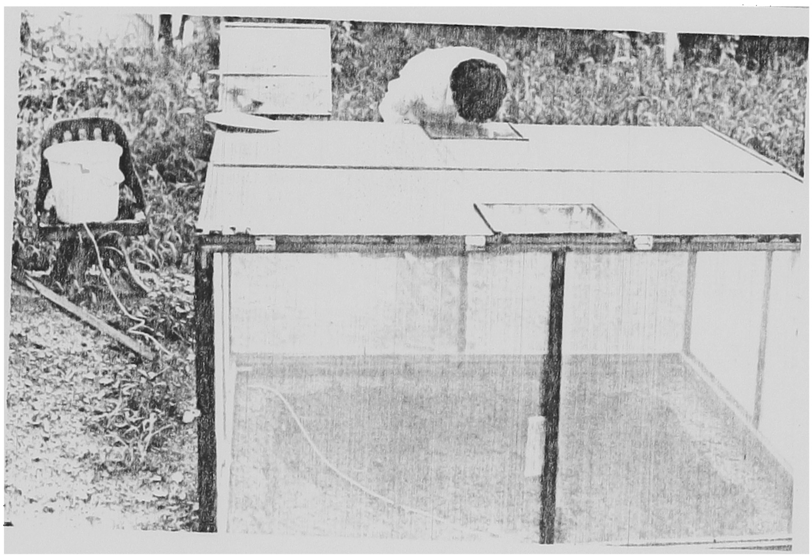

Plate 8.