POPULATION STUDIES OF TWO SPECIES OF PSYLLIDAE ON BROOM

by

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ABSTRACT

The population dynamics of two species of psyllid, *Arytaina spartii* Guérin-Menéville and *Arytaina genistae* Latreille on broom, *Sarothamnus scoparius* (L) Wimmer were studied during 1960 - 63 in a 2½ acre broom plantation at Silwood Park, Berkshire. Some information about the psyllid population between 1957, when the broom was planted, and 1960 was also available.

A. genistae has two generations each year and overwinters as an adult while *A. spartii* has only one and overwinters in the egg stage.

Both psyllid species colonised the broom rapidly in 1957 and increased in numbers. *A. genistae* reached its maximum numbers in the summer of 1959 and then crashed in the following summer. *A. spartii* increased until 1960 - 61 and crashed in 1961 after achieving far higher numbers than *A. genistae*. Both species fluctuated at much lower levels after their numbers had dropped.

Psyllid numbers began increasing in 1957 probably because of the good state of the young bushes and the low numbers of predators present. *A. genistae* numbers dropped in 1960 probably because of the increase of predators, competition with *A. spartii* and the emigration of adults. The crash of *A. spartii* in 1961 was caused by competition among nymphs and adults arising from over-exploitation of the habitat. Many *A. spartii* adults emigrated and the shortage of oviposition sites probably reduced the fecundity of those remaining.

Predation was an important cause of mortality in both broom psyllids, mirids and anthocorids (Hemiptera, Heteroptera) being perhaps the most important. The presence of large numbers of one psyllid probably tended at times to protect the other from predation. The more protected egg of *A. spartii* embedded in broom stems, gives it an advantage over *A. genistae* which has an exposed, superficial egg very vulnerable to predation.

A. genistae suffered more from mortality caused by unfavourable weather than *A. spartii*. Frost in autumn, winter and spring killed many *A. genistae* nymphs and eggs. *A. spartii* is at an advantage in spring should any interspecific competition occur because it can develop at lower temperatures than *A. genistae*. This advantage would be lost in a warmer climate since laboratory studies show that *A. spartii* does not survive as well as *A. genistae* when nymphs of the same age are competing.

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I. INTRODUCTION.

The object of this work was to study the populations of two species of psyllid, Arytaina spartii Guérin-Menéville and Arytaina genistae Latreille occurring together on broom, Sarothamnus scoparius (L) Wimmer. These two species utilise the same habitat though they have different life histories.

This study concentrated on obtaining measurements of population size of both species throughout the year between October 1960 and July 1963. Data from three generations of A. spartii and five generations of A. genistae are described and analysed in an attempt to understand the factors determining abundance. These factors are competition, predation, emigration, immigration and weather. Parasites were absent during the period of this work.

The psyllids are but a small part of the large and interesting fauna associated with broom. Richards and Waloff (1958 and 1961) have studied the biology and population dynamics of Phytodecta olivacea Förster on broom at Silwood Park and they are at present engaged together with Dempster on a study of broom mirid populations. Parnell (1962) investigated the large broom pod fauna. A series of investigations on other insect species living on broom have also been made at Silwood Park by Dempster (1960), M.R. Smith (1958), B.D. Smith (1957) and White (1958).

Distribution: Arytaina genistae occurs over most of the British Isles and is widely distributed in Europe being recorded from Scandinavia, Germany, France, Czechoslovakia, Spain, Corsica, Sicily, Rumania and North Africa

(Vondráček 1957, Dobreanu and Manolache 1962, Heslop-Harrison 1951 and 1961). Heslop-Harrison (1951) suggests that many southern records for *A. genistae* may in fact be closely similar but distinct species such as *Arytaina africana* Heslop-Harrison, *Arytaina spartii* is not as widespread as *A. genistae*, the most northerly limit of distribution being reached in Britain (Heslop-Harrison, 1951). *A. spartii* has been recorded from France, Spain, Portugal, Holland, north to the north of Scotland and east from Southern Germany through parts of Austria to the Balkans. *A. spartii* has not been recorded from Czechoslovakia (Vondráček 1957) or Rumania (Dobreanu and Manolache 1962). Both *A. genistae* and *A. spartii* have been introduced together with their food plant, *Sarothamnus scoparius* into North America (Heslop-Harrison 1951 and 1961).

The genus *Arytaina* is associated only with broom (*Sarothamnus*) and closely related plants throughout its range which includes the shores of the Mediterranean and the European and Western Asiatic temperate region (Heslop-Harrison 1951).

Habitat: The present study was carried out in 2½ acres of broom on a low hill in the grounds of Silwood Park, Sunninghill, Berkshire. This area was planted in 1957 in 24 rows containing a total of 1609 bushes and is rather unusual from an ecological point of view because all the bushes are of the same age. The possible effects of this on the size of the psyllid population will be considered later.

A. spartii has been recorded only on *Sarothamnus scoparius*

(Heslop-Harrison 1951) and A. genistae is also probably largely confined to this plant and possibly other Sarothamnus species. Heslop-Harrison (1951) records a single instance of a breeding colony of A. genistae on Genista tinctoria L., a plant related to broom. There are also records of A. genistae on Ulex europaeus (Vondráček 1957) but I have never found it on this plant and Heslop-Harrison has not been able to establish breeding colonies on Ulex. During the period 1961 - 1963 A. spartii nymphs were much more numerous than A. genistae nymphs at Silwood Park.

The nymphs of the broom psyllids occur in the buds and on the tender actively growing parts of the plant. They are rather flattened and are generally found packed between the bud scales or, at times when shoot extension has occurred, in the leaf axils. The adults move about much more freely and spend much of their time sitting on the younger green stems, moving round to the other side when disturbed. Both species jump and fly readily.

Sarothamnus occurs on acid soils of heaths and woodlands and is sometimes locally abundant. It is typically associated with disturbed ground where the natural vegetation has been destroyed. Bushes live 10 - 15 years and, on disturbed ground, are often replaced as the natural vegetation regenerates. Areas of broom are therefore often relatively temporary habitats.

Sarothamnus forms a shrub up to 10 ft. high with numerous branches. There are two main growth periods in the year, one in spring just before flowering and another in summer when most of the growth takes place.

Flowering occurs in April or May and often causes an arresting of growth. In older bushes heavy flowering may result in the loss of the growing points on many branches. The green stems of these branches may persist to the following year alive but often without any shoot growth. There is usually also a minor flowering period in early autumn, but this is of little importance in the reproduction of the broom plant.

Separation of psyllid nymphal stages: It is easy to separate the nymphal instars of the two species by the relative size of the wing pads (Norman 1959). Also since *A. genistae* nymphs have greater bristle development than *A. spartii* nymphs the two species can be readily separated. The adults of the two species are also easily identified. *A. genistae* is larger than *A. spartii* and has a conspicuous, variable, brown band covering nearly the whole of the area of the forewing between the radial and median veins. The wings of *A. spartii* are of a fairly uniform smoky yellow colour (Figs. 1, 2 and 3).

Life histories of the broom psyllids: *A. spartii* and *A. genistae* are the only two psyllids found regularly on broom at Silwood Park. Another psyllid, *Trioza urticae* L. is occasionally found on broom in autumn when its food plant, the nettle, is dying off, but this species does not breed on broom.

A. spartii has only one generation per year and has a long diapause in the egg stage lasting five or six months. The eggs are laid singly embedded in the concave surfaces of young actively growing stems. The

Fig. 1. Nymphs of Arytaina spartii. Instars 1 - 5.

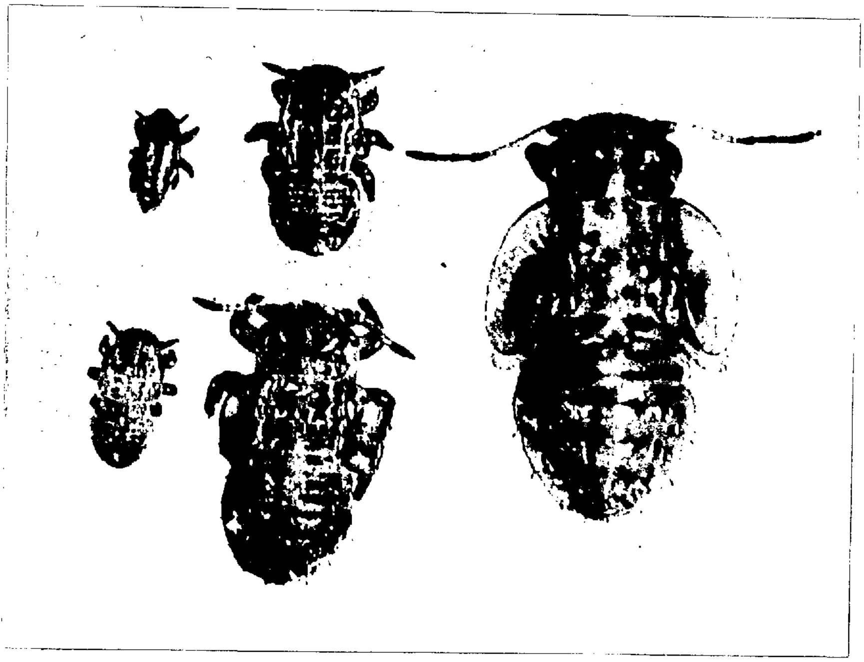


Fig. 2. Eggs and nymphs of Arytaina genistae.

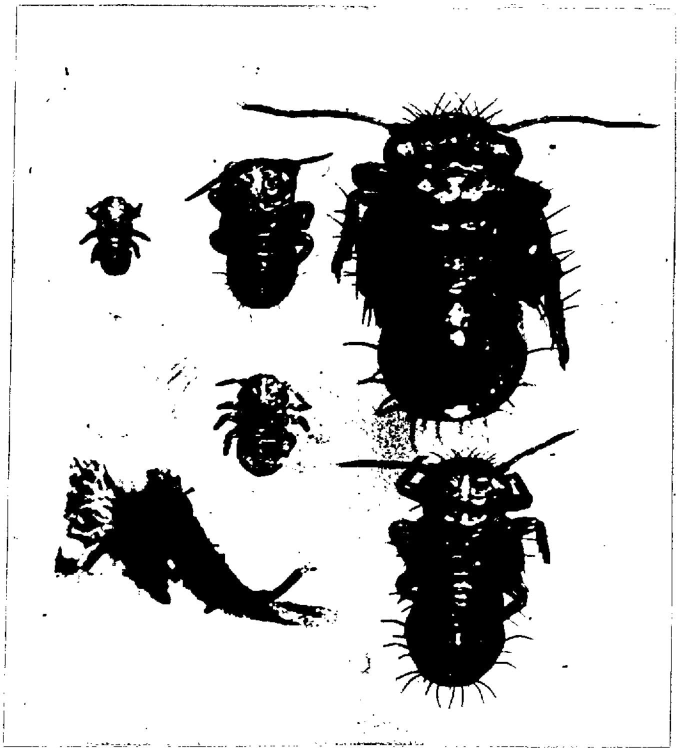
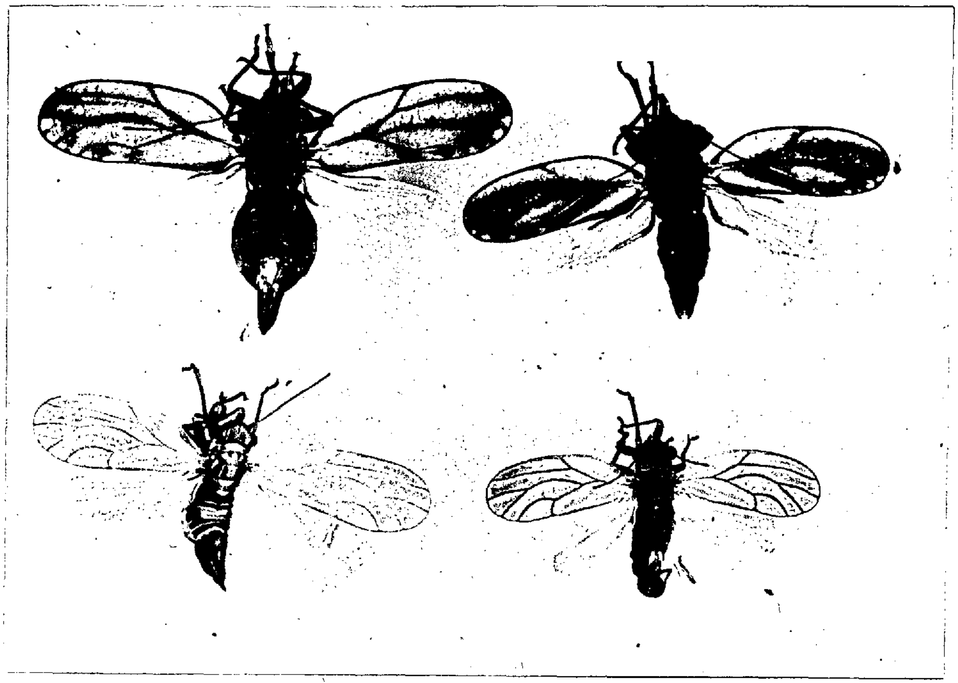


Fig. 3. Adults of *Arytaina genistae* (upper) and *A. spartii* (lower). Females on left.



females make many trial incisions with their ovipositors besides those in which they place their eggs, so that the surface of a broom stem containing eggs has a scarred appearance. After being laid between June and August the egg develops fairly rapidly so that the first instar nymph is fully formed inside the egg shell by September, when diapause commences. The exposed side of the egg is covered by a waxy protective layer which may adhere like a cap to the first instar nymph for a short while after it hatches.

The eggs hatch in the following spring between February and May depending upon the weather. Hatching is very protracted and may continue for several weeks. This results in a wide overlapping of stages. As soon as it hatches the nymph which is bright orange in colour, creeps along the stem until it finds a bud where the scales are separating. It then crawls in and begins to feed. The nymph produces a clear liquid honey dew from the anus and this is enclosed by a layer of waxy excretion produced by a circumanal ring of pores, the openings of wax glands.

The adults of A. spartii appear in May or June depending on the weather and a portion of the population may then disperse into the surrounding country. The adults die by late July or early August.

A. genistae has two generations each year with sometimes a third generation if the autumn is mild. In the southern parts of its range A. genistae is probably multivoltine. This species overwinters as an adult and has no diapause in any stage. The eggs are laid superficially with only the pedicel embedded in the plant. They are placed on leaves, in leaf axils and in buds, singly or in groups of up to fifteen, but more usually of two, three or four.

The first generation occurs between March and late June and the second in the period July to November. This summer-autumn generation produces adults which overwinter on the broom in a mature state. They will lay eggs at any time in the winter if the weather is mild enough. The adults appear to be the only stage capable of surviving winters in Britain although the eggs can survive many weeks of cold weather. Any nymphs hatching in winter are usually killed by frost and the spring generation of nymphs can only develop when frosts are mild and infrequent.

Some of the first generation adults disperse but those of the second generation have been observed to disperse only in small numbers in autumn and not at all after they have overwintered.

Heslop-Harrison working in Northern England, reports that the second generation females of _A. genistae_ are smaller and darker than the first generation females (Heslop-Harrison 1951). In the present study second generation females were not noticeably smaller than those of the first generation but a higher proportion of the second generation females had dark instead of pale green or brown abdominal sternites. It appears that the abdominal sternites tend often to darken as the insects get older.

II. METHODS OF STUDYING THE PSYLLID POPULATIONS.

Methods of Sampling Eggs and Nymphs.

Population estimates for eggs and nymphs were obtained by carefully sorting through weighed cuttings of green broom under a dissecting microscope. A mounted needle was used to dissect the buds and push aside the leaves to expose eggs and nymphs. All population estimates are expressed as the number per 100 grammes of green broom.

For the purpose of sampling, the bushes were divided horizontally into equal upper, middle and lower layers. The cuttings were taken in turn from each of the three layers, only green broom with buds on it being sampled. An equal number of samples was taken from each of the upper, middle and lower levels and from each of the four aspects, North, South, East and West. In 1961 the centres of bushes were also sampled, but this was abandoned in 1962 and 1963. The whole broom area was sampled as evenly as possible each sampling day by taking an equal number of cuttings from each row of bushes.

It was found that the most reliable results were obtained when the number of cuttings was highest (see Tables 1 and 2). The weights of the separate cuttings have comparatively little influence on the standard error. The last three sets of figures in the table (Table 1) (with 135, 172 and 307 cuttings respectively) were obtained from a low density population in 1963 while the other figures came from a high density population in 1961. The standard error is less with higher population densities. In the low

Table 1. Reliability of Different Numbers and Weights of Samples for Psyllid Nymphs.

(a) A. spartii.

No. cuttings	Wt. each cutting in gm.	Mean number of psyllids per sample ± 95% Fiducial limits	Standard error as % of mean	Date
24	2.5	164.7 ± 55.80	17.29	9/3/61
24	5.0	189.0 ± 91.63	24.74	9/3/61
24	10.0	334.8 ± 133.16	20.29	9/3/61
48	1.0	79.1 ± 24.21	15.61	20/3/61
72	2.5	114.3 ± 28.07	12.53	9/3/61
135	0.55	0.6519 ± 0.2601	20.36	24/5/63
172	0.64	0.5581 ± 0.23	20.75	24/5/63
307	0.60	1.5271 ± 0.17	14.55	24/5/63

density population of 1963, 172 and 135 cuttings gave less reliable estimates than 48 and 72 cuttings from the high density population of 1961. The A. genistae data are poorer than the A. spartii data because the distribution of the former species is more patchy (Table 2).

The number of separate cuttings was increased as far as possible. Up until 9th March 1961, 24 cuttings each weighing five grammes were taken on each sampling day. After this date 48 one-gramme cuttings were taken on each sampling day. The cuttings of one or five grammes each were weighed separately up to 27th April 1961 so that the numbers of psyllids on each aspect and level of the bushes could be compared. After this, however, the cuttings were weighed together en masse. In 1962 and 1963, 144 cuttings of approximately one gramme each were taken on each sampling day. In the spring and summer of 1961 when the number of A. spartii was very high it was found that sorting more than 40 - 60 grammes of broom per day was impossible and samples had to be stored in the deep freeze. After the spring and summer of 1961, however, when psyllid numbers were much lower, it was possible to sort through a sample on the day it was collected.

The numbers of all five nymphal instars of each of the two psyllid species, and the eggs of A. genistae, were counted on each sampling day, twice a week during the summer and once a week in winter. The numbers of living nymphs were kept separate from the numbers of dead nymphs. The numbers of A. spartii eggs were estimated twice a year in 1960 - 61 and 1961 - 62 and once in 1963. The cuttings taken for the counting of A. spartii eggs were always weighed separately and 100 - 200 were taken at a time. The eggs were counted by close examination of the stems under a dissecting microscope, probing with a mounted needle where necessary. The cuttings taken for the counting of A. spartii eggs were stored in 70% alcohol as it was impossible to sort through them all in a day.

At the start of the sampling programme in the spring of 1961 two extraction techniques were tried without success. These were the Berlese Funnel method and a method using turpentine vapour which was found to be suitable for extracting thrips (Lewis 1960). Both these methods were very

Table 2. Reliability of Different Numbers and Weights of Samples for Psyllid Nymphs.

(b) A. genistae (numbers include eggs and nymphs in this species).

Date	No. cuttings	Wt. per cutting in gm.	Mean number of psyllids per sample ± 95% Fiducial Limits	Standard error as % of mean
9/3/61	24	2.5	4.29 ± 3.72	44.29
9/3/61	24	5.0	4.46 ± 6.55	74.89
9/3/61	24	10.0	2.13 ± 2.14	51.17
20/3/61	48	1.0	0.40 ± 0.43	55.00
24/5/63	135	0.55	0.9333 ± 0.6045	33.04
24/5/63	172	0.64	0.3140 ± 0.207	33.63
24/5/63	307	0.60	0.5863 ± 0.2895	25.19

inefficient since psyllid nymphs died inside the buds. A simple extraction technique would have made the counting of psyllid nymphs in samples easier.

Methods of Sampling Adults.

Three methods of sampling psyllid adults were tried. These were by beating broom bushes, marking and recapture and a carbon dioxide sampling apparatus.

(a) Beating Method: A quarter of a bush in every 20 bushes throughout the area was shaken over a 3 ft. square cloth tray. Eighty quarter bushes were beaten on each sampling day, the quarters being estimated by eye. Equal numbers of the quarters were taken from North, South, East and West sides of the bushes. The psyllids falling on to the beating tray were counted, sexed and released. The number of psyllids per hundred grammes and the total population in the study area were estimated and compared with estimates obtained by marking and recapture and by the carbon dioxide sampler.

The beating method is not suitable for the estimation of psyllid adult populations in warm weather because the insects readily jump and fly. When the adults of A. spartii became very numerous in the summer of 1961 it was only possible to count the numbers falling on a small area of the beating tray which was divided into equal squares by ruled pencil lines. The beating method does have the advantage of including a large volume of broom which makes for greater accuracy when populations are low. Because of the activity of the psyllid adults, however, the beating method was abandoned in the summer of 1961. Beating also involves considerable disturbance of the habitat.

(b) Marking and Recapture (Bailey 1952): In this method the total population is taken as containing N individuals from which n_1 individuals are taken, marked and released. A few days later when the marked individuals have dispersed throughout the area, n_2 are captured. If n_3 out of these are found to be marked, n_3 is to n_2 as n_1 is to N, the total population according to the formula below.

$$N = \frac{n_1 \times n_2}{n_3}$$

Bailey (1952) has shown that if n_3 is relatively small a better estimate of N is obtained from

$$N = \frac{n_1 \times (n_2 + 1)}{n_3 + 1}$$

It was this modification of the Lincoln index which was used in the estimation of psyllid populations.

This method depends on marked and unmarked animals having equal survival rates and equal chances of being captured. The population must also occupy a defined area with no movement in or out. During the period when the marking and recapture technique was used on A. genistae this condition was fulfilled, but it was not for A. spartii which disperses rapidly after the adults appear. Marking and recapture was tried simultaneously with the beating method on a number of occasions for comparison with the other methods.

Adults of A. genistae were marked with a touch of red, yellow or green Reeves oil paint which was found to be non toxic to caged individuals. A. spartii adults are too delicate to mark in this way and were therefore dusted with Rotor Red powder (Macleod & Donnelly 1957). A marked insect then leaves a red mark on filter paper when wetted with acetone. The marking and recapture method was unsuccessful with A. spartii because of the large numbers present and the fact that they were dispersing rapidly.

The marked psyllids were released in equal numbers in the centres of ten equal areas covering the entire extent of broom. They were taken to the study area in stoppered 4" x 1" specimen tubes which were then emptied on to bushes. An estimate by beating was obtained one or two days after marked individuals had been released and the adults so caught were examined for marks. The marking and recapture technique cannot be used on A. spartii adults and is rather laborious. The capture of a sufficient number of psyllids for marking by beating also involves considerable disturbance of the habitat. For these reasons this method was discontinued.

(c) The Carbon Dioxide Sampler: This is a hinged metal box with a foam rubber rim to seal the edges when it is clamped on to a broom branch. Carbon dioxide is blown in through a small hole in the box from a small cylinder and anaesthetises insects within the box (Dempster 1961a). When this technique was first taken over from Dr. Dempster the inert insects inside the box were emptied on to a white enamel tray and then brushed with a small paint brush into a 4" x 1" specimen tube. Later an electrically driven "pooter" was used to suck them up.

This method was adopted exclusively in the summer of 1961 when the beating and marking and recapture were abandoned. Eighty samples were taken on each sampling day, one bush in twenty being sampled. Only branches with live green stems, leaves and buds were sampled, dead stems being avoided. The samples were divided into high, middle and low samples. High samples were from within a foot of the tip of a branch, low samples came from within a foot of the base and middle samples came from the parts between these two. Out of eighty samples fifty four were middle samples, nineteen high and seven low, the numbers being according to the frequency of occurrence of the three types. This sampling method was adopted from Professor Richards, Dr. N. Waloff and Dr. J.P. Dempster who were using the technique to study the broom Miridae. They were kind enough to give me the psyllid numbers in their carbon dioxide samples in the summer. I continued sampling independently during the autumn, winter and spring. In 1963 the system of high, middle and low samples was discontinued as much broom in the parts where the middle and low samples came from had died. Carbon dioxide samples were then taken from the outer layers of the bushes where the green stems were concentrated, equal numbers being taken from each aspect and each of three equal levels, top, middle and bottom. The numbers of psyllid adults per 100 grammes of green growth was worked out as shown in Table 3 where the fraction of green growth present in each year is given. The figures for 1961 and 1962 were obtained by Professor Richards, Dr. Waloff and Dr. Dempster for their work. Different sets of figures are used for two sizes of carbon dioxide sampler. The large sampler was used by myself in 1961, 1962 and 1963 and by Professor Richards, Dr. Dempster and Dr. Waloff in 1961. In 1962 they adopted the smaller carbon dioxide sampler which they then used exclusively.

The carbon dioxide sampler does not allow active insects to escape, is easy to handle and does not cause much disturbance of the habitat. The quantity of broom sampled can be measured with greater accuracy than is possible with the beating method. The quantity of broom sampled is, however, much smaller than with the beating method and this makes the accurate measurement of sparse populations difficult.

Table 3: Figures used to convert numbers of psyllids in small and large carbon dioxide samples.

	Large sampler			Small sampler	
	1961	1962	1963	1961	1962
Average weight of broom in sampler in grammes	48.55	48.43	50.80	-	12.15
Fraction of green in samples.	0.6559	0.7402	0.7738	-	0.6201

The standard errors for different numbers of carbon dioxide samples are shown in Table 4. The reliability of the carbon dioxide sampler is determined, as is that of the cuttings for nymphs and eggs, more by the number than by the size of the samples. The density of the population is also an important factor. In both the A. spartii and the A. genistae estimates for 6th June 1961, 60 samples give more reliable results than 20 samples. In A. spartii, 288 samples taken on 18th June 1962 had a standard error little different from that of 60 samples taken a year previously from a much denser population. The same can be said for the 144 samples taken for A. genistae on 12th July 1962 except that the population was denser in 1962 instead of 1961. It appears that reliability is not much improved in psyllid adult population estimates when more than 60 carbon dioxide samples are taken. It therefore seems that 80 samples is a reasonable number to be taken on each sampling day.

Table 4. Reliability of CO_2 Sampler for Psyllid Adults.

(a) *A. genistae*.

Date	No. samples	Wt. per sample in gm.	Mean number psyllids per sample ± 95% Fiducial limits	Standard error as % of mean
6/6/61	60	48.55	0.60 ± 0.25	21.03
6/6/61	40	48.55	0.58 ± 0.27	24.03
6/6/61	20	48.55	0.65 ± 0.52	40.66
12/7/62	144	12.15	0.31 ± 0.12	19.44
12/7/62	60	12.15	0.32 ± 0.12	19.89

(b) *A. spartii*.

6/6/61	60	48.55	9.15 ± 2.39	13.34
6/6/61	40	48.55	9.08 ± 2.91	16.37
6/6/61	20	48.55	9.30 ± 4.29	23.57
18/6/62	288	12.15	0.45 ± 0.114	12.87
18/6/62	60	12.15	0.40 ± 0.21	27.35

Comparison of Results from Different Methods of Sampling.

Results obtained by the three methods of estimating numbers of psyllid adults are shown in Table 5. The results from beating and the marking and recapture technique agree fairly closely. The carbon dioxide sampler, however, gives far higher numbers than the beating method. Psyllids were often observed flying off the beating tray and it is certain that many were missed. The marking and recapture technique was not repeated after 22nd February and it is therefore impossible to say how it would compare with the beating method at higher temperatures. The carbon dioxide method does not allow the escape of adults and is therefore likely to be much more reliable than beating. The main disadvantage of the carbon dioxide sampler is that it is relatively insensitive when populations are low. When one psyllid is found in 80 carbon dioxide samples this gives an estimate of 1,767 for the whole study area. The beating method, because it deals with a far larger amount of broom, can give estimates far lower than 1,767.

Table 5. Results Obtained by Three Methods of Estimating Numbers of Psyllid Adults.

Total Number in Study Area by Beating		Total Number in Study Area by Marking & Recapture		Total Number in Study Area by Carbon Dioxide Sampler		Date
A. genistae	A. spartii	A. genistae	A. spartii	A. genistae	A. spartii	
9,886						10-17/10/60
8,045		5,786				21-24/10/60
11,760		13,900				9-11/11/60
8,634		13,824				21-23/12/60
6,907						19/12/60
3,942		4,225				22/ 2/61
1,256				1,767		5/ 4/61
785				1,767		7/ 4/61
724				1,767		16/ 4/61
724				1,767		17/ 4/61
471				0		2/ 5/61
276	85,228			1,767	565,376	8/ 5/61
119	330,395			1,767	1,270,329	11/ 5/61
26,388	245,855			73,023	577,116	13/ 6/61
4,317	23,547			37,689	94,223	20/ 6/61

Estimation of Recruitment of Individuals to the Population.

(a) A. spartii: A number of broom branches with A. spartii eggs on them were each isolated by a sticky band round the base and cleared of buds with a razor blade. These branches were from one to three feet long and were numbered. The buds were removed so that hatching psyllid nymphs, having nowhere to hide, could easily be seen, removed with a small brush and counted. In 1961 twelve branches were used and in 1962 and 1963 this number was doubled. The branches were chosen at random in 1961, but in 1962 and 1963 the number of eggs was so low that branches with sufficient eggs on them had to be carefully chosen. The prepared branches were distributed over the entire broom area and the aspect and any other features of the position of each branch were noted.

The numbers of nymphs hatching daily were plotted on a graph (Figs. 7, 8 and 9). In 1961 hatching records were started on 18th February, a short while after hatching had begun. It appears from the data, however, that an insignificant fraction of the total number hatching was missed. The same applies to 1962 and 1963 in spite of efforts to obtain a record of the initiation of hatching. In both 1962 and 1963 branches were prepared about a month before hatching started, but nymphs appeared in samples before hatching started on these branches. Further branches had therefore to be prepared. In 1962 and 1963 hatching started on a few of the original branches before more were prepared. These branches were used to calculate the expected total hatch for all the branches for the initial period when the compliment of branches was not complete. It was found that the few original branches followed the hatching pattern of the rest fairly closely. The reason for this difficulty was most probably due to having too few branches. It was not practicable, however, to search more.

The daily "total" of nymphs hatching on all branches is accumulated as a grand total. The numbers of nymphs hatching between sampling days are then calculated as decimal fractions of the grand total. The fraction of the total population hatching in any period is thus known.

(b) A. genistae: The eggs of A. genistae are laid throughout the year in buds and on leaves. This makes it impossible to study hatching in the same way as described for A. spartii. An attempt was made to study recruitment in A. genistae by estimating the rate of egg laying. Twenty female A. genistae were captured in the study area each week throughout the year and enclosed singly in 6 - 9 inch long muslin sleeves of 4 - 5 inches in diameter. These sleeves were placed on fresh young shoots and tied at both ends with string. The eggs laid by each female were counted each week and plotted in the form of a histogram (Figs. 30 and 31). The sleeves, except in a few cases, were tied in position 10 to 14 days before the introduction of the psyllid females to ensure that any eggs already on the enclosed shoots would develop sufficiently to be distinguishable from eggs laid by the captive insect. Fresh eggs were counted and a figure for the number laid per female per day was worked out from the total in all sleeves containing live females. The eggs in sleeves where the psyllids had died were ignored. Eggs which showed eye spots were also ignored as it was assumed that these were laid before the sleeves were placed in position. Eggs in the field take from 8 to 14 days to develop to the stage where eye spots are visible at summer temperatures. The numbers of eggs with eye spots in the sleeves agreed fairly closely with the numbers of eggs in the samples taken for eggs and nymphs, showing that the omission of these eggs from calculations of egg-laying rate was justified.

To obtain the rate of egg laying of the whole A. genistae adult population in terms of numbers of eggs laid per hundred grammes of broom between sampling days the average rate per female per day is multiplied by the product of the number of adults per hundred grammes, corrected for the sex ratio and the number of days between samples. The number of eggs laid in 100 grammes between two sampling days is expressed as a fraction of the total laid in the generation concerned.

During most weeks between a quarter and three quarters of the psyllids in the sleeves died. The numbers dying were apparently not related to temperature, humidity or the age of the insects. The fact that death did occur in so many cases suggests that conditions inside the sleeves were not as favourable as they should have been. In the spring-summer generation of 1962 the females inside the sleeves laid far fewer eggs than would be expected from the peak number of eggs in the samples and the totals obtained by analysis of the population data. In the summer-autumn generation of 1962 the number of eggs laid in the sleeves is much larger than the peak number in the samples, but still smaller than the total calculated (see

Table 6). The spring-summer generation of 1963 again shows that the number of eggs laid in the sleeves is too low. The number of eggs laid in the sleeves is therefore probably not very closely related to the number laid by females under natural conditions.

Table 6. Number of Eggs Laid by Females in Sleeves Compared with Peak Numbers of Eggs in Samples and Calculated Totals.

Generation of *A. genistae*	Total No. eggs laid per 100 gm. by females in sleeves	Peak No. eggs per 100 gm.	Total No. eggs laid in period of generation by calculation (cf Section III).
Spring-Summer 1962	633	1,102	(1) 2,043 (2) 5,019
Summer-Autumn 1962	1,313	262	(1) 5,661 (2) ?
Spring-Summer 1963	191	508	(1) 485 (2) 695

Method of Assessing Adult Movement.

The number of psyllid adults caught each year in a Vent Axia, propeller type suction trap of 18" diameter were counted. This trap was situated in a hollow 90 yards south east of the study area and was 4 feet above ground level. It is probable that most of the psyllids caught were from the study area as the nearest other broom areas were about a quarter of a mile away and much smaller. The number of A. spartii or A. genistae caught in the suction trap between any two sampling days is expressed as a fraction of the total number caught during the particular generation.

The suction trap samples were brought in at 9 a.m. each day except on Saturdays and Sundays. Daily records are therefore available for all days except Fridays, Saturdays and Sundays. The number of adults caught in the suction trap on each day during a weekend was estimated by dividing the total for the week end by three if weather conditions were similar throughout the three days. If the weather was variable the total for the three days was divided up according to the maximum temperatures reached on each of the days. Errors arising from this are not considered to be large.

Methods of Analysis of the Sampling Data.

Three methods were used to analyse the psyllid population data. Analysis of the data is necessary because hatching, death and moulting from one stage to the next occur simultaneously and make it difficult to estimate mortality from the original successive population estimates. The three methods used are described below.

(a) The Simultaneous Equation Method (Dempster 1961b).

For this method the rate of build-up and fall-off of the population as well as the rate at which new individuals are being added by hatching or egg-laying must be known. It is assumed that mortality during each larval instar is constant. The population changes between sampling days are represented in terms of the accumulated mortalities of the instars present.

The number of any one stage dying between sampling days is given by the product of the number of that stage present, the fraction dying per day and the number of days. The number present is taken as the average of the numbers on the two sampling days. As the fall-off is exponential good results are only obtained if sampling is frequent. If then Io is the number of first instar nymphs present on day o and It is the number present t days later, the number of first instar nymphs dying during that time is $\frac{(Io + It)}{2} tu_1$ where u_1 is the average daily mortality of first stage nymphs. The number of second stage nymphs dying between days o and t = $\frac{(IIo + IIt)}{2} tu_2$ while the number of thirds dying = $\frac{(IIIo + IIIt)}{2} tu_3$ and so on. The effect of moulting is accounted for by considering all the stages together.

The total change in the size of the population between days o and t may be represented by the expression

$$- \frac{(Io + It)}{2} tu_1 - \frac{(IIo + IIt)}{2} tu_2 - \frac{(IIIo + IIIt)}{2} tu_3$$

$$\ldots\ldots\ldots\ldots \frac{(Ado + Adt)}{2} tu_{ad}$$

This will only apply when hatching or egg laying has been completed. While recruitment is still in progress the addition of new individuals will tend to reduce the effects of mortality. The number of first instar nymphs hatching, or eggs laid, between days o and t is given by the formula $P\alpha(o \rightarrow t)$ where α is the fraction of the total number P hatching or laid during that time. The methods of obtaining α for broom psyllid populations have already been described. The accumulated mortalities of each stage between days o and t are subtracted from $P\alpha(o \rightarrow t)$.

Equations can be obtained for the change in numbers between each of successive sampling days, giving a set of simultaneous equations from which the total number hatching (P) and the daily mortalities of the various stages, u_1, u_2, u_3 etc., can be calculated. The right hand side of each equation is the observed total change in the population between sampling days, positive if the population has increased or negative if the population has decreased. Each equation is therefore built up as below:

$$P\alpha(o - t) - \frac{(Io + It)}{2}tu_1 - \frac{(IIo + IIt)}{2}tu_2 - \frac{(IIIo + IIIt)}{2}tu_3$$

$$\ldots\ldots\ldots\ldots \frac{(Ado - Adt)}{2}tu_{ad} = \text{Total population change.}$$

The equations can also include a term representing the movement of adult psyllids into or out of the area. The influence of movement on the population may be estimated as follows. The total number moving into or out of the area can be taken as D. The fraction of the total immigration or emigration occurring between days o and t will be reflected by the numbers flying at that time. A curve for flight activity was obtained as already described from the numbers caught in a suction trap close to the study area. From this curve the fraction flying between days o and t can be calculated as follows:

$$\text{fraction of total flying between days o and t} \quad (x) = \frac{\text{the number trapped between days o and t}}{\text{total number trapped}}$$

The number of individuals leaving or entering the area between days o and t may then be represented by

$$Dx\ (o \rightarrow t)$$

Values for x, for the period between other sampling days, may be estimated and put into the appropriate equation in the same way as the hatching data was used. The value of D will be given on solution of the equations. If D is negative an emigration is indicated. A positive sign for D indicates an immigration.

When the equations are solved they are reduced by the method of least squares to a matrix including a column each for $P, u_1 — u_{adult}$ and D. The matrix can be solved by a desk calculating machine or more quickly by an electronic computer. The number of equations must at least be equal to the number of unknowns and larger numbers are desirable.

This method of analysis was applied to all the *A. spartii* data and to three of the five sets of *A. genistae* data for which recruitment data is available. [illegible]

(b) The Regression Method (Richards and Waloff, 1954; Dempster, 1956)

This is based on the calculation of the slope of fall-off of numbers after the peak has been reached. If it is assumed that when once hatching or egg laying is completed, there is an approximately steady mortality, the time trend of the population will fit the formula $Y = nk^x$, where Y is the population occurring on day x, n is the total number of nymphs hatching or eggs laid, and k is the fraction surviving each day. The logarithm of Y (for values after the peak in numbers) will follow a straight line, since Y = log n + x log k. A linear regression equation can be determined for the logarithm of successive population estimates together with values of x, and the regression coefficient is the logarithm of the average fraction of the population surviving each day. The size of the original population can be calculated by substituting the value of x at the beginning of the generation in the regression equation. A calculation for the population less the egg or first instar,(i.e. for successive accumulated totals of the first or second instars depending on whether eggs or first instar nymphs are treated as the first stage) gives an estimate of the total number of nymphs which have entered the first or second instar. A corresponding total can be determined for each subsequent instar. The mortality during each stage may be calculated from the estimates of the number of nymphs entering it.

In the treatment of the psyllid data by this method the value of x at the beginning of any stage is taken as the number of days between the start of the generation and the sampling day preceding that on which that stage was first found. It is assumed that a given stage first appeared between the two sampling days. If the period between successive sampling days is greater than three or four days the value of x on the day before the sampling day on which the stage was first recorded is taken.

One of the weaknesses of this method arises from the fact that mortality is not constant for the whole generation. If the logarithm of the total population is plotted against time a sigmoid curve and not a straight line results. This is because mortality is highest at the beginning and end of a generation. To avoid this difficulty as far as possible in the treatment of the psyllid data the total fall-off was cut into separate segmentx each corresponding with the period of occurrence of a different stage. The regression equation for each stage was calculated from the accumulated population totals after the peak while that stage was present.

The regression method works best with populations which build up rapidly to a well marked peak with a short period of recruitment (Dempster 1956). A long period of recruitment such as is present in broom psyllid populations results in a wide overlapping of stages. With this wide overlap comes the difficulty of separating mortalities of each of the stages occurring together. The greater the overlap, the greater the influence of mortality in one stage on the estimate of mortality in the next.

This method was applied to all the psyllid population data. Results obtained by this method for the initial numbers of A. spartii in three generations are given in Table 9.

(c) A Graphical Method of Estimating Mortality (Dempster, not published)

If the numbers of each stage are plotted on squared paper, the area under the curve equals the number of individuals entering that stage multiplied by the length of time that they stay in that stage. The total number of any stage produced can be estimated by dividing the area under the curve by the mean length of the stage in days. The average length of that stage is the difference between its mean day of occurrence and that of the following instar.

Because the adult stage lasts very much longer than the fifth instar the mean length of the fifth instar is too long if the mean day of occurrence of the adults is used. For this reason the mean length of the fifth instar was taken as the number of days between the mean day of occurrence of the fifth instar and the peak day of occurrence of the adults. The chief difficulty in this method is due to failure in obtaining reasonable values for the mean lengths of many of the stages. In some cases these calculated values proved to be negative.

III. DESCRIPTION OF THE POPULATION DATA.

The Population Changes in Arytaina spartii.

All population figures given here are for the numbers in 100 grammes of broom except where otherwise stated.

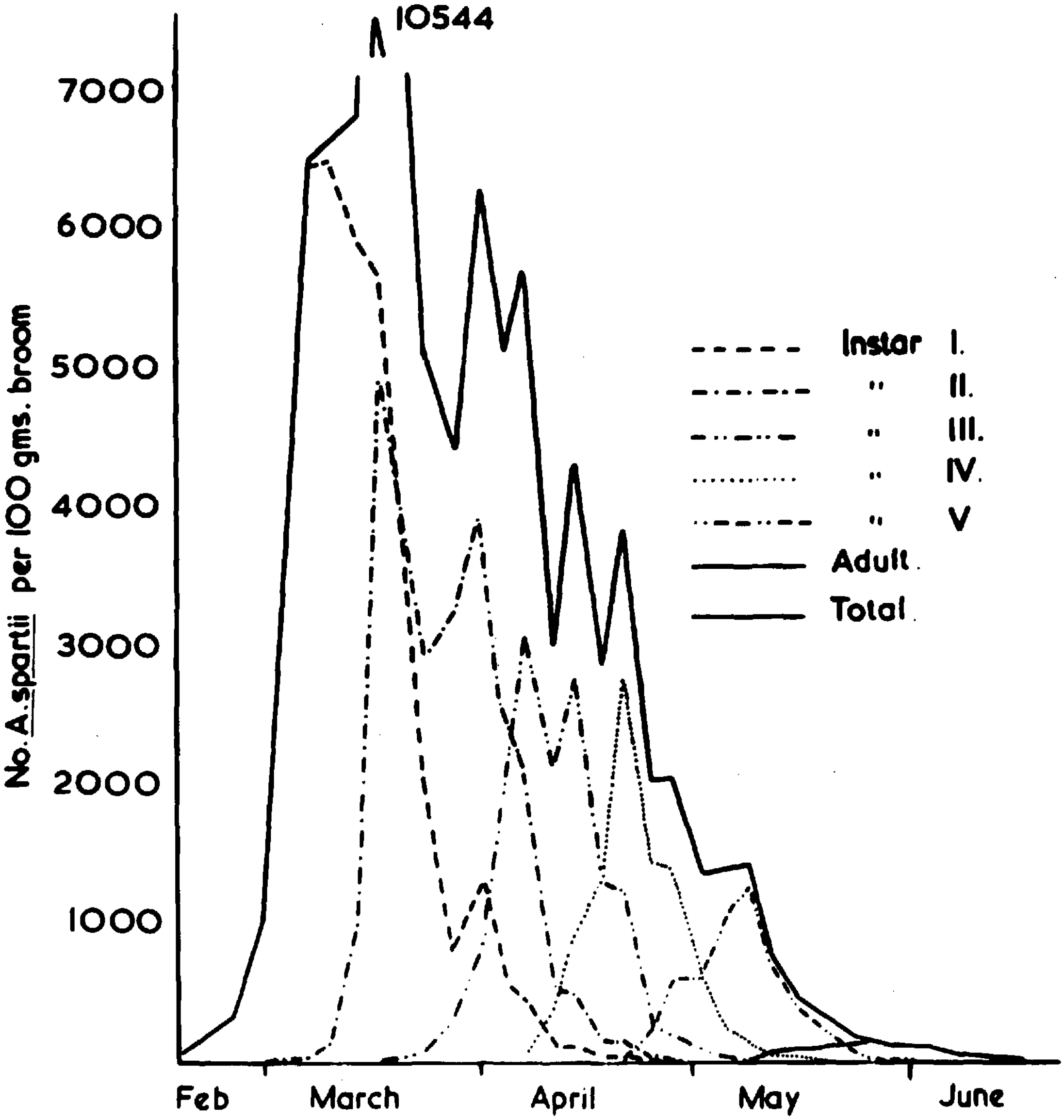
When the eggs of A. spartii were estimated in the autumn of 1960 and again in the spring of 1961 it was obvious that the nymphal population would reach a very high level in the spring and summer of 1961. The autumn 1960 (1 November) egg estimate was 21,701 eggs per 100 grammes, while the spring 1961 (10 February) estimate was 21,891. This meant that the total number of eggs in the study area was about 913,078,000.

A. spartii began hatching about 10 February 1961. The first population sample was taken on 13 February when there were 37 first instar nymphs per 100 grammes. Hatching records were begun on 18 February and hatching continued for 69 days after this until 28 April. As a result of rapid hatching the population reached a peak of 10,544 nymphs by 16 March (see Fig. 4). After this the nymphal population fell almost as rapidly as it had risen in spite of the fact that only half the total number had hatched and hatching continued at a similar rate (see Fig. 7). The peak figures reached by each nymphal instar and the adults are shown in Table 7.

The numbers of the first instar reached a peak 23 days after sampling began and about 28 days after hatching probably started. The numbers of first instar nymphs fell much more rapidly than would be expected from the rate of hatching (Fig. 7).

Fig. 4

A. spartii population estimates 1961.



The first adults appeared on 5 May, 85 days after hatching started and their numbers increased to the peak after 20 days. On 18 May, 13 days after the adults had first appeared, A. spartii was first found in the suction trap. Between 18 May and 19 June large numbers of adults left the study area and the population fell rapidly (Fig. 12).

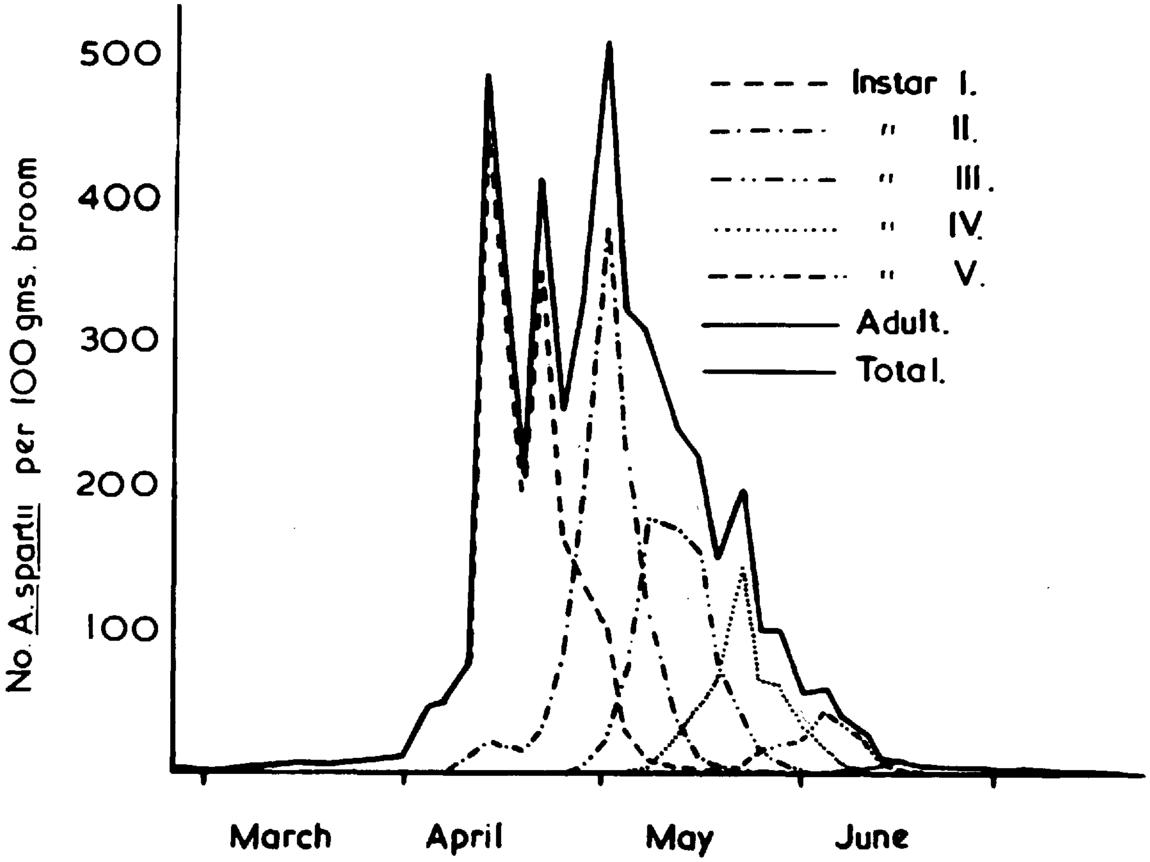
By the time adults appeared many of the broom bushes in the area were in poor condition with their leaves and stems discoloured by psyllid honey dew and fungus. The bushes made a fair amount of growth by August, however.

Estimates of the number of eggs laid by the adults gave numbers of only 1,419 (7 August 1961) and 1,199 (21 March 1962) eggs per 100 grammes, far fewer than would be expected from the number of adults present. The mean of these two estimates indicates a total of 80,244,000 eggs in the entire study area.

In 1962 A. spartii (Fig. 5) began hatching about 23 February, the first nymph being found in the samples on that day. Hatching only became appreciable, however, by 27 March (Fig. 8) after which it increased to a maximum on 9, 10 and 11 April. This peak in hatching was far more distinct than in the previous year. The peak number of nymphs was 508 recorded on 1 May when about 90% of the total number had hatched. As can be seen from the graph (Fig. 8) the number of first instar nymphs follows the numbers hatching more closely than in 1961. Hatching in 1962 continued for 88 days from 23 February to 21 May. The hatching period in 1962 was then apparently longer than that of 1961 but this may be a false impression since

Fig. 5

A. spartii population estimates 1962.



the beginning of hatching is not included in 1961. After the peak the population fell off rapidly as in 1961 and disappeared shortly after 20 July. The peak numbers reached by each of the nymphal instars and adults are shown in Table 7.

The first adults were seen in the suction trap samples on 15 June, three days after they first appeared. Dispersal of the adults therefore started more quickly than in 1961 (Fig. 13).

By the time adults appeared in 1962 the broom was still in good condition. The 1962 adults laid rather more eggs than those of the previous year suggesting that a larger proportion stayed in the study area to lay.

In the spring of 1963 there were 1,613 eggs per 100 grammes (95,750,000 in the entire area). Hatching started in early April and was completed more quickly than in the previous two years (49 days) because of higher temperatures. The peak hatching days were the 19th and 23rd of April so that a maximum hatching rate was achieved more quickly than in 1962 (Fig. 7). The peak number of nymphs was 505 on 30 April after about 77% of the total had hatched. The fall off from this well marked peak was similar to that in the previous two years (Fig. 6). The peak numbers reached by instars 1-5 and adults are shown in Table 7.

The first 1963 adults appeared quicker than in either of the previous two years on account of higher temperatures (Table 8). Dispersal began on 12 June, 5 days after the adults first appeared and continued until 23 June. The adults of the 1963 generation disappeared shortly after 5 July (Fig. 14).

Fig. 6

A. spartii population estimates 1963

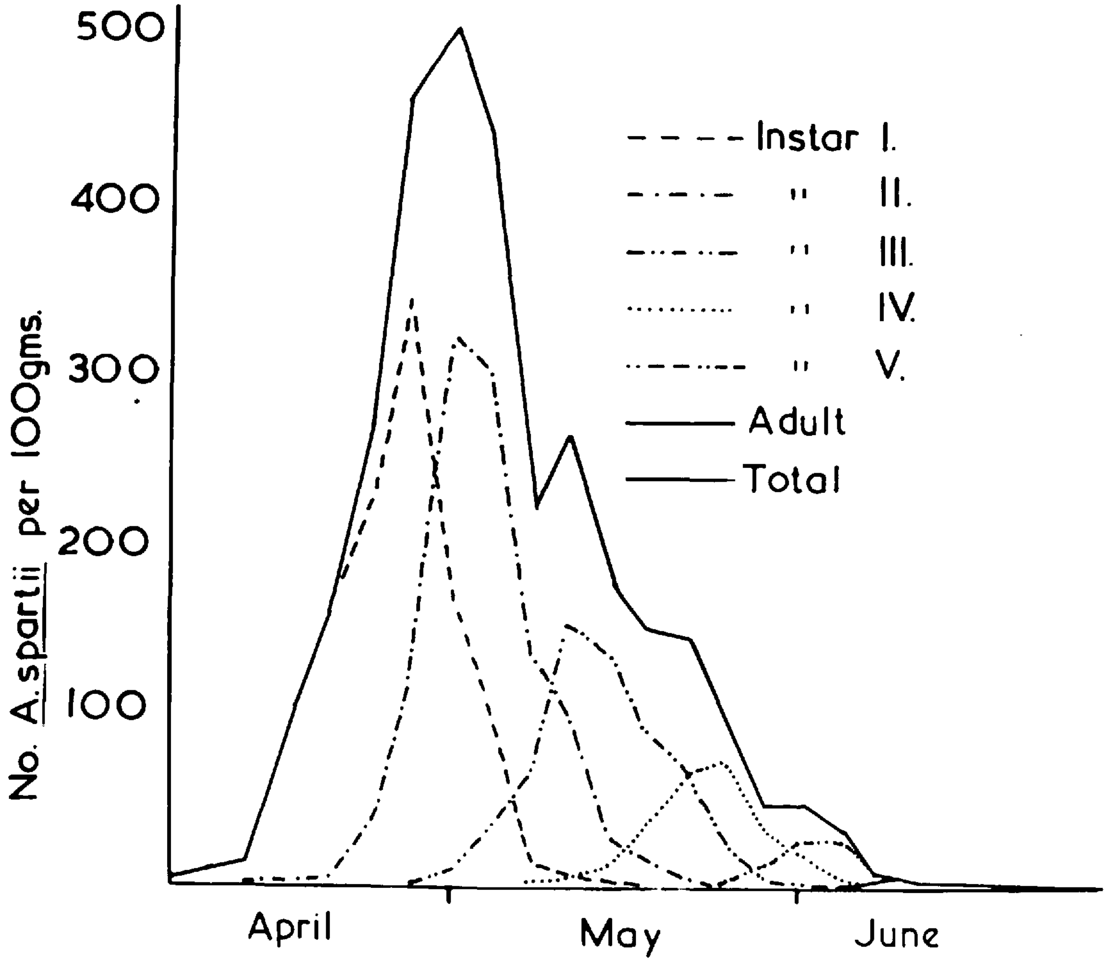


Table 7. Peak number per 100 grammes of broom of each stage in three A. spartii generations (1961 - 1963).

Stage	1961		1962		1963	
	Date	Peak Number	Date	Peak Number	Date	Peak Number
Instar I	9/3	6,446	13/4	460	26/4	346
II	16/3	4,923	1/5	382	30/4	324
III	6/4	3,106	8/4	178	10/5	157
IV	20/4	2,372	22/5	145	24/5	78
V	8/5	1,276	1/6	23	4/6	28
Adult	25/5	204	19/6	5	11/6	2

Table 8. Time taken for nymphal development in 1961 - 1963, compared with average daily maximum and mean temperatures.

Year	Number of days between start of hatch and appearance of first adults	Average daily maximum temperature	Average daily mean temperature in °C.
1961	85	14.15	8.38
1962	110	12.39	6.24
1963	64	16.42	10.01

Fig 7

The relation between the numbers of *A. spartii* hatching daily, daily maximum temperature and the number of 1st instar nymphs per 100 gms broom in the study area (1961)

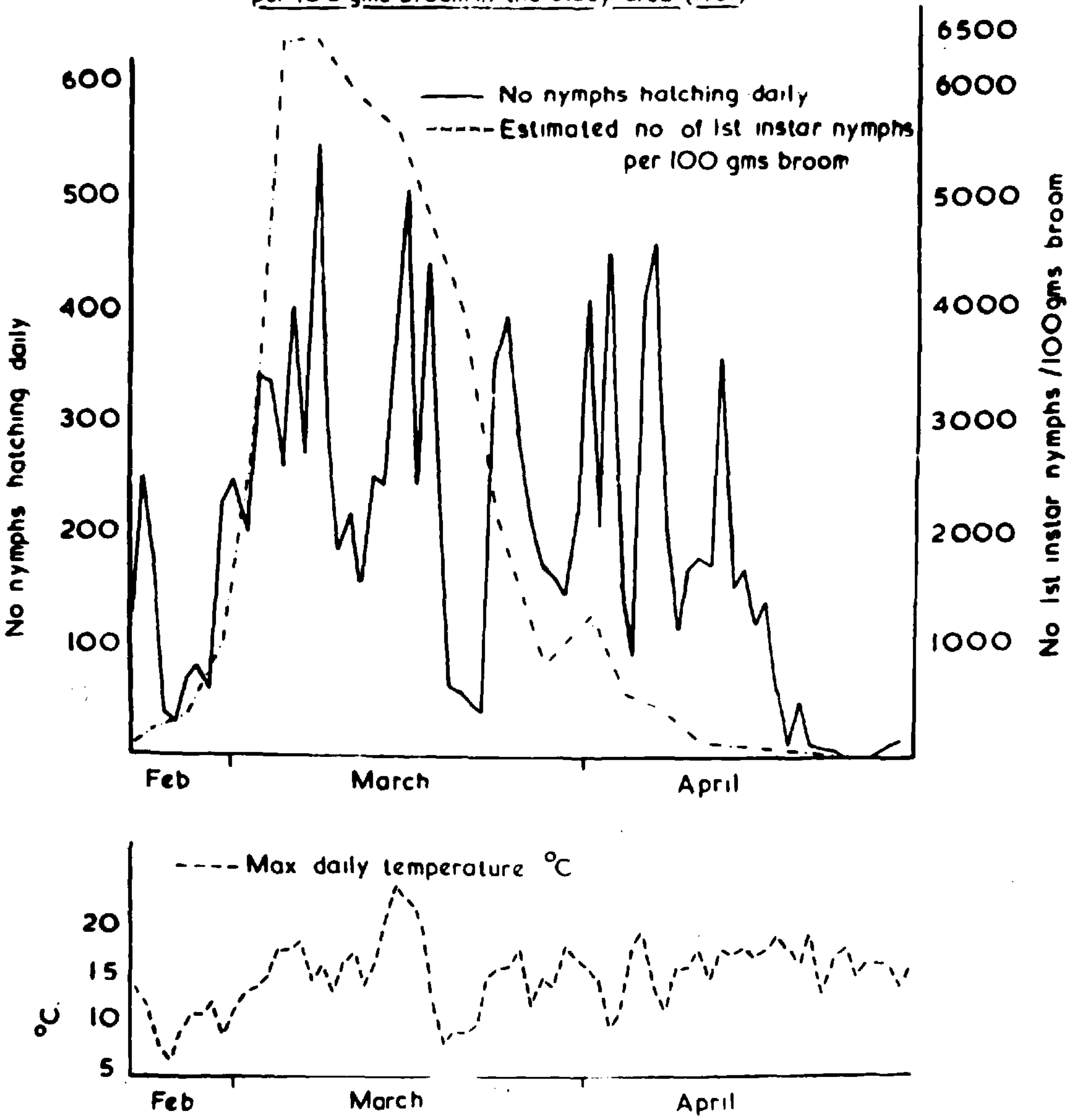


Fig. 8

The relation between the numbers of *Arytaina spartii* hatching daily, temperature and the number of 1st. instar nymphs per 100 gm. broom in the study area 1962

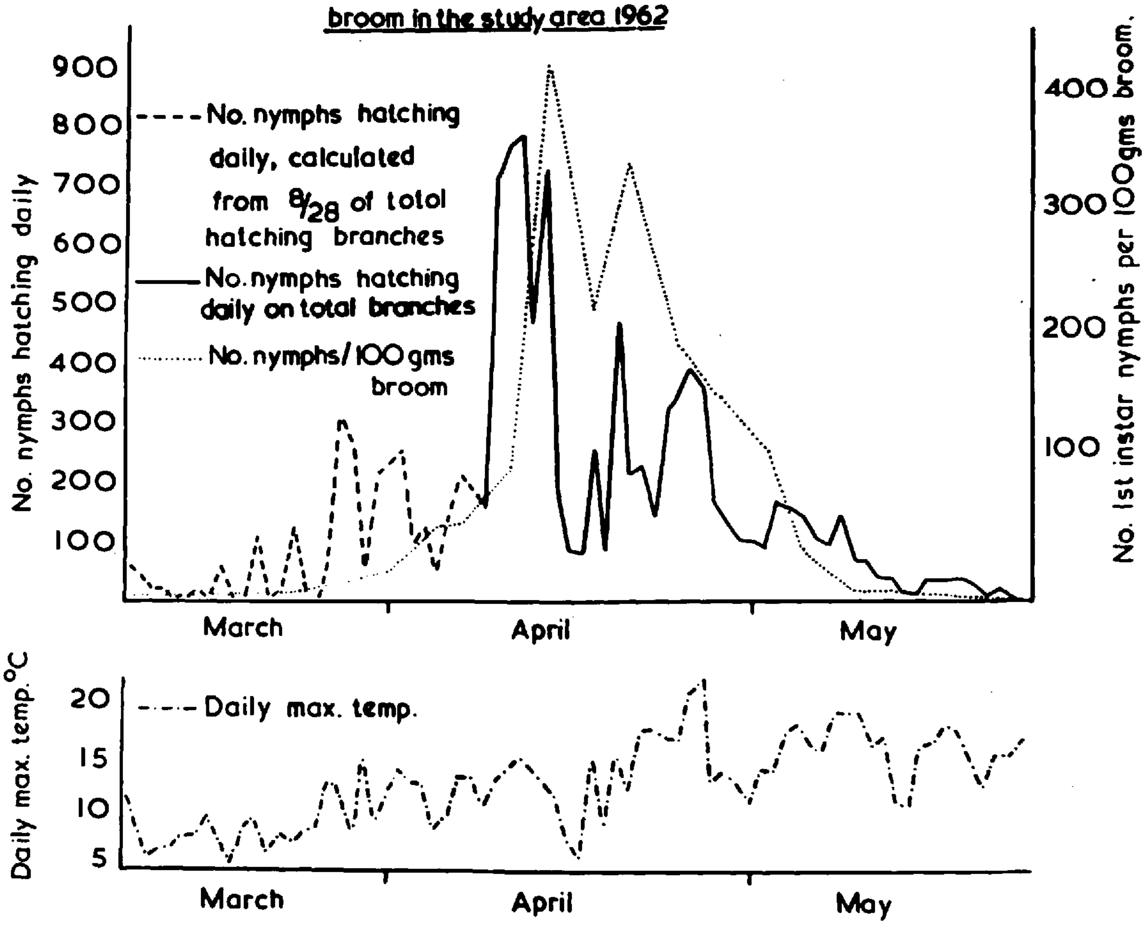
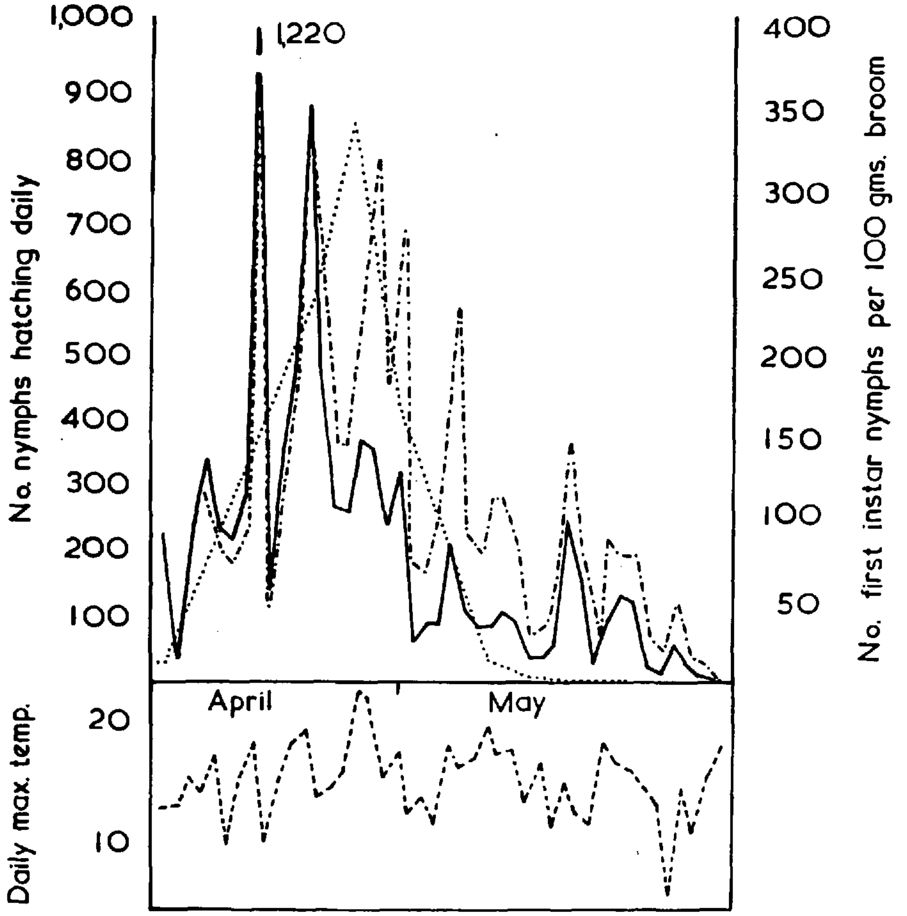


Fig. 9

Relation between numbers of *A. spartii* hatching daily, the daily maximum temperature & the number of Ist. instar nymphs per 100 gms. broom in the study area – 1963



—— No. nymphs hatching daily, shaded branches excluded

-.-.-.- No. nymphs hatching daily on all hatching branches

.... No. Ist. instar nymphs per 100 gms.

- - - - Daily maximum temperature

The average numbers of A. spartii nymphs present during the three years 1961 - 1963 were 3,032,130 and 166 respectively. These figures show that the population crash in 1961 resulted in a reduction of twenty times in the number of nymphs produced in 1962. The same reduction is evident in the number of eggs laid in the two years. The 1963 generation was similar in size to the 1962 generation and there was no evidence of any build up to another high population level.

Mortality in A. spartii.

Estimates of the number of eggs present in late summer, autumn or spring agree closely with one another. The figures for the numbers of nymphs hatching obtained by means of the equation method of data analysis in 1961 and 1962 are also similar and this suggests that virtually all the eggs hatch and that egg mortality is small. This is also supported by the small numbers of dead eggs found in samples (Table 14).

Discoloured, decomposing and shrivelled eggs were classed as dead in samples which were stored in alcohol. The proportion of dead eggs appears to have been largest in 1962.

The population graphs indicate a very high nymphal mortality. The results obtained by the three methods of analysis of the sampling data (cf section II) are shown in Tables 9 and 10. The estimated number hatching obtained by the simultaneous equation method is very close to the number of eggs present in 1961 and 1962. In 1963, however, the equation method gave an estimate which is far too low. The results from the regression method are not as good and the estimated hatch in 1962 is obviously too high. This has resulted in the estimated mortality during the early nymphal period obtained by this method being too high in that year. The regression method also appears to have given a poor estimate of the number of adults produced in 1962. The graphical method gives estimates of about half those one would expect from the number of eggs present, but the trend in the nymphal mortality is similar to that indicated by the simultaneous equation method except in 1963.

The results obtained indicate that about 25,000 nymphs hatched in 1961 and that 90 - 95% of them died before becoming adult. Most of them (60 - 65%) died during the first two instars. In 1962 about 1,300 nymphs probably hatched and there was a somewhat lower nymphal mortality (80 - 90%). In the first two instars mortality was greater in 1961 (66%) than in 1962 (52%). In 1963 the equation and regression methods are obviously unreliable. The graphical method indicates that total nymphal mortality was similar in 1962 and 1963 and that mortality in the first two instars was similar in 1961 and 1963. Other evidence discussed later suggests that nymphal mortality was highest in 1963.

The equation method then worked well in 1961 and 1962 but not in the third year. The reason for failure in 1963 was probably because of weakness in the recruitment data. This was partly because a third of the 24 hatching branches used were in the shade of trees. Hatching on the shaded branches was somewhat delayed and gave the impression of a fairly high hatching rate even when the number of first instar nymphs had fallen to a low level (Fig. 42). Most of the study area was unshaded. A better result can probably be obtained by removing the shaded branches from the calculations, but time was not available to test this.

The maximum density reached by nymphs in 1961 was 10,544, twenty times the peak densities present in 1962 and 1963. As has already been noted the numbers of first instar nymphs fell off more rapidly in 1961 than would have been expected from their rate of hatching (Fig. 7). In 1961 half of the total number had hatched by the time the peak in numbers had been reached while in 1962 and 1963 90% and 77% had hatched by this time. This suggests that A. spartii was suffering from overcrowding in 1961 and this, acting through increased mortality, prevented the numbers rising after only half of the nymphs had hatched. The rapid decrease in the numbers of first instar nymphs was most probably caused by their not being able to find buds not already packed with other larger individuals in a later stage of development. As many as 50 to 70 nymphs were often found in a single bud in 1961, while in 1962 and 1963 buds containing more than 4 to 6 nymphs were rare. It is most probable that mortality caused by crowding accounts for the difference between nymphal mortality in 1961 and 1962 (cf Section IV). Some other factor, possibly increased predation, must be responsible for the high nymphal mortality in 1963. A high nymphal mortality in 1963 was also indicated by the low peak number of adults produced (2 per 100 grammes) compared with 1962 (5 per 100 grammes). The 1962 and 1963 generations had a similar average number of nymphs. The ratio of the peak number

Table 9. Numbers of *A. spartii* produced per 100 grammes broom and percentage mortality calculated by different methods of analysis.

Year	Stage	Method of Analysis					
		Equations		Regression		Areas under curves	
		No. Produced	% mortality	No. Produced	% mortality	No. Produced	% mortality
1961	Instar I	26,781	16.70	25,110	40.14	10,028	39.83
	" II	22,317	49.00	15,031	15.66	6,034	19.27
	" III	9,201	21.60	11,100	11.14	4,102	18.84
	" IV	3,414	2.60	8,302	+18.60	2,213	11.54
	" V	2,722	+0.40	12,972	48.48	1,055	10.52
	Adult	2,832	10.57	799.29	3.18		
Nymphal mortality	Instars I & II	65.70%		55.80%		59.10%	
	Total Nymphal Mortality	89.43%		96.82%		89.48%	
1962	Instar I	1,356	57.41	4,415	68.15	449	22.03
	" II	577	+5.23	1,406	17.30	350	25.50
	" III	648	25.57	642	4.42	236	24.86
	" IV	302	+2.06	447	+6.18	124	20.72
	" V	330	5.82	720	+28.88	31	6.89
	Adult	251	18.50	1,995	45.19		
Nymphal mortality	Instars I & II	52.18%		85.45%		47.53%	
	Total Nymphal Mortality	81.46%		54.81%		93.11%	
1963	Instar I	993	+166.79	2,249	81.33	513	27.23
	" II	2,649	-80.58	420	+1.37	373	32.41
	" III	1,849	+29.95	451	+21.86	207	20.99
	" IV	2,146	-18.47	943	33.05	99	14.15
	" V	1,963	-2.15	199	7.79	27	5.21
	Adult	1,942	-2.13	24	1.08		
Nymphal mortality	Instars I & II	+86.21%		79.96%		59.64%	
	Total Nymphal Mortality	+93.41%		98.92%		94.79%	

Table 10. Estimations of the total number of *A. spartii* nymphs hatching by three methods of analysis.

Year	Total expected from actual numbers of eggs in samples	Total calculated by equations	Total calculated by regression	Total calculated by graphical method
1961	21,701 - 21,891	26,781	25,110	10,028
1962	1,199 - 1,419	1,356	4,415	449
1963	1,613	993	2,249	513

of adults to the average number of nymphs is also lower in 1963 than in 1961.

Many predaceous Arthropods are present on the broom during the time of occurrence of the nymphs and adults of *A. spartii* (e.g. Heteroptera, Coccinellids, Dermaptera, mites, harvestmen and spiders). Although the actual numbers of psyllids taken by each predator could not be estimated, the predators which do take psyllids in the field were identified by means of the precipitin test described later in Section III. Mortality caused by these predators appears to have been substantial in all three years.

Dead nymphs found in the samples are those killed by predators, unfavourable weather or other causes. Predators likely to leave shrunken dead nymphs inside buds are Heteroptera, neuropteron larvae, mites, spiders and harvestmen which suck the juices of their prey leaving the integument intact. Predators such as coccinellids and Dermaptera which have biting mouthparts could not be expected to leave any remains of a psyllid meal. The numbers of dead nymphs present follow the numbers of live nymphs fairly closely (Figs. 15, 16 and 17). Only low numbers of dead nymphs persist for more than a few days after living nymphs have disappeared. This indicates that dead nymphs do not accumulate and are easily lost. Any estimates of mortality based on the numbers of dead nymphs present are likely to be too low. The higher proportions of dead first and second instar nymphs in the 1961 samples suggest, however, that mortality in the first two instars was higher than in 1962 or 1963 (Table 11). This gives support to the results of analysis of the sampling data.

<u>Table 11.</u> <u>Comparison of numbers of dead and live *A. spartii* nymphs in samples.</u>

Year	The numbers of dead nymphs as a fraction of the numbers of live nymphs				
	Instar I	II	III	IV	V
1961	0.59	0.09	0.02	0.02	0.05
1962	0.06	0.07	0.08	0.02	0.06
1963	0.08	0.04	0.08	0.11	0.00

In 1961 dead nymphs were not counted before 23 March but it was noted that there were large numbers of dead first instar nymphs present even before this date. The dead first instar nymphs in 1961 were possibly killed by the effects of crowding and this would account for the apparent large disappearance of first instar nymphs already described.

Another mortality factor in 1961 could have been frost which occurred on 15 nights in March 1961 while the numbers of A. spartii nymphs were highest (Fig. 36). Fewer frosty nights occurred while numbers of the first two instars were high in 1962 and 1963 (Figs. 38 and 41). On four nights in March 1961 the temperature fell to - 3.3°C. and on two other nights it fell to -3.9 and -4.4°C. The later series of frosty nights coincided with a fall in numbers of live nymphs and a rise in numbers of dead nymphs (Figs. 15 and 36). In 1962 the lowest temperature reached while nymphal numbers were high was -3.9°C. on 1 May but there were only half the 1961 number of frosty nights while the first two instars were present. In 1963 the amount of frost (lowest temperature = -1.1°C.) was even less than in 1962 after nymphal numbers had risen above 13 per 100 grammes (Fig. 41). Frost then could have caused a higher nymphal mortality in 1961 than in other years.

The numbers of dead nymphs in the 1961 samples fell rapidly after the frosty period in March (Fig. 15). In spite of this the numbers of dead first instar nymphs was 1.13 times the numbers of live first instar nymphs. As in other years the dead first instar nymphs disappeared quickly after live nymphs were no longer present. This shows that mortality of first instar nymphs must have continued at a high rate after the frost. This mortality was most probably caused by crowding. Hatching continued at a high rate for some time after the frosts in March (Fig. 7).

Many of the dead nymphs, in various stages of decomposition, were embedded in the honey dew produced by older nymphs. The desiccated bodies of others were adhering loosely to stems and bud scales, mostly on heavily

Number of *Arytaina spartii* adults in 100 gms. broom in study area and in suction trap (1959 & 1960)

Fig 10

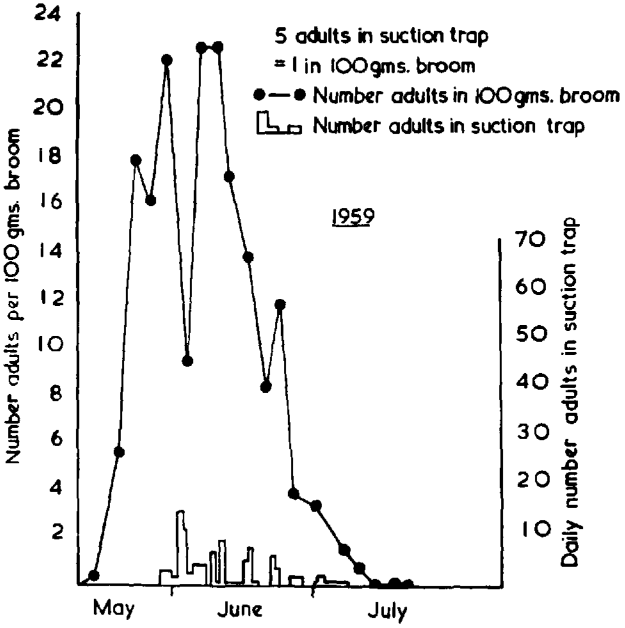
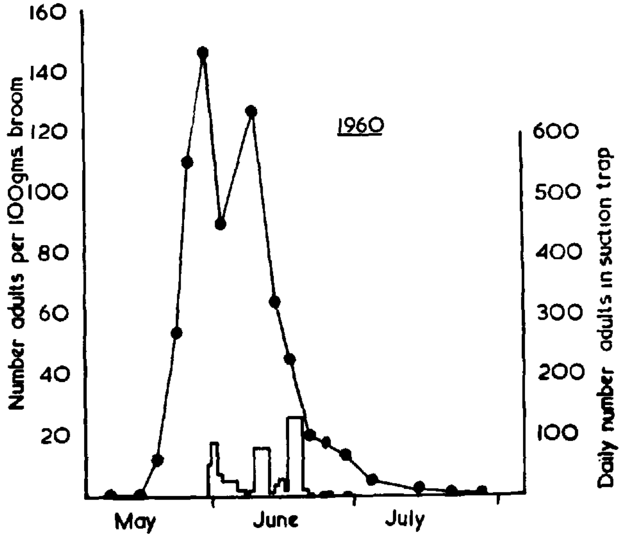
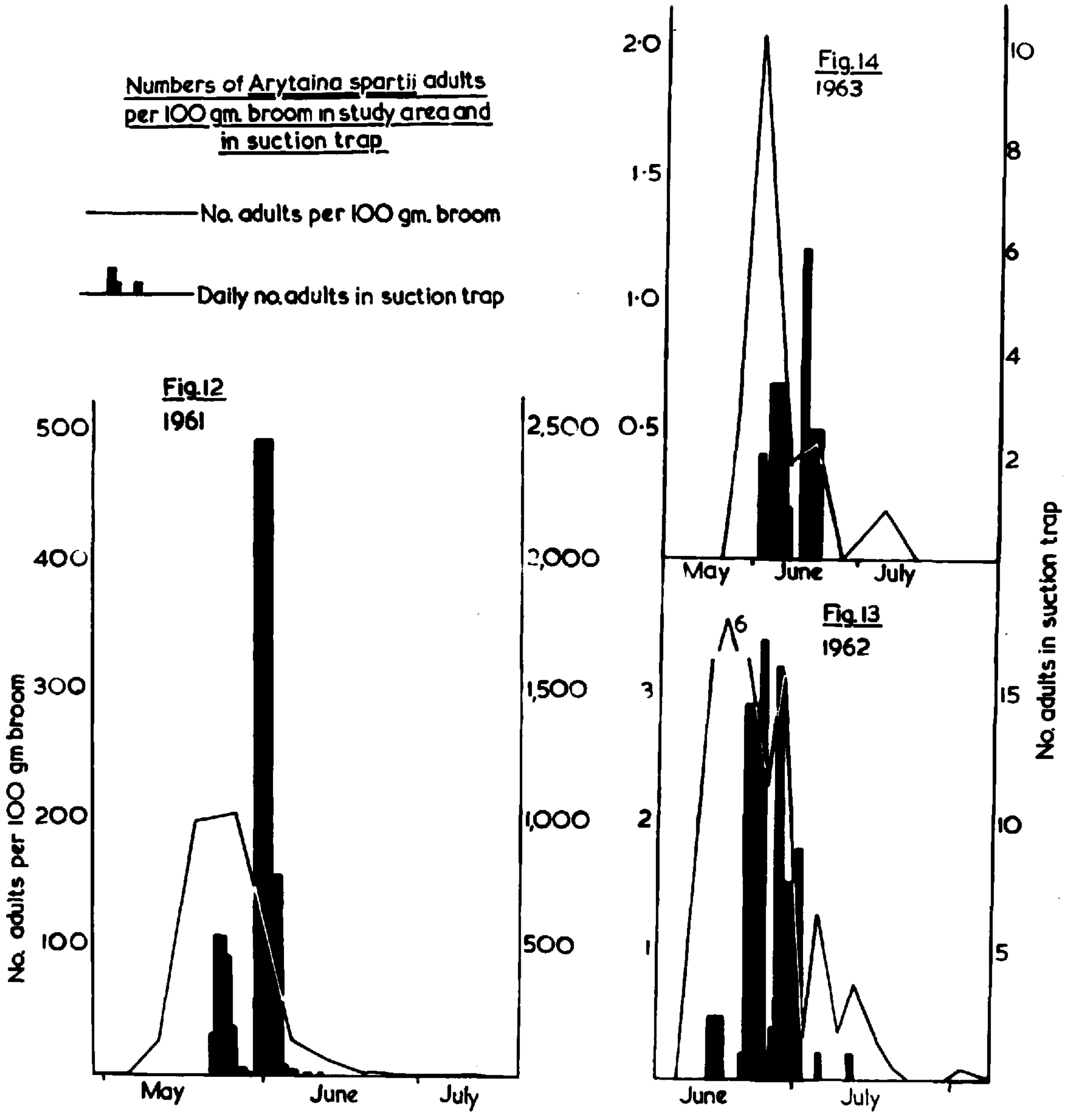


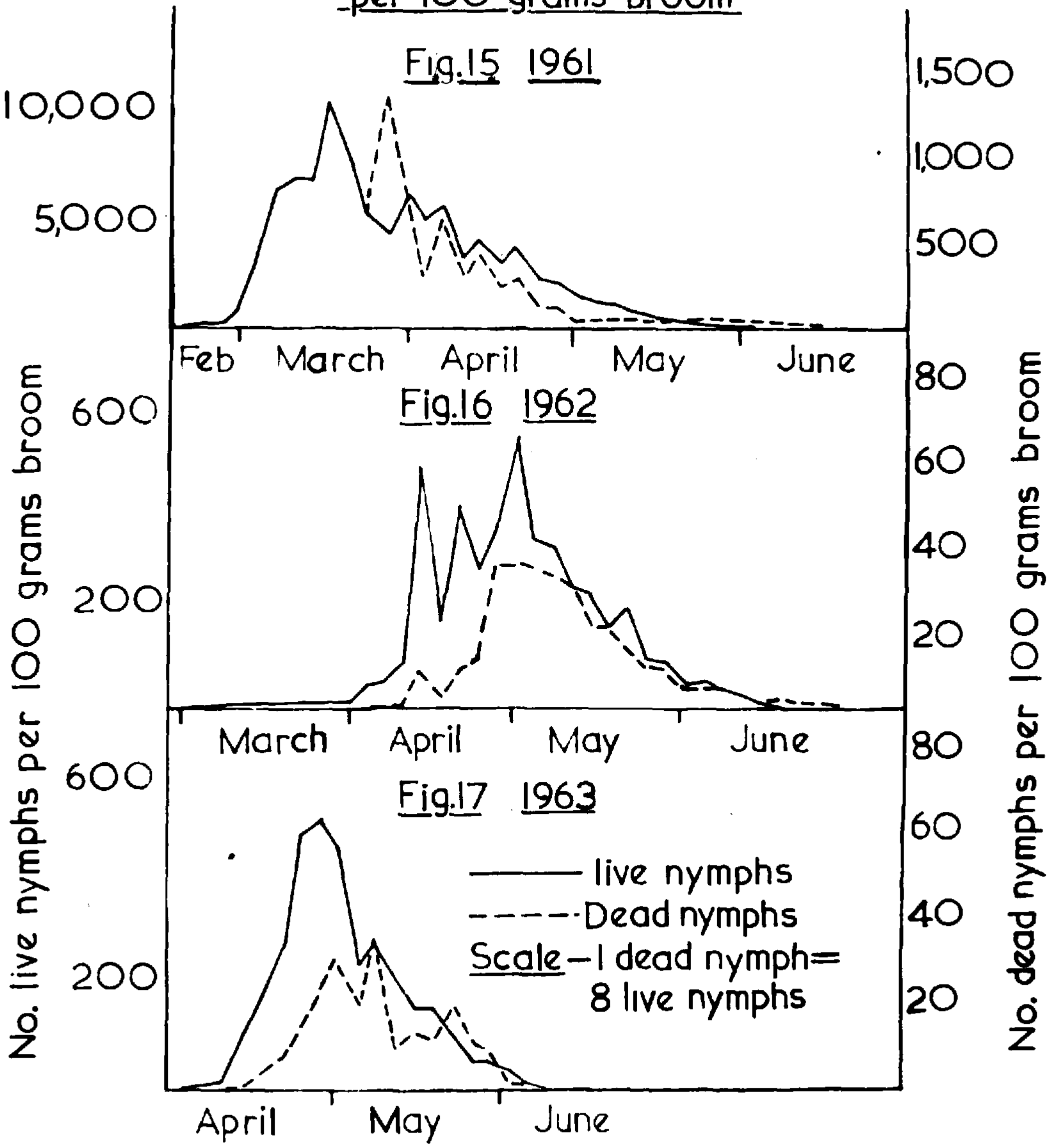
Fig 11



Numbers of Arytaina spartii adults per 100 gm. broom in study area and in suction trap



Numbers of live and dead Arytaina spartii nymphs per 100 grams broom



infested bushes. Mortality after the second instar in 1961 is rather lower than in other years according to Table 11. Dead nymphs in the 1962 and 1963 samples were probably mostly killed by predators. In 1963 there was a tendency for a higher percentage of dead nymphs near the end of the nymphal period. The average percentage of dead nymphs in 1962 and 1963 is rather similar (6.6% in 1962 and 7.1% in 1963). It is possible, however, that a high death rate in the fourth instar in 1963 could have cancelled the effects of lower mortality in other stages (Table 11).

The adults of A. spartii decrease fairly rapidly after they reach their peak numbers. The equation method indicates that 68 adults per 100 grammes of broom left the study area in 1961. This seems an insignificant number when there was a total of 2,832 adults produced per 100 grammes according to the equation method. The peak number of adults in the samples, however, was only 204 per 100 grammes and so the figure given by the equations seems far too high. If the peak figure from the samples is taken as indicating more accurately the number of adults produced, the emigration of 68 adults per 100 grammes appears more substantial and perhaps gives a better indication of what was happening. Almost the entire emigration (99% of total movement) occurred between 22 May and 6 June when the numbers of adults in the samples fell from 204 to 29 (see Fig. 12). After 6 June when emigration virtually ceased the rate of fall off of the adult population was less rapid. It appears therefore that emigration caused the rapid reduction of adults in 1961. The majority of adults which disperse probably die because of the small chance they have of being carried by air movements to another broom plant. In 1962 the equation method indicates a movement of 6.7 adults into the study area. In that year most of the adult movement (93% of the total) occurred while the numbers of adults in the study area were falling from the peak number of 6 per 100 grammes on 18 June to 1 per 100 grammes on 3 July (see Fig. 13). While movement was taking place in 1962 therefore the adult population fell by 83% compared with 86% for the period of adult movement in 1961. This does not indicate any less emigration in 1962. The 1962 adults laid rather more eggs than the far more numerous 1961 adults, however, and this suggests that a higher proportion of the adults may have remained to lay eggs in 1962. It is also possible that fecundity in 1961 and 1962 was different because of the crowding of adults on restricted oviposition sites in 1961 (Section IV).

In 1963 all adult movement occurred between 11 and 23 June, a time during which the adult population decreased from its peak level of 2 to 0.24, a fall of 88%. The number of eggs laid by the 1963 adults is not known.

The equation method of analysis indicates that 11 adults per 100 grammes left the study area in 1963. This figure seems far too high in relation to the peak number of adults in samples.

The occurrence of dispersal of adults in each year shows that this is a regular feature in the life cycle of A. spartii. Psyllid adults do not occur in the suction trap samples on every day during a flight period. The numbers in the suction trap vary widely from day to day and the period of dispersal is short, being marked by a few peak days. The numbers in the

Table 12. Wind direction during period of adult dispersal 1960 - 1963.

Year	Number of days in dispersal period	Fraction of days with wind blowing A.spartii from study area away from trap	Fraction of days of light variable wind	Calm days	Fraction of days with wind blowing from study area towards suction trap (westerly or northerly wind)
1959	40	0.10	0.08	0.13	0.70
1960	22	0.50	0.27	0.05	0.18
1961	21	0.42	0.14	0.05	0.37
1962	18	0.50	0.06	0.06	0.38
1963	12	0.58	0.17	-	0.25

Table 13. Comparison of numbers of A. spartii adults in suction trap with maximum number per bush in study area.

Year	Maximum number of adults per bush	Total number adults in suction trap	Ratio of maximum number adults per bush to total number in suction trap
1959	316	118	1 : 0.37
1960	3,880	850	1 : 0.22
1961	7,792	10,572	1 : 1.36
1962	223	131	1 : 0.59
1963	74	26	1 : 0.35

suction trap were influenced by wind direction and temperature. The days with the most adults dispersing were warm and sunny. Because the suction trap was situated south east of the study area a westerly or northerly wind was required to blow flying adults from the study area to the suction trap. A north west wind was the best. Winds coming from other directions blew psyllids from the study area away from the suction trap so that few or none were caught. Days with light variable winds were marked by fairly high numbers of psyllids in the suction trap often equal to the numbers on days with northerly or westerly winds. The fraction of the number of days in the dispersal period in each year when winds blew psyllids away from the suction trap are shown in Table 12. Only the main period of dispersal is considered, single adults on a few days after the main period being ignored. In 1959 the suction trap was 50 yards nearer the study area than in other years. This accounts for the greater frequency of winds blowing psyllids towards the suction trap in that year. Winds blowing psyllids away from the suction trap were most frequent in 1963 and occurred on half the days during dispersal in 1960 and 1962.

The numbers of adults found in the suction trap from 1959 - 1963 were related to the peak numbers of adults per bush in the study area as shown in Table 13. Winds are likely to have made the 1959 and 1961 figures high and the 1963 figures low. The large number of adults trapped in 1961 suggests that the proportion of the population emigrating may be density dependent.

The 1959 and 1960 figures for the numbers of psyllid adults in the study area are from carbon dioxide samples taken by Professor Richards, Dr. Waloff and Dr. Dempster. In 1959 and 1960 the pattern of adult movement was similar to that in other years (Figs. 10 and 11) occurring while the adult population was falling rapidly from the peak level. In both 1959 and 1960, however, the daily average numbers of adults in the suction trap during the dispersal period were much lower than in other years. This is easily seen by comparison of Figs. 10 and 11 with Figs. 12, 13 and 14. The 1959 figures are low in spite of the fact that the suction trap was 50 yards nearer the study area in that year. The dispersal period in 1959 was apparently much longer than in other years, however (Table 12). This might be a false impression gained because the suction trap could have sampled the dispersing adults better in that year through being closer to the study area.

The population of *A. spartii* increased between 1959 and 1961 (Table 13) and this suggests that a higher proportion of the adults remained to lay eggs in 1959 and 1960 than in 1961. The production of eggs by the 1962 adults suggests that fewer flew out than in 1961. The number of eggs laid each year indicates a similar number emigrating as data from the suction trap, in spite of possible wind effects.

The peak numbers of adults of *A. spartii* are one fourteenth to one fifth the peak number of fifth instar nymphs, a difference usually greater than that between the peaks of successive nymphal instars (see Table 7). It seems that there is a substantial disappearance of fifth instar nymphs and/or adults. The peak number of *A. spartii* adults is always reached before most of the movement and after most of the fifth instar nymphs have disappeared. This indicates that the disappearance is not caused by movement but most probably by death in the study area. The peak numbers of adults in A. genistae are much closer to the peak numbers of fifth instar nymphs (Table 15). Web spinning spiders might be responsible for this disappearance of A. spartii adults (Section IV.).

A. spartii females do not lay an egg in every incision they make and there are always more oviposition scars than eggs. The numerous females of the 1961 generation made about 17 trial incisions to every one in which they placed an egg (Table 14). The spring 1962 sample gives an estimate of 13 trial incisions to every egg. This fall off is most probably due to the missing of oviposition scars on stems covered with dirt after overwintering. Even though it is likely that the 1961 and 1963 spring figures for numbers of oviposition scars are too low it appears that the 1961 adults laid far fewer eggs per scar than in other years. This seems to be associated with the high density of the 1961 adults and their crowding on a restricted amount of young growth suitable for oviposition. Total rainfall in March - June 1960 was similar to that in 1961, but May 1961 had only half the amount of rain recorded in May 1960 (42.6 mm. in May 1960 and 20.1 mm. in May 1961). Adults appeared in mid-May 1960 and early May 1961. It is possible that the smaller amount of rainfall in May 1961 checked new growth on the already exhausted bushes at a time when the A. spartii population was densest. In May 1961 there was a period of 21 days without appreciable rain. The 1960 adults apparently had much more

Table 14. Dead *A. spartii* eggs and the number of trial oviposition sites in samples.

Date	Number of oviposition scars per 100 grammes	Number of dead eggs per 100 gm.	Fraction of dead eggs	Number of scars per egg
10/2/61	43,130	416	0.019	1.99
7/8/61	24,812	24	0.02	17.19
1/3/62	18,306	155	0.11	13.52
7/3/63	7,847	130	0.07	4.50

favourable conditions for oviposition on a large quantity of young shoots.

It is then possible that the great increase in the number of scars per egg in 1961 was due to the high density of the adult population aggravated by the restriction of oviposition sites. Egg-laying females in 1961 might have been disturbed by other adults and this might have been one of the factors involved in the reduction of the numbers of eggs laid. The effects of crowding on the number of eggs laid are discussed later (Section IV).

Emigration and possibly the reduction of fecundity of the 1961 adults were then probably responsible for the reduction of the 1962 generation to a small fraction of that of the previous year.

The Sex Ratio of *A. spartii*.

The numbers of the two sexes are more or less equal at the beginning of a generation but the males tend to die off more quickly than the females. One male can copulate many times and most females are fertilised within two weeks of their appearance.

The numbers of males in the suction trap are always less than the numbers of females. In 1960 - 1963 the numbers of males trapped varied from 27% of the total in 1963 to 41% in 1961 (mean = 34%). This suggests that the males are less active in dispersal than the females. All the females caught in the suction trap were mature with fully developed eggs in their oviducts - all had mated.

Population Changes in *Arytaina genistae*. 1960 - 1963.

Fluctuations of the population of *A. genistae* in the study area over five complete and one partial generation are now described. All figures are again given in terms of the numbers per 100 grammes of broom. Total numbers for the whole study area are given in Table 15.

(a) First Generation, 1961. (See Figs. 18 and 19 for egg and nymph population estimates).

When sampling for adults began on 10 October, 1960, there was a population of 0.15 per 100 grammes (Fig. 27), much lower than the numbers present earlier in 1960. The highest estimate for the adult population in

Fig. 18

Estimates of numbers of *A. genistae* eggs and nymphs per 100 gms. broom in the study area — 1961.

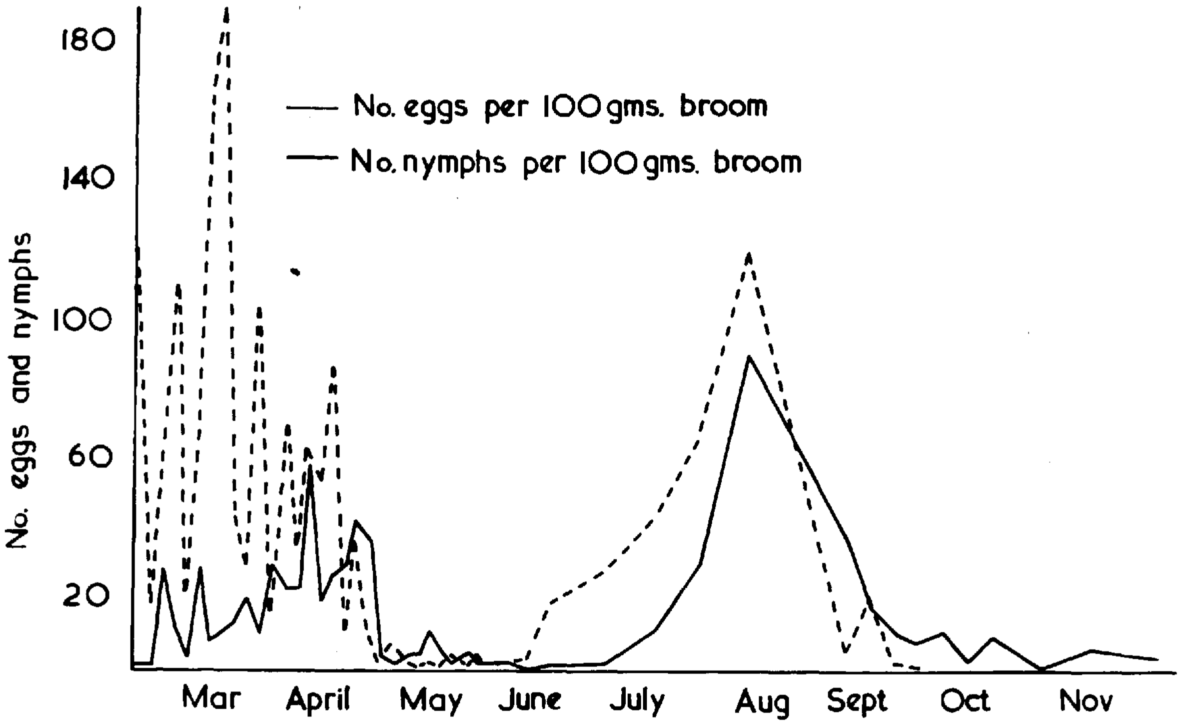


Fig. 19

A. genistae population estimates. 1st generation 1961

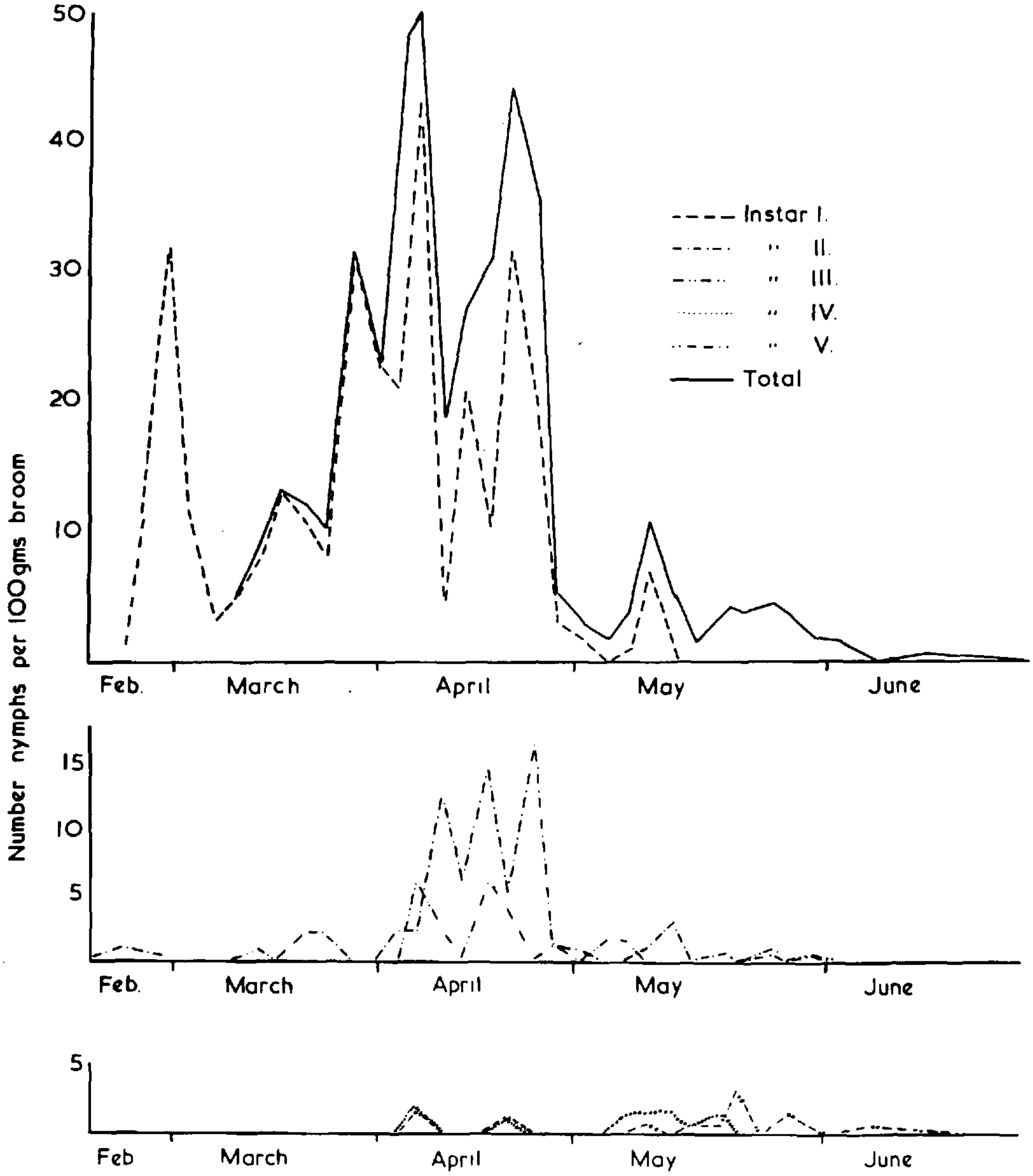


Table 15. Peak numbers reached by each of nymphal instars and adults of A. genistae in each generation.

Stage	1961				1962				1963	
	First generation		Second generation		First generation		Second generation		First generation	
	Date	Peak Number	Date	Peak Number	Date	Peak Number	Date	Peak Number	Date	Peak Number
Fresh Eggs	13/3	192	10/8	78	31/3	951	31/7	241	12/4	474
Eggs with eyespots	-	-	10/8	41	24/4	268	16/8	58	23/4	94
Instar I	6/4	46	10/8	47	8/5	166	12/9	45	17/5	93
II	24/4	17	10/8	28	18/5	81	12/9	27	24/5	23
III	6 & 17/4	6.25	10/8	7.83	1/6	27	12/9	20	4/6	7.07
IV	6/4	2.08	10/8	6.91	12/6	20	28/9	7.41	7/6	4.19
V	25/5	3.51	5/10	5.18	19/6	5.75	21/9	2.22	11/6	1.33
Adults	6/6	1.88	26/10	5.38	3/7	5.25	24/10	2.30	27/6	0.28
Average number nymphs present in generation per 100 gm.	51		39		243		137		180	
Average total number present in generation in entire study area	2,135,000		1,717,000		14,896,000		8,459,000		10,685,000	

the autumn of 1960 was 0.17 between 9 and 11 November. After this the numbers decreased steadily through the winter until there were only about half this number when sampling for eggs and nymphs started on 15 February 1961.

The data for this generation is very variable because of the large sampling errors arising from the low numbers of samples taken (see Section II). The peak numbers reached by eggs, the nymphal instars and adults in this and other generations are shown in Table 15. The dates of the peaks of successive stages do not form a series because of the low numbers present and the large sampling errors.

The adults which had overwintered continued to decrease until they died out about 5 May. The egg numbers declined with the adult numbers until none were found on 15 May. The first new adults appeared between 8 and 11 May, 86 days after sampling started at the beginning of the generation.

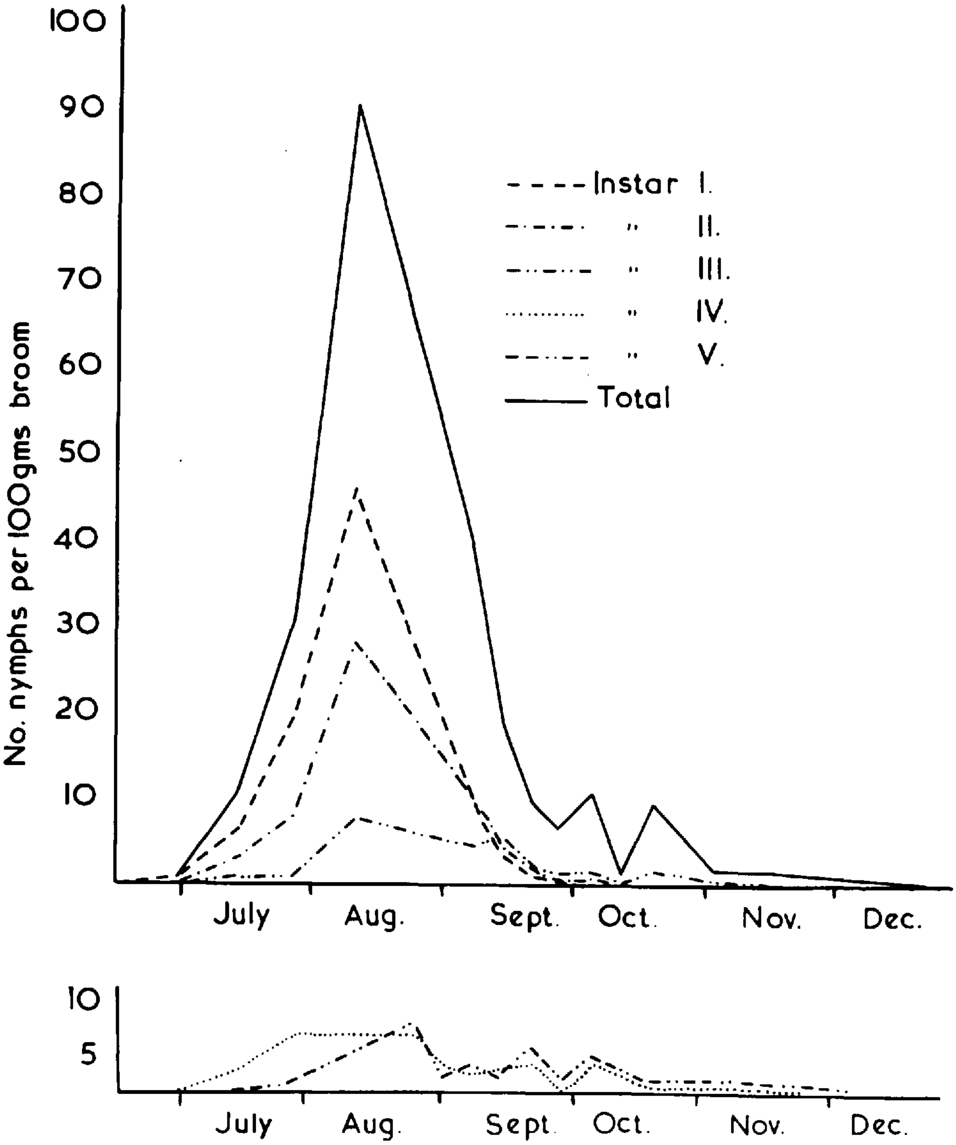
(b) Second generation, 1961 (Figs. 18 and 20).

The adults produced by the first generation started laying by 18 May, ten days after they first appeared (Table 16). Between 23 June and 13 August a few adults dispersed but it is probable that the numbers flying out were insignificant (Fig. 28).

The numbers of eggs present steadily increased after 18 May until the peak of 119 eggs was reached, 85 days after laying had started. After 21 September no eggs were present and it is most probable that the first generation adults had died out by that time.

Fig. 20

A. genistae population estimates (2nd generation 1961)



In spite of the fact that this generation was somewhat smaller than the previous one, many more adults were produced, the peak of adult numbers being almost three times that of the first generation (Table 15). The coincidence of the peaks of the eggs, first, second, third and fourth instars in this generation is caused by the long periods between samples taken. The peaks of some stages have therefore been missed. The second generation adults appeared on 10 August, 41 days after the first nymphs hatched and far more quickly than in the preceding generation (Table 17). The length of the generation from the time the first nymphs appear to the time when the first adults appear is closely correlated with the average mean daily temperature ($P < 0.05\%$. See equation at the bottom of Table 17). This generation developed more quickly than any other because of high temperatures. Only two adults of this generation were found in the suction trap compared with 9 from the previous generation (Fig. 28). These two were at the beginning of the adult period when adult numbers were still low. This indicates that hardly any of the second generation adults emigrated in spite of the fact that the density reached was much higher than in the previous generation. Temperatures were not much lower in September and early October when the second generation adults reached peak numbers than in June when first generation adults dispersed. Daily maximum temperatures were between 17 and 19°C. up to mid October. It was not low temperatures then that prevented the second generation adults from dispersing.

(c) First Generation, 1962 (Figs. 21 and 22).

The adults of the second generation of 1961 began laying about 2 November 1961. The numbers of eggs rose gradually throughout the winter, but no appreciable hatching took place until 8 February, when 19 first instar nymphs per 100 grammes were present. Low temperatures, however, kept the numbers of first instar nymphs at a low level until after 20 April. Records of the numbers of eggs laid by females in sleeves started on 8 December 1961 and egg-laying was more or less uninterrupted throughout the winter. After 15 January the egg-laying rate rose steadily from between 0.4 to 0.7 eggs per female per day until a maximum rate of between 8 and 16 eggs per day was reached after 18 April (Fig. 30).

By the time the peak of egg numbers had been reached in the first 1962 generation, 60% of the total number of eggs for the generation had been laid and this was 6 days before the number of first instar nymphs began rising appreciably.

The numbers of eggs and nymphs fell off rapidly as the number of laying adults decreased. By the time the maximum rate of egg-laying had been reached after 18 April the number of adults was between 0.4 and 0.5 per 100 grammes and steadily decreased until none occurred on 4 June (Fig. 28). The last nymphs of this generation were recorded on 13 July.

The average number of individuals (including eggs) present in this generation was much larger than in the 1961 generations. In spite of this the first 1962 generation produced a peak number of adults similar to that of the second 1961 generation (Table 15). Some of the adults of the first

Fig. 21.

A. genistae. Estimates of total eggs and nymphs per 100gms broom 1961–62

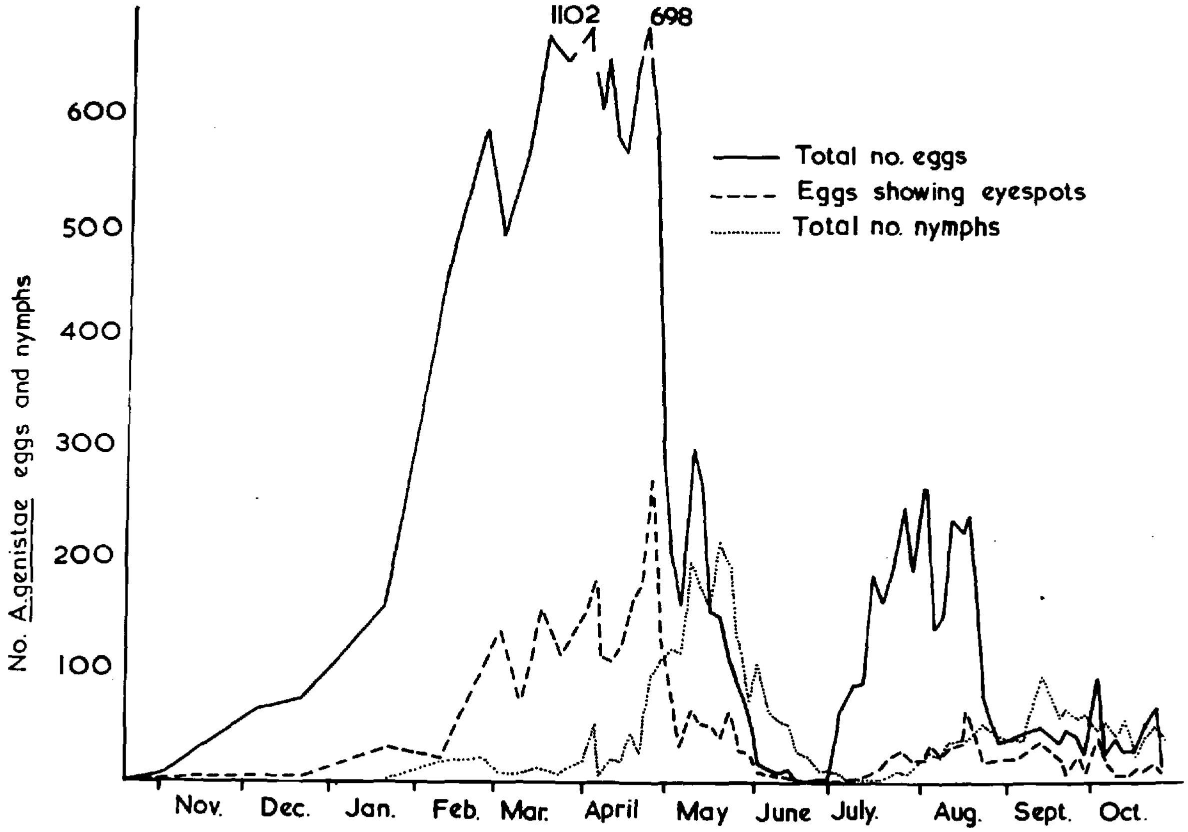
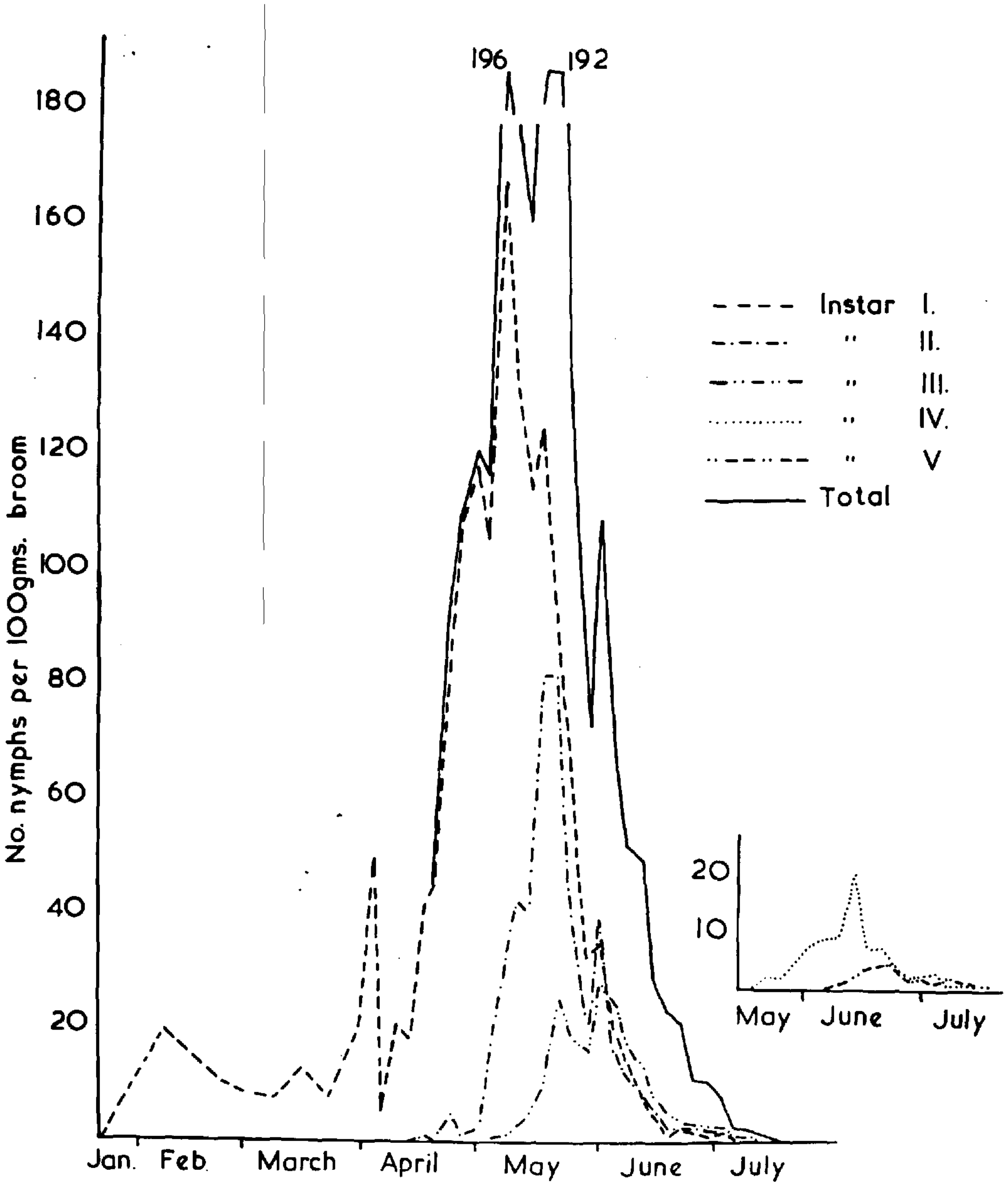


Fig. 22

A. genistae population estimates. First generation 1962



1962 generation dispersed between 27 June and 3 August, a total of 58 adults being found in the suction trap compared with only 9 for the first 1961 generation (Figs. 28 and 29).

(d) Second Generation, 1962 (Figs. 21 and 23).

The first eggs of this generation were found on 22 June. After this the average number of eggs laid per female per day rose quickly from 9 between 26 June and 3 July, to 17 between 4 and 10 July (Fig. 30). The highest number of eggs laid per female was a daily average of 19 between 25 and 31 July. The peak in egg numbers was reached at a time when the number of eggs laid per female per day began to fall. The number of adults was 3 compared with 0.6 at the much higher peak in egg numbers in the preceding generation so that fecundity was undoubtedly lower. After the peak in egg numbers in the second 1962 generation the number remained fairly constant for 16 days after which it fell sharply to one sixth of the peak number (peak number = 240 per 100 grammes) on 28 August. After this the number of eggs remained fairly constant for two months (Fig. 21).

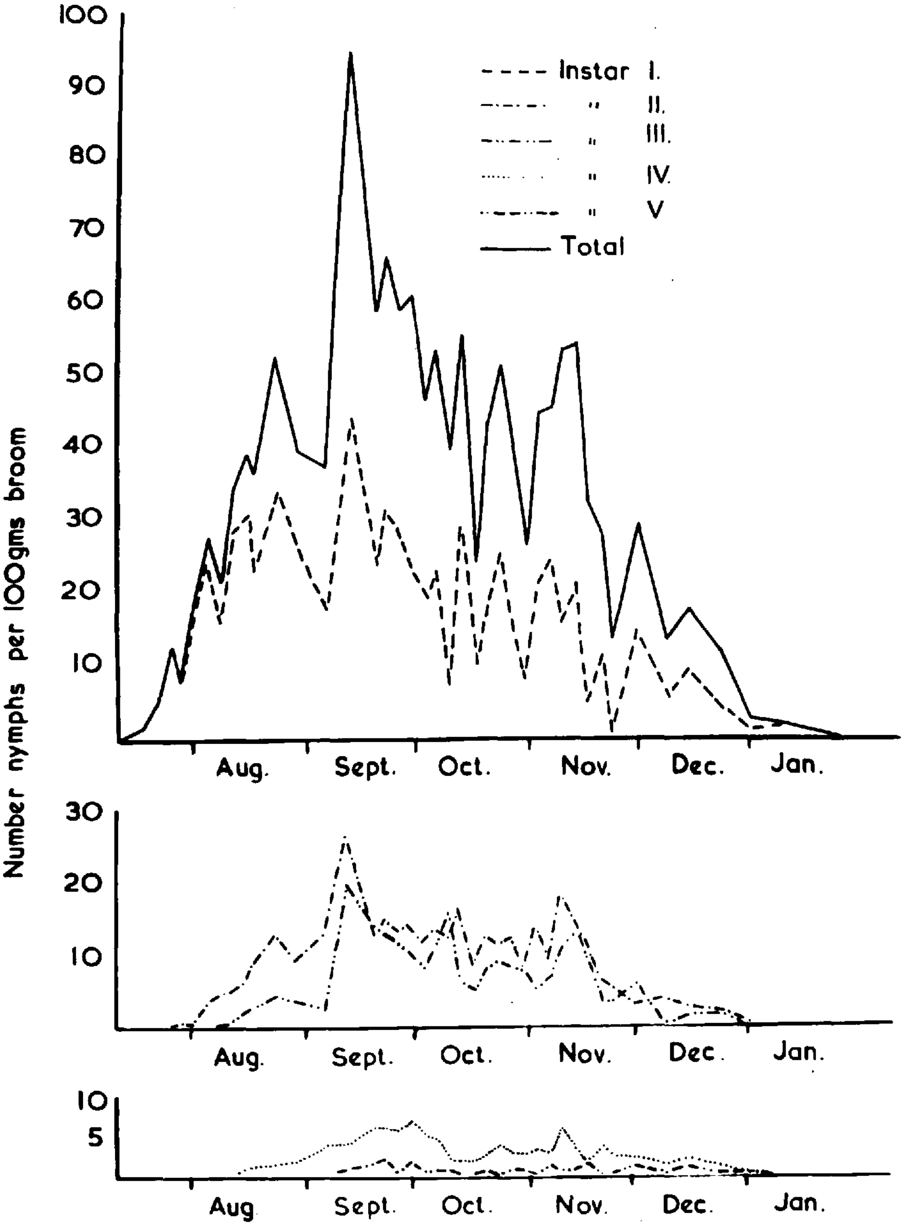
By the time the first adults of this generation appeared it is probable that the adults of the first generation had almost died out. The egg-laying rate had fallen to between 0.5 and 1 egg per female per day (Fig. 30).

(e) Partial Third Generation, 1962 (Figs. 24 and 23).

The numbers of eggs which had been fairly constant for some time, began to rise at the end of October. From a level of between 30 and 60

Fig. 23

A. genistae population estimates (2nd and partial 3rd generation 1962)



the numbers of eggs rose to 185 by 8 December (Fig. 24). This rise in numbers was due to the start of laying by the new adults of the second 1962 generation. This was about 35 days after they had first appeared. At this time there were eggs and nymphs of all stages of their own generation still present so that it was impossible to separate the two generations. In the second generation of 1961 the new adults took more than twice as long to lay their first eggs (Table 16) in spite of the fact that temperatures were higher. This ensured that the eggs of the 1961 adults only appeared after eggs and younger nymphs of the preceding generation had disappeared. In the first generation of 1961 and 1962 the new adults laid about a week after they first appeared. As can be seen from Table 16, the time taken for the adults to lay their first eggs is not related to temperature. Some other factor such as decreasing day length during nymphal development or adult maturation might be responsible. The 1962 second generation started about a month later than the second 1961 generation but the reason why the adults started laying sooner in 1962 is obscure.

The last nymphs were found on 15 January 1963 and there was ample time between the end of October and then for nymphs of a third generation to hatch. Temperatures were lower in the autumn of 1962 than in 1961 and it therefore appears unlikely that any of the third generation nymphs reached the adult stage. The time between the first appearance of first instar nymphs and the first adults in other generations varied from 41 to 127 days. The number of days between 31 October 1962 and 15 January 1963

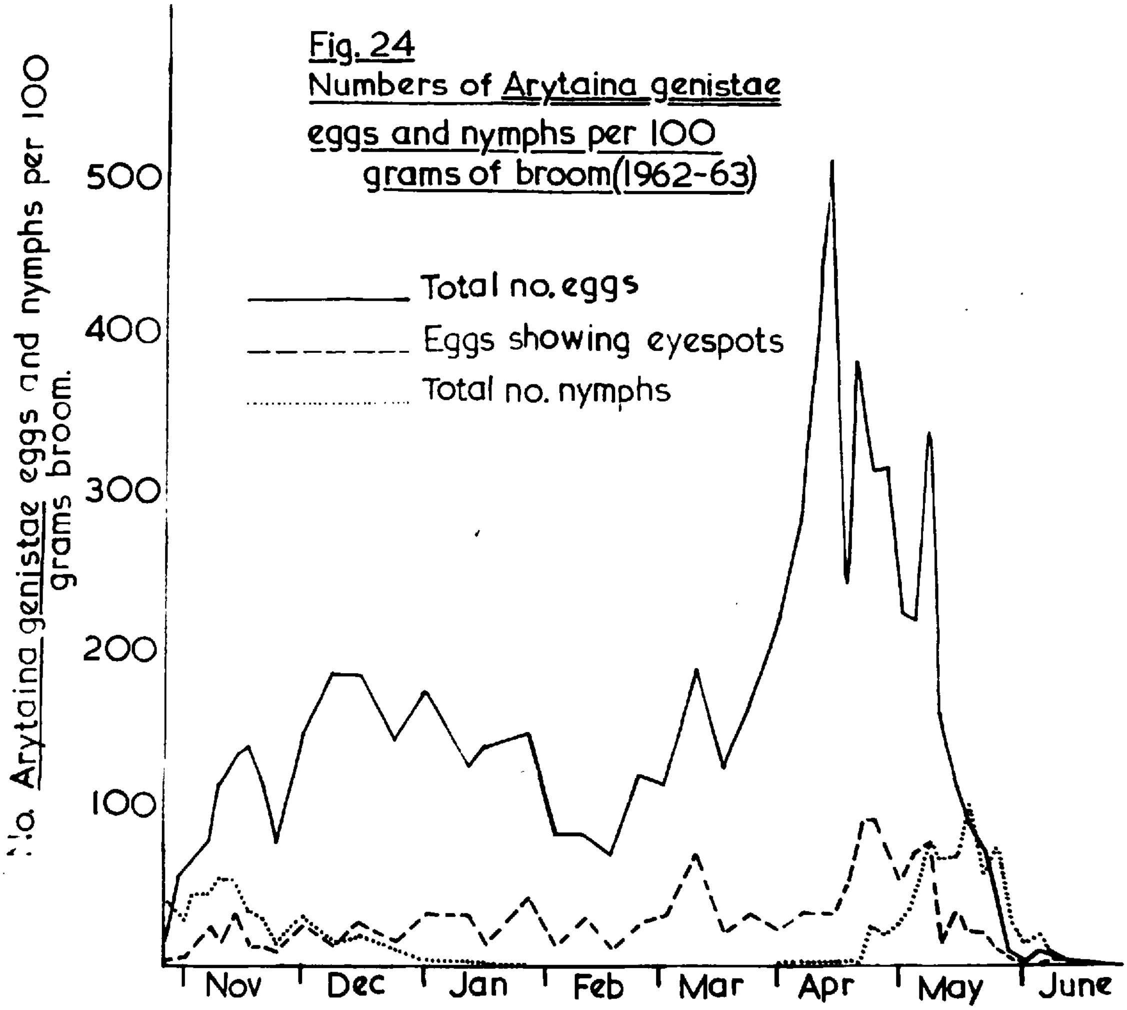


Fig. 24
Numbers of *Arytaina genistae* eggs and nymphs per 100 grams of broom (1962-63)

Table 16. The time taken for maturation in *A. genistae* and temperature in °C.

Generation	Time between first adults and first eggs	Average mean daily temperature	Average maximum daily temperature
First 1961	10	11.35	18.71
First 1962	7	16.04	22.11
Second 1961	84	13.07	19.39
Second 1962	35	9.55	15.83

is 76 and this is clearly too short a time for the third generation to have produced adults with the low temperatures prevailing at the time (Table 17).

During the period of this partial third generation of 1962 the rate of egg laying per adult female remained at a fairly constant low level of between 1.8 and 0.3 eggs per day (Figs. 30 and 31). Laying stopped altogether after 23 December when a prolonged spell of very cold weather set in.

The fall off in numbers of the first generation of 1962 is steeper than that of the second generation. This is connected partly with the dying out of the overwintered adults producing the first generation eggs. In the second generation adult recruitment continued for a longer period after peak numbers had been reached and eggs were

Table 17. Relation of temperature in °C. to time between first nymphs and first adults produced by five generations of *A. genistae*.

Generation	Number of days taken for nymphal development	Average daily mean temperature. °C.	Average daily maximum temperature °C.
	y	x	
First Generation 1961	86	8.49	14.47
Second Generation 1961	41	15.89	22.94
First Generation 1962	127	6.22	12.19
Second Generation 1962	77	13.78	19.95
First Generation 1963	67	10.43	17.03

Regression equation: $y = -7.1002 (x - 10.9656) + 79.60$

present for the whole time.

The data for the period between 20 October and 30 November are more variable than those for the first generation, probably because the nymphs and eggs had a more patchy distribution. For much of the second 1962 generation numbers did not change quickly and this would have also tended to make sampling error more conspicuous.

(f) First Generation, 1963 (Figs. 24 and 25).

After 23 December 1962 when laying by the overwintering adults ceased the numbers of eggs declined gradually from the peak of 185 per 100 grammes reached in the partial third generation until the lowest level of 70 per 100 grammes was reached on 16 February. Sixty per cent of the eggs present on 8 December had therefore been lost by 16 February without any hatching taking place. It is probable that laying started again after 16 February as egg numbers show a rise to 113 per 100 grammes by 2 March in spite of the fact that snow only disappeared on 4 March. Very few eggs (3 in 7 sleeves with surviving females) had been laid in sleeves which were buried under the snow for the entire period.

The egg-laying rate rose steadily after 26 February from 1.8 per female per day between 26 February and 12 March to 22 eggs per female per day between 23 and 30 April. The numbers of eggs in the samples rose to the peak of 508 by 12 April by which time about half the total number of eggs for the generation had been laid (Fig. 31).

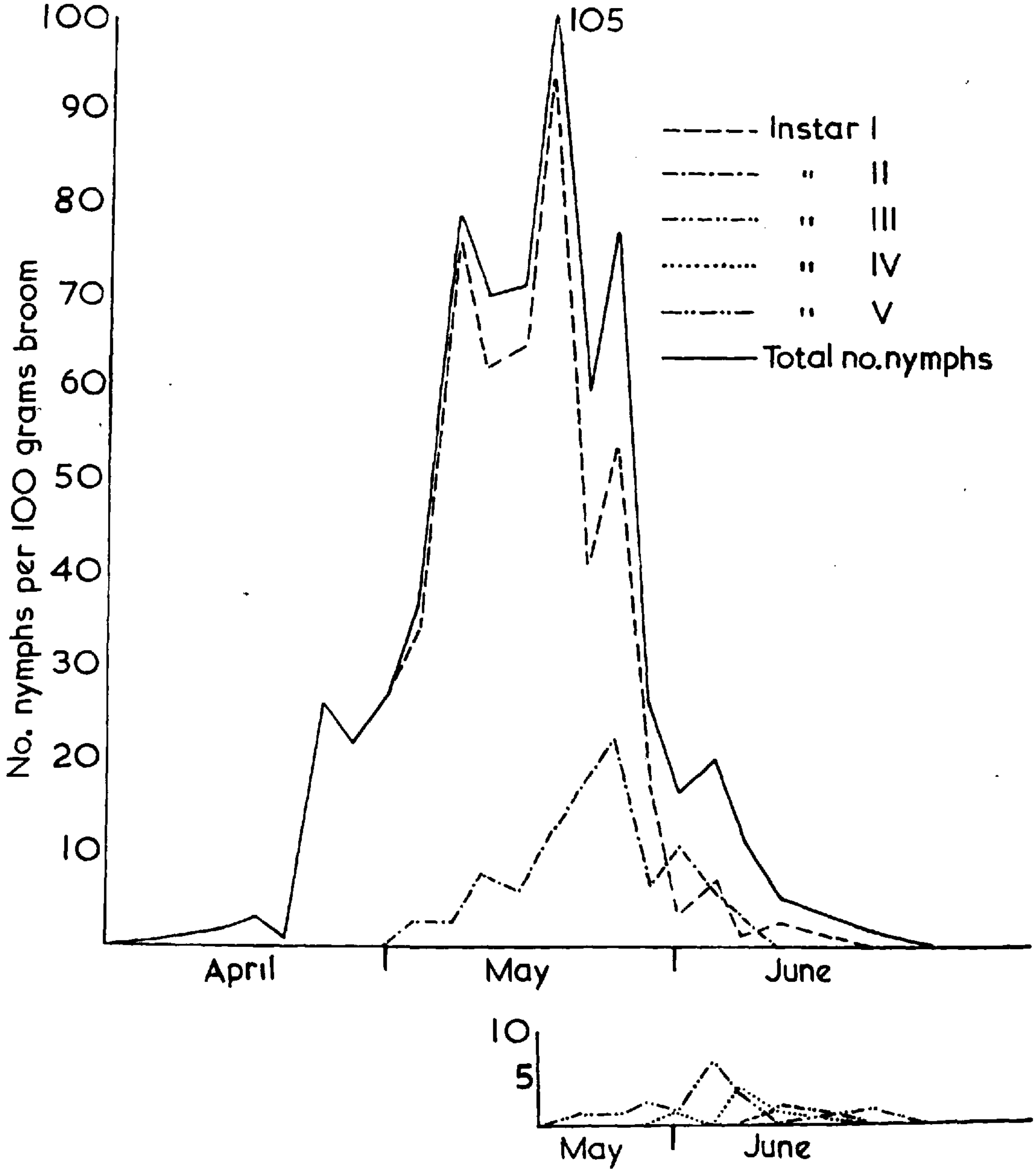
In spite of the fact that the average number of eggs and nymphs present in this generation was the second highest of all the five generations observed, the number of adults produced was the smallest recorded (Fig. 29). This suggests that mortality was highest in this generation. Only one fifth instar nymph was found in all the samples.

As can be seen from the description of the data from each of the generations studied, the number of adults produced is not closely related to the number of eggs laid, which in turn is not necessarily related to the number

Fig. 25

Arytaina genistae population estimates

First generation 1963



of adults present. Mortality and fecundity both varied considerably from generation to generation. The highest numbers were reached in the spring of 1962 after a build up over two generations from the spring of 1961. After the spring of 1962 the numbers of *A. genistae* fell to a low level again by the middle of 1963. An attempt to explain some of the possible causes for these population changes is made below.

(g) The *Arytaina genistae* population in the study area in 1959 - 1960.

Figures for the psyllid adult population in the study area were obtained in 1959 and 1960 by Professor O.W. Richards, Dr. N. Waloff and Dr. J.P. Dempster (Figs. 26 and 27). The broom in the study area was planted early in 1957 and colonised rapidly by psyllids. By 1959 the numbers of *A. genistae* had reached a high level (Table 18). High numbers were repeated in three generations until there was a crash in numbers at the end of the first generation in 1960. *A. genistae* therefore stopped increasing sooner than *A. spartii* and did not achieve such high densities (Table 18).

In 1959 *A. genistae* seems to have had three complete generations, each represented by a separate peak (cf Fig. 26). The summer of 1959 was very warm (average daily mean temperature in June - September = 16°C.) and psyllids ~~c~~would have developed quickly (see regression equation under Table 17). The warm weather continued into October and there was probably enough time to complete a third generation between early August, when the second generation adults were near peak numbers, and the end of September. In the warmer climates of southern Europe *A. genistae* probably

Numbers of *A. genistae* adults per 100 gms. broom in study area and in suction trap

Fig. 26

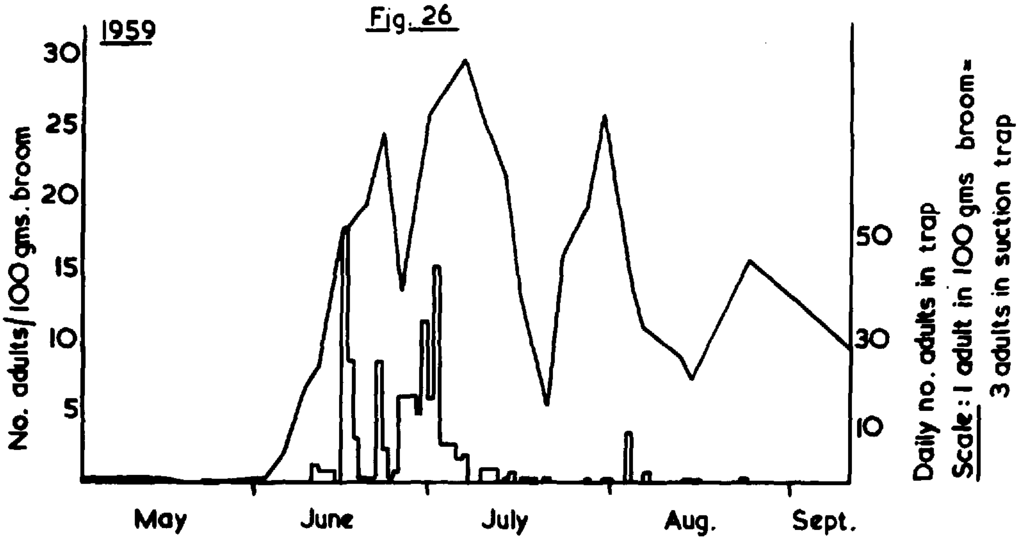


Fig. 27

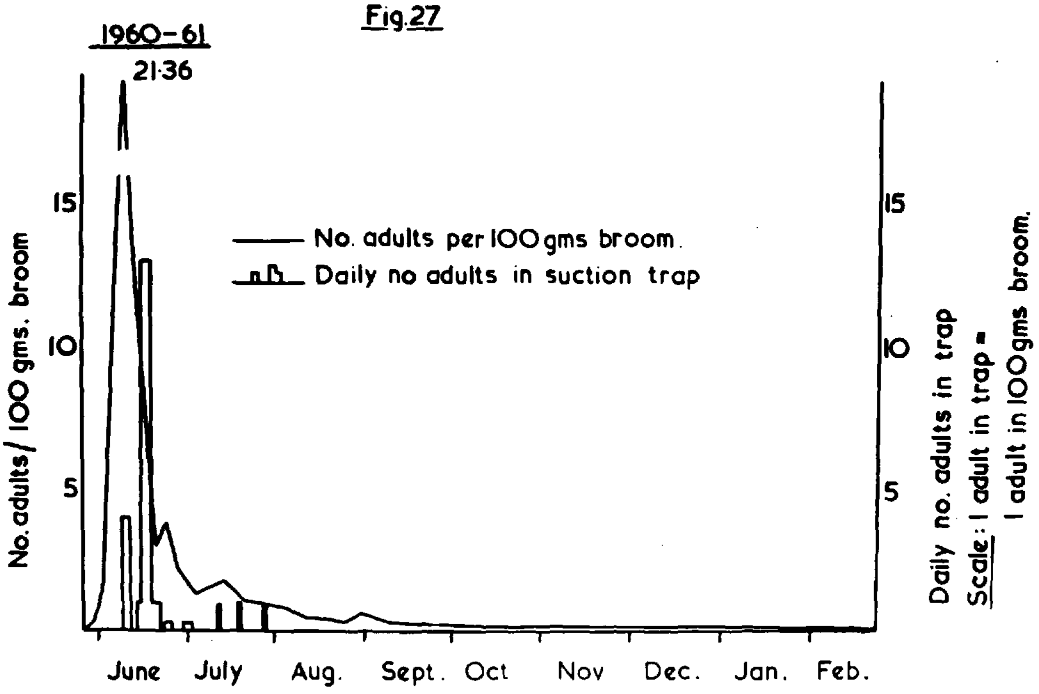


Fig. 28

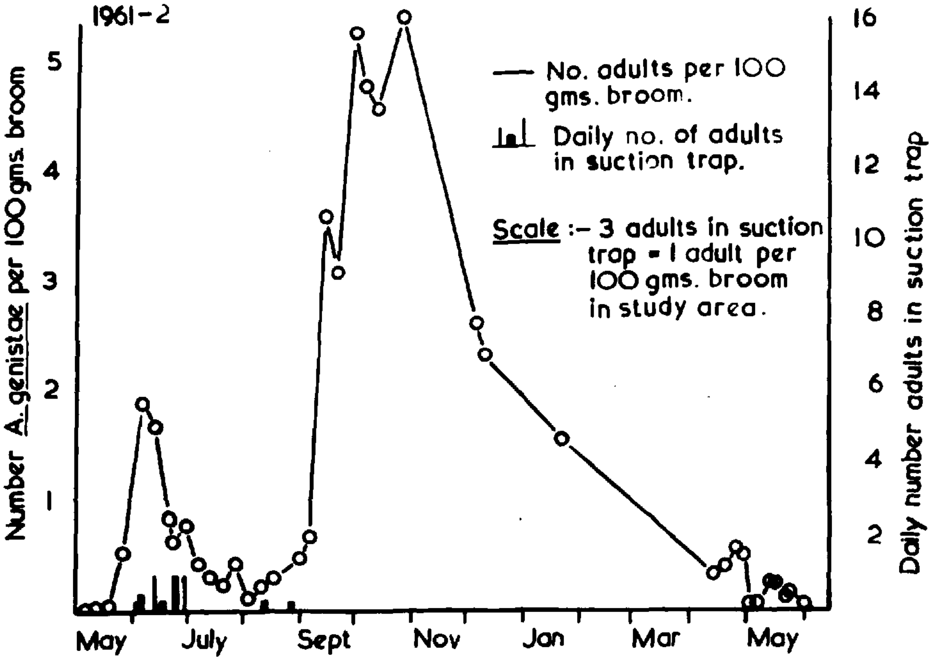

1961-2
Number A. genistae per 100 gms. broom
5
4
3
2
1
Daily number adults in suction trap
16
14
12
10
8
6
4
2
— No. adults per 100 gms. broom.
Daily no. of adults in suction trap.
Scale :- 3 adults in suction trap = 1 adult per 100 gms. broom in study area.
May
July
Sept
Nov
Jan
Mar
May

Fig. 29

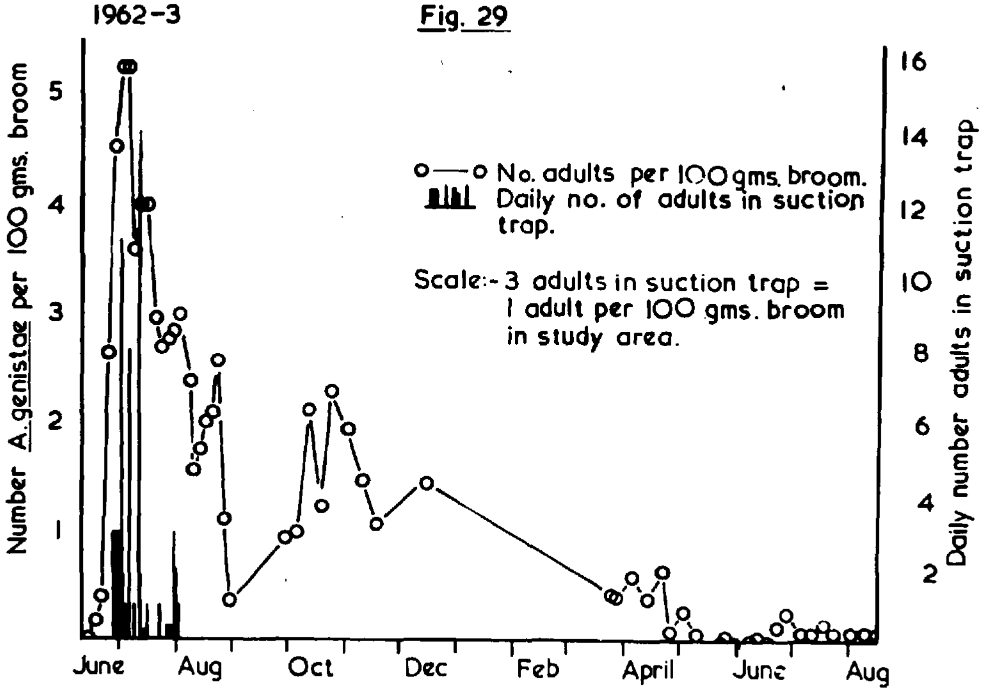

1962-3
Number A. genistae per 100 gms. broom
5
4
3
2
1
Daily number adults in suction trap
16
14
12
10
8
6
4
2
o—o No. adults per 100 gms. broom.
Daily no. of adults in suction trap.
Scale:- 3 adults in suction trap = 1 adult per 100 gms. broom in study area.
June
Aug
Oct
Dec
Feb
April
June
Aug

Table 18. Peak numbers of *A. genistae* adults per 100 grammes broom in 1959 - 1963.

Year	Peak number of *A. genistae* adults		Peak number of *A. spartii* adults
	1st Generation	2nd Generation	
1959	30	26	23
1960	21	0.17	149
1961	2	5	204
1962	5	2	5
1963	0.3	-	2

has generations following one another continuously.

Mortality in *Arytaina genistae*.

The figures for percentage mortality in this species obtained by the three methods of analysis are shown in Table 19. The Equation and Regression methods gave poor results which appear unreliable. The Graphical Method gave more consistent results (Table 19) but the total egg and nymphal mortality (up to the fourth instar only in the graphical method) indicated is much the same in all generations (over 99%). Other evidence discussed later suggests strongly that this was not so. The results from the graphical method depend on whether the numbers of fresh eggs are combined with or separated from the numbers of eggs with eyespots. All the results from the methods of data analysis used with the A. genistae data are therefore suspect.

There is then no available figure for the total number of eggs laid in any generation. The number indicated by the equation method is always much too low while the regression and graphical methods give variable results which cannot be checked. The reason for the failure of the equation method in the analysis of the A. genistae data most probably lies in the recruitment data. The sleeves enclosing the laying females might have affected their rate of egg production and possibly too few females were used to obtain a reliable estimation. The differences between the peaks of successive stages in the graphs indicate a very high mortality, particularly in the egg stage. A. genistae never reached the high density of the A. spartii 1961 generation, the highest density of A. genistae eggs and nymphs in 1961 - 1963 being respectively 1,102 on 31 March 1962 and 214 on 18 May 1962.

The numbers of dead nymphs and eggs found in samples are expressed as fractions of the number of live nymphs and eggs in Table 20. The data for the two 1961 generations are poor or absent because very few dead A. genistae nymphs were recognised in the first generation and they were ignored in the second generation. The data for the two 1962 generations and the 1963 generation indicate that the eggs sustain the highest mortality. In 1961 and 1962 a larger proportion of eggs were lost in the first generation than in the second. Egg mortality appears to have been highest in the first generation of 1963. Nymphal mortality appears to be higher in the second generation of 1962 than in either the first generation of that year or the 1963 generation.

Dead eggs are not found in the samples long after the live eggs have disappeared (Figs. 32, 33 and 34). The numbers of dead eggs also follow the numbers of live eggs fairly closely. This suggests a fairly constant egg mortality throughout each generation. An exception was the second and partial third generations of 1962 (Fig. 33). Egg mortality seems to have been fairly constant until the adults produced by the second generation started laying at the end of October. At this time the proportion of dead eggs fell, but began rising gradually again as the winter progressed.

Dead eggs in the samples could have died through predation, infertility or unfavourable weather conditions. Mortality in winter would most probably be due largely to unfavourable weather, as predators are almost absent and inactive at this time. The fall in the proportion of dead eggs after the end of October in 1962 could have been caused by a reduction of predation. A large proportion of the eggs can survive even the most severe frosts. When laying ceased about 23 December 1962 at the beginning of freezing conditions there were between 140 and 170 live eggs per 100 grammes of broom. On 16 February, just before laying was resumed there were 70 live eggs per 100 grammes. About half the eggs present on 23 December had therefore died during 56 days when the average daily mean temperature was -1.9°C. and the lowest temperature reached was -13.9°C. on 23 January. Healthy eggs showing eyespots brought into the warmth of the laboratory for counting during this cold period frequently hatched.

Table 19. Mortality in *Arytaina genistae* 1961 - 1963 as shown by three methods of data analysis.

Egg I = Fresh eggs with no signs of development.

Egg II = Eggs with the eyespots of the developing first instar nymph visible.

Generation and Year	Stage	Equations No. Produced	Equations % mortality	Regression No. Produced	Regression % mortality	Graphical method No. Produced	Graphical method % mortality Egg I & Egg II together	Graphical method % mortality Egg I & Egg II separat
1st Generation 1961	Egg I							
	Egg II							
	Egg I + Egg II					291.6	-71.53	
	Instar I					83.0	+11.59	
	II					116.8	-36.88	
	III					9.3	-2.33	
	IV					2.5	-0.31	
	V					1.6	-0.54	
	Adult							
	Egg mortality						-71.53	
	Nymphal mortality						-27.93	
	Egg + nymphal mortality						-99.46	
2nd Generation 1961	Egg I			242.8	+872.20	2007.1		-65.98
	Egg II			1115.0	-489.40	682.9		-23.21
	Egg I + Egg II					341.3	-36.39	
	Instar I			625.6	+274.10	217.1	-47.91	-8.15
	II			899.7	-556.00	53.6	+0.77	+0.13
	III			343.7	-39.00	56.2	-10.75	-1.83
	IV			304.7	-29.32	19.5	-0.38	-0.06
	V			11.5	+2.80	18.2	-5.34	-0.91
	Adult			14.3	-14.30			
	Egg mortality				+382.80		-36.39	-89.19
	Nymphal mortality				-347.42		-58.27	-9.91
	Egg + Nymphal mortality				-35.38		-94.66	-99.10

Table 19 Cont.

Generation and Year	Stage	Equations		Regression		Graphical method		
		No. Produced	% mortality	No. Produced	% mortality	No. Produced	% mortality	
							Egg I & Egg II together	Egg I & Egg II separate
1st Generation 1962	Egg I	379	+131.35	437700.0	-96.48	5018.7		-89.85
	Egg II	5349	-1147.76	15410.0	+28.17	509.6		-3.95
	Egg I + Egg II					2043.5	-84.77	
	Instar I	999	+2.37	138700.0	-31.68	311.3	-8.69	-3.54
	II	1008	+49.34	40.9	+0.25	133.7	-3.71	-1.51
	III	1195	-131.13	148.5	-0.26	57.9	-1.70	-0.61
	IV	698	+54.09	34.9	-0.06	23.1	-0.70	-0.29
	V	903	-16.62	7.1	-0.002	8.7	-0.43	-0.17
	Adult	840	-0.88	7.0	-0.02			
	Egg mortality		-1016.41		-68.31		-84.77	-93.80
	Nymphal mortality		-42.83		-31.75		-14.80	-5.95
	Egg + Nymphal mortality		-1054.24		-100.06		-99.57	-99.75
2nd Generation 1962	Egg I	627	+84.05	561.1				
	Egg II	1154	+25.68	7893.0				
	Egg I + Egg II					5661.3	-96.00	
	Instar I	1315	+173.36			226.4	+0.25	
	II	2402	-126.48			240.4	+0.05	
	III	1609	+145.93			243.2	-3.60	
	IV	2524	-143.06			39.2	-0.58	
	V	1627	-55.02			6.5	-0.11	
	Adult	1281	-26.95					
	Egg mortality		+109.73				-96.00	
	Nymphal mortality		-32.22				-3.88	
	Egg + Nymphal mortality		+77.51				-99.88	

Table 19 Cont.

Generation and Year	Stage	Equations		Regression		Graphical method		
		No. Produced	% mortality	No. Produced	% mortality	No. Produced	% mortality	
							Egg I & Egg II together	Egg I & Egg II separate
1st Generation 1963	Egg I	392	-29.59	9721.0	-62.09	695.0		-76.65
	Egg II	276	+18.37	3685.0	+225.54	162.3		-9.13
	Egg I + Egg II					485.1	-79.63	
	Instar I	348	+75.51	25610.0	-225.12	98.8	-14.96	-10.44
	II	644	+28.06	41.0	-0.11	26.2	-0.60	-0.42
	III	754	-4.08	30.0	-0.18	23.3	-3.48	-2.43
	IV	738	+4.08	12.7	-0.11	6.4	-1.21	-0.84
	V	722	+0.99	2.0		0.6	-0.12	-0.08
	Adult	726	+0.43					
	Egg mortality		-11.22		+163.45		-79.63	-85.78
	Nymphal mortality		+104.56		-225.52		-20.25	-14.13
	Egg + Nymphal mortality		+93.34		-62.07		-99.88	-99.91

Dead A. genistae eggs in the field can either be completely dried out or shrivelled with a wrinkled corion still containing some liquid. The proportion of shrivelled eggs tends to be highest in late autumn, winter and early spring, probably because lower temperatures tend to slow down the drying out process. In the first generation of both 1962 and 1963 the percentage of shrivelled eggs fell steadily as temperatures rose. In the second generation of 1962 the percentage of

Average daily number of eggs laid per female *A. genistae* compared with total number eggs per 100gms broom in study area.

Fig. 30

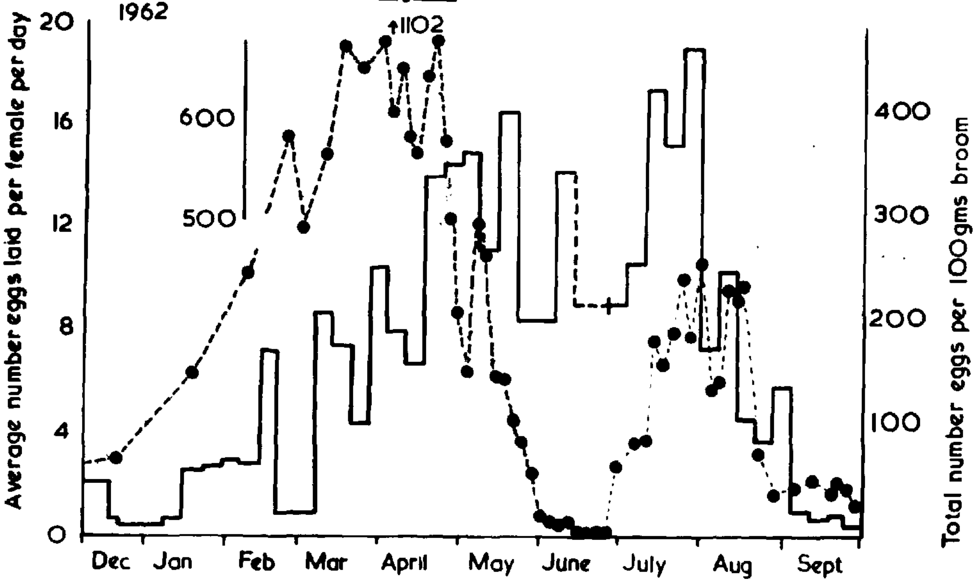
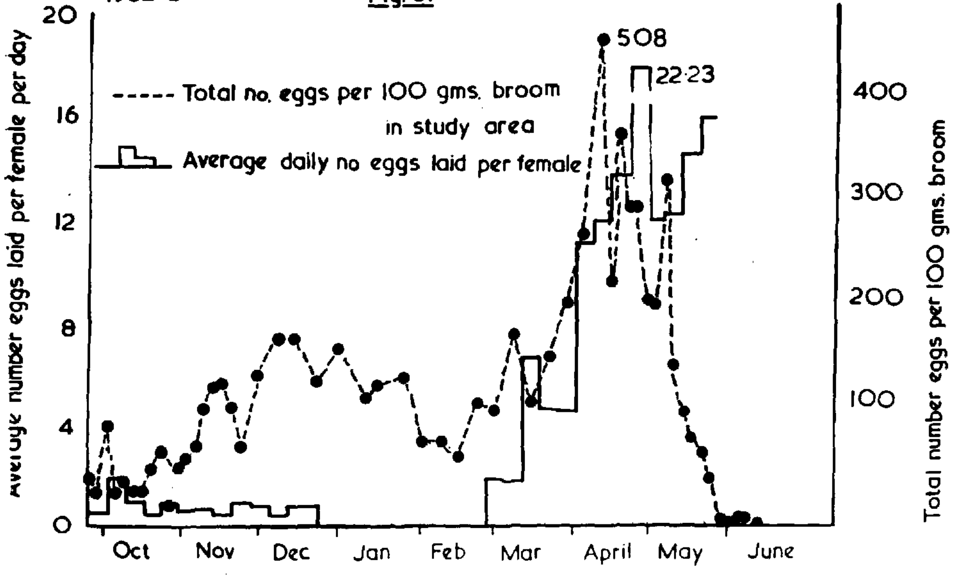


Fig. 31



Numbers of live and dead A. genistae eggs per 100 gms broom

Fig. 32

1st generation 1962

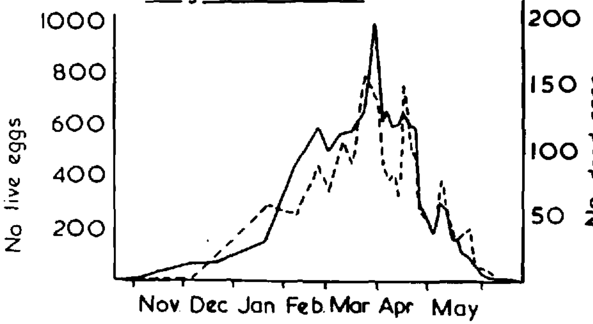


Fig. 34

1st generation 1963

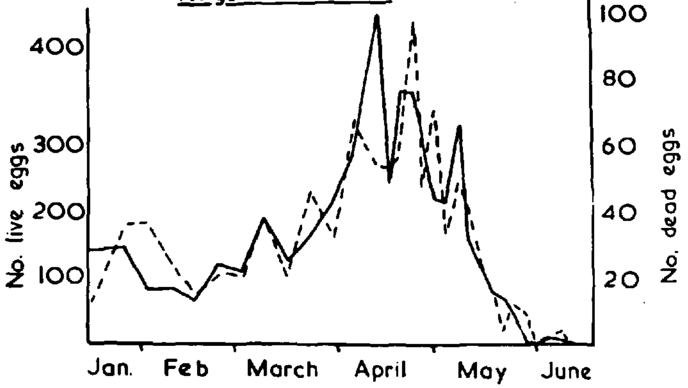


Fig. 33

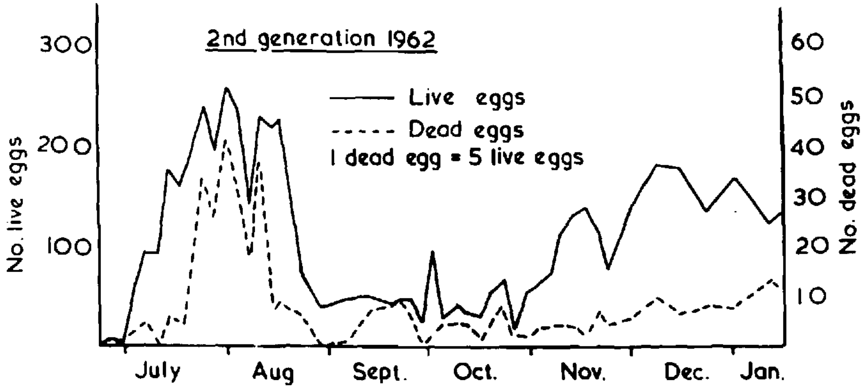


Table 20. Comparison of numbers of dead and live *A. genistae* eggs and nymphs in samples.

Generation	Dead nymph numbers as a fraction of live nymph numbers					
	Egg	Instar I	Instar II	Instar III	Instar IV	Instar V
1st Generation 1961	0.05	0.02	0	0	0.07	0
2nd Generation 1961	0.03	-	-	-	-	-
1st Generation 1962	0.17	0.06	0.02	0.02	0.01	0.03
2nd Generation 1962	0.08	0.07	0.07	0.07	0.03	0.04
1st Generation 1963	0.19	0.04	0.04	0	0	0

shrivelled eggs tended to rise as winter came on but fluctuated widely. Dried out eggs can be distinguished fairly easily from egg shells left by hatching nymphs. The former are opaque or with traces of dried cytoplasm while the latter are transparent and often with a blackish apical region. Dead *A. genistae* nymphs do not occur in samples long after live nymphs have disappeared. An exception was the very cold winter of 1962 - 1963 when dead nymphs persisted in fair numbers long after living ones had disappeared, probably because low temperatures prevented decay. The numbers of dead nymphs do not follow the numbers of live nymphs closely and this suggests that mortality is variable. The numbers of dead nymphs are highest at the beginning of hatching in the spring generations of

1962 and 1963 and at the end of the autumn generation of 1962. This suggests that mortality was probably highest at these times (Figs. 38, 39 and 40).

The relation between average daily mean temperature and the build up of nymphal numbers in the spring generations of 1961, 1962 and 1963 and the fall off of numbers in the autumn generations of 1961 and 1962, is shown in Figs. 35, 37, 38, 39 and 40. Temperature is important in both spring and autumn. In spring the rise in nymphal numbers only really starts when average daily mean temperatures are above 7°C. In the spring generations of 1962 and 1963 the proportion of dead nymphs is highest at the beginning when low temperatures are preventing the build up of the population. Hatching occurs at favourable day temperatures and many young nymphs are killed by frost at night. A. genistae will hatch when maximum day temperatures are around 10°C. Falling temperatures and frosts also appear to have been very important in killing off the nymphs of the 1962 autumn generation.

The trend in the fall off of nymphal numbers in this generation follows the fall of temperature closely (Fig. 39). The numbers of dead nymphs rose as soon as frosts occurred towards the end of October and the nymphs died out completely when frosts occurred every night. Temperature does not appear to have affected the fall off in nymphal numbers in the autumn generation of 1961 (Fig. 37). In the 1961 generation the last eggs were recorded on 21 September so that a rapid fall off in nymphal numbers would have occurred without the influence of

Fig.35 The relation between the number of *Arytaina genistae* nymphs per 100 gms. broom and the average daily mean temperature between sampling days. 1st generation 1961.

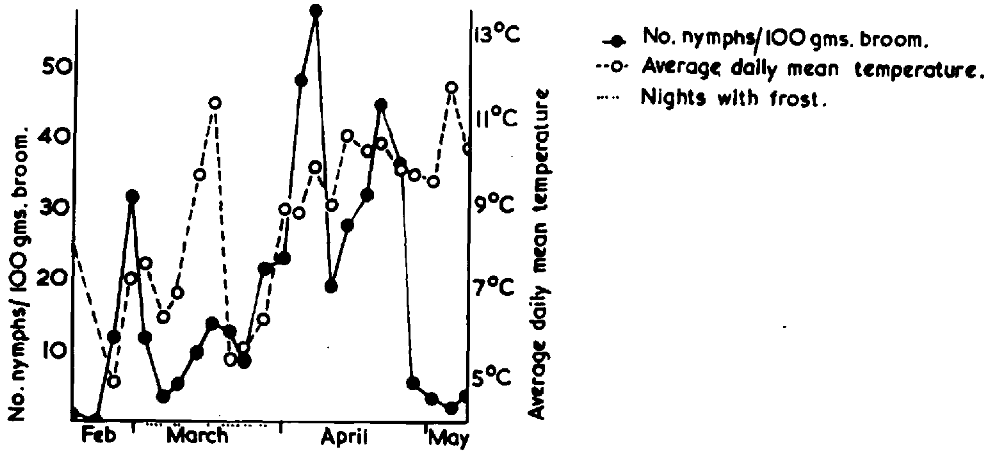


Fig.36 The relation between the number of *Arytaina spartii* nymphs and average daily mean temperature between sampling days. 1961.

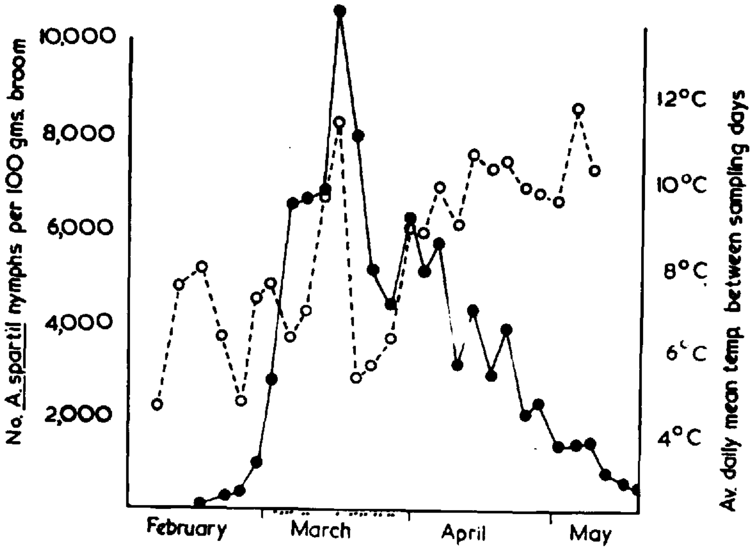


Fig. 37

The relation between the number of A genistae nymphs per 100 gms. broom and the average daily mean temperature between sampling days (second generation 1961)

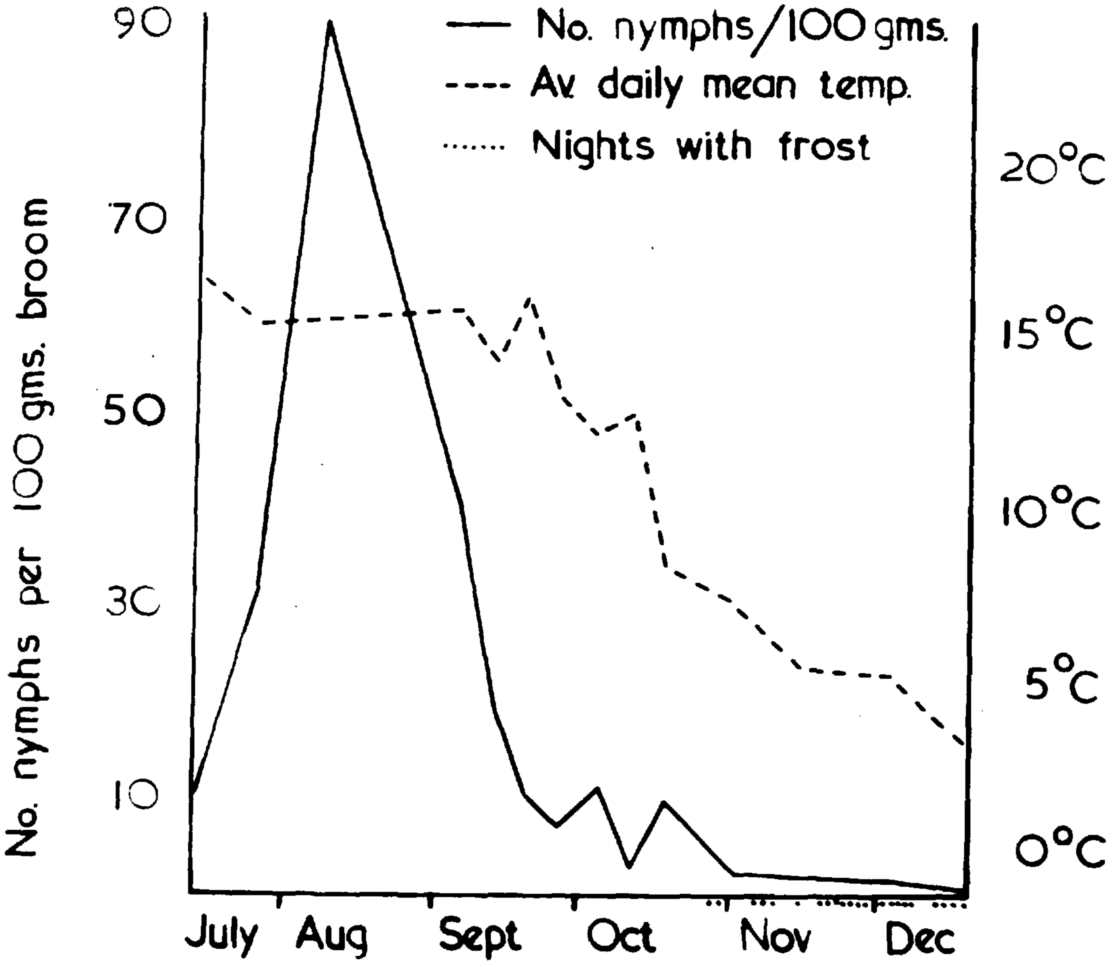


Fig. 38

The relation between the number of *Arytaina genistae* & *Arytaina spartii* nymphs/100gms broom and average daily temperature between sampling days – First generation 1962.

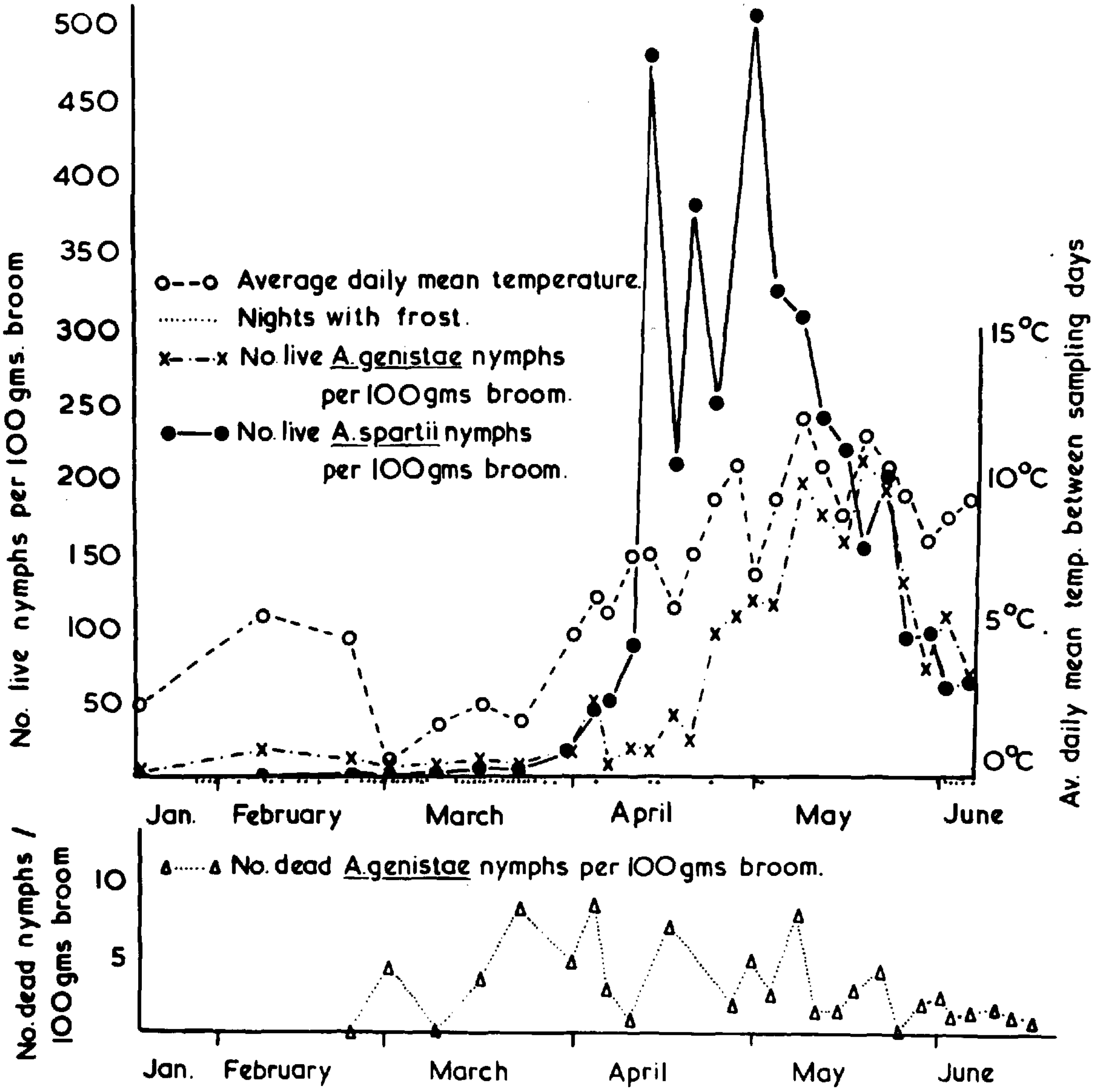
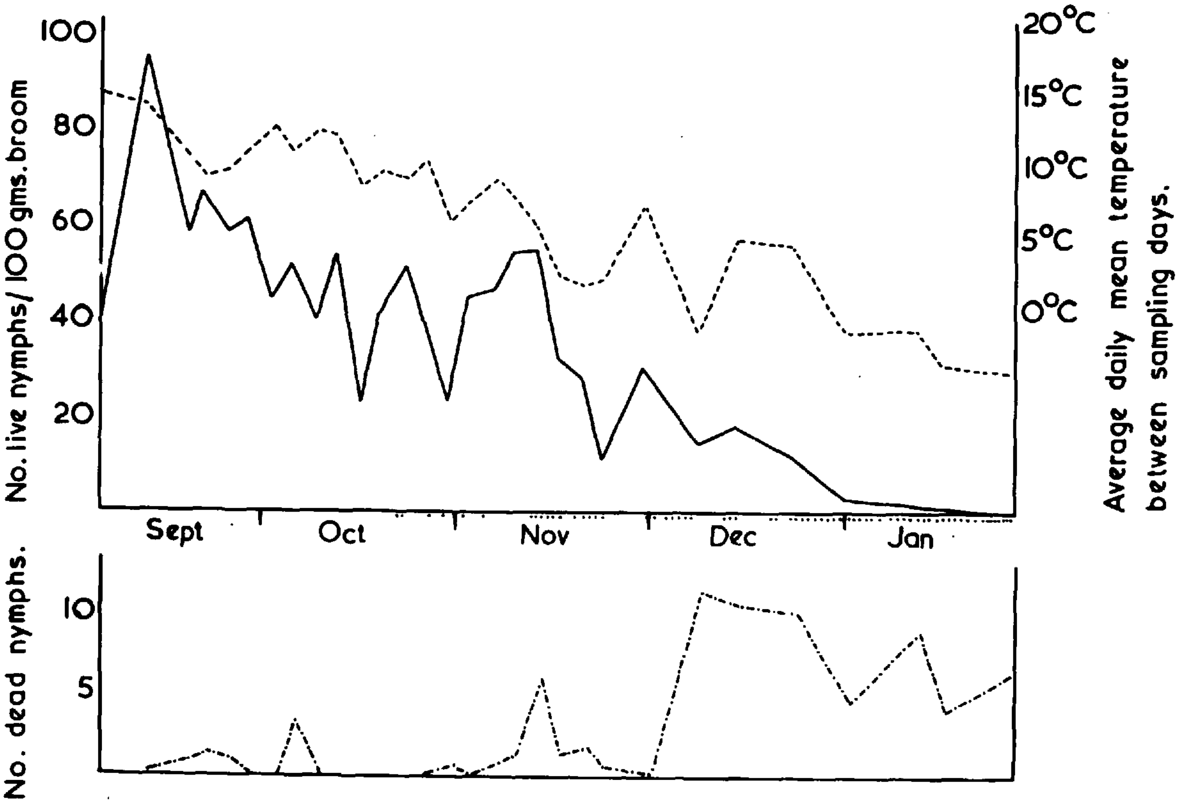


Fig. 39

The relation between the number of *Arytaina genistae* nymphs per 100 gms. broom and average daily mean temperature. 2nd generation 1962



— No. live nymphs/100 gms. broom.
---- Average daily mean temperature between sampling days.
-·-· Number of dead nymphs per 100 gms. broom.

The relation between psyllid nymph numbers and average daily mean temperature between sampling days 1963

Fig. 40 Arytaina genistae

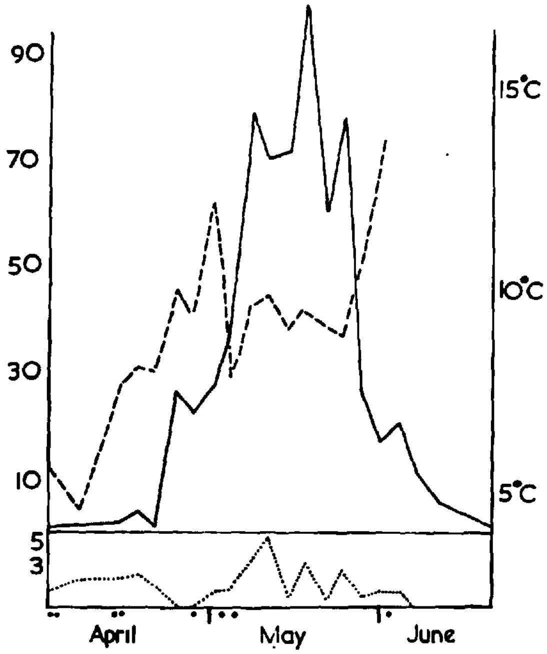
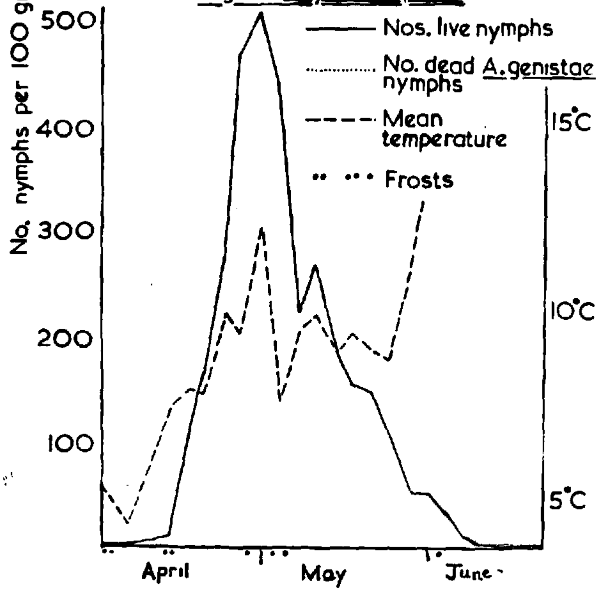


Fig 41.—Arytaina spartii



lower temperatures. Low temperatures did, however, prevent hatching of eggs laid by the overwintering adults. *A. spartii* nymphs seem to be able to develop at lower temperatures than *A. genistae* nymphs. *A. spartii* nymphal numbers increase rapidly at average daily mean temperatures above 4°C. (Figs. 36, 38 and 41). Some mortality was, however, probably caused in *A. spartii* by low temperatures in 1961. In 1962 *A. spartii* started hatching about two weeks later than *A. genistae* and the number of nymphs of this species only became equal to the number of *A. genistae* nymphs after 4 weeks (Fig. 38). After this, however, *A. spartii* nymphal numbers rapidly exceeded *A. genistae* nymphal numbers. The slower start of *A. spartii* hatching in 1962 probably enabled this species to escape much of the mortality caused by frost in *A. genistae*. In 1963 both psyllid species started hatching at the same time, as they ~~might~~ appear also to have done in 1961. *A. genistae* nymphs are more easily killed by low temperatures than eggs, and *A. spartii* eggs suffer no mortality from cold unless the broom stems are killed.

The first generation of *A. genistae* in 1961 occurred with a very high density of *A. spartii* nymphs which were themselves suffering from crowding. It is possible that *A. genistae* was crowded out to a certain extent by *A. spartii* as both species occupy the same ecological niche and appear to have identical food requirements. In the spring of 1961, 1962 and 1963 the numbers of *A. spartii* nymphs rose more rapidly to a peak than the *A. genistae* nymphs. The date of the peak in *A. spartii* nymphal numbers always precedes that of *A. genistae* by 18 to 21 days

(Table 21). Because *A. spartii* is able to develop at lower temperatures than *A. genistae* it is at an advantage if any interspecific competition occurs. When nymphs of the same age are crowded together experimentally, however, *A. genistae* gains the upper hand over *A. spartii* (see Section IV). Under natural conditions *A. spartii* probably has the advantage because its nymphs are older and larger than those of *A. genistae* when competition is likely to occur.

Predators are very important in causing mortality of *A. genistae* nymphs as also in *A. spartii*. A wide range of predators occurs on broom.

Table 21. Dates of peak numbers of *A. spartii* and *A. genistae* in different years.

Year	Date of *A. spartii* peak in nymph numbers	Date of *A. genistae* peak in nymph numbers
1961	16 March	6 April
1962	1 May	18 May
1963	30 April	17 May

The peak numbers of adults produced by each generation are compared with the average egg and nymph numbers in Table 22. The number of adults produced in the second generation of 1961 is larger in relation to the average number of nymphs present than in all the other generations. More nymphs produced adults in the first generation of 1961 than in any other generation except the second generation of that year. This suggests that if competition with A. spartii were important in the first generation of 1961 some other mortality factor had as big an effect in the other years.

The average number of nymphs expressed as a fraction of the average number of eggs seems higher in the first generation of 1961 than in the first generation of the following two years. This is in spite of the fact that the average for the numbers of eggs present in the first generation of 1961 does not include eggs present before hatching started. Exclusion of eggs present before hatching started in the other two years makes the average number of eggs appear even higher increasing the apparent egg mortality. The figures in Table 22 therefore suggest lower nymphal and egg mortality in the first generation of 1961 than in the first generation of the following two years. The large numbers of A. spartii possibly protected A. genistae to a certain extent from predation (Section IV) and this may have outweighed harmful effects due to competition.

In the second generation there is no prolonged period with eggs only present and hatching is rapid by the time peak numbers are reached. This quick hatching would tend to depress the average number of eggs present and reduce the apparent egg mortality.

Adults of the first generation were found in the suction trap in each of the years 1959 to 1962. In 1963, however, when the numbers in the study area were very low, none was found in the suction trap.

The numbers of adults in the suction trap correspond with the

Table 22. Average numbers of eggs and nymphs compared with the peak numbers of adults produced in five generations of A. genistae.

Year	Generation	Average number eggs present	Average number nymphs present	Ratio of egg numbers to nymph numbers	Peak number of adults	Ratio nymph numbers to adult numbers
1961	1st	51	14	1 : 0.27	1.88	1 : 0.13
	2nd	37	20	1 : 0.54	5.38	1 : 0.27
1962	1st	251	48	1 : 0.19	5.25	1 : 0.11
	2nd	108	32	1 : 0.30	2.13	1 : 0.08
1963	1st	177	29	1 : 0.16	0.28	1 : 0.01

density present in the study area in 1959, and 1961 - 1963. In 1960, however, relatively few adults were found in the suction trap compared with the high density present in the study area.

The numbers of A. genistae in the suction trap were affected by wind direction and temperature. Most A. genistae adults fly on warm sunny days. In 1960 there was a smaller proportion of days with winds blowing A. genistae towards the suction trap than in other years (Table 24). In Table 24 the dispersal period is taken as the time when the highest numbers of A. genistae were found in the suction trap; the period when only one or two were found on occasional days is ignored. In 1961 one or two A. genistae were found occasionally throughout 28 days with no apparent peak. Winds blowing psyllids away from the suction trap are likely to have had the greatest effect in 1960 and the least in 1959 and 1962. In 1959 the suction trap was 50 yards nearer the study area than in other years and this could have increased the number caught.

The relation between the numbers of adults in the suction trap and the number in the study area is shown in Table 23. The 1960 figure for adults in the suction trap is perhaps too low because of the effect of wind during the main dispersal period.

The peak of first generation *A. genistae* adults in 1960 occurred at a time when the *A. spartii* adult numbers were still high (130 per 100 grammes). Crowding with *A. spartii* adults could have caused many *A. genistae* to fly out. In other years the peak of the first generation *A. genistae* adults came after the main dispersal period of *A. spartii* when *A. spartii* adult numbers were low. There were 2 *A. sparti* adults per 100 grammes at the peak of *A. genistae* adult numbers in 1959, 29 in 1961 and about 0.4 in 1962 and 1963.

Most of the adult movement in *A. genistae* usually occurs, as in *A. spartii*, after the peak adult density has been reached (Figs. 27, 28 and 29). An exception is the year 1959 when most of the dispersal occurred before the peak had been reached (Fig. 26). Dispersal in that year might have delayed and reduced the peak. Dispersal seems to have been an important cause of loss of first generation adults from the study area in 1959 - 1962. In 1960 the number of adults fell in 11 days from their peak density of 21 per 100 grammes on 9 June to 3 per 100 grammes

Table 23. Numbers of *A. genistae* in the suction trap compared with the maximum number of adults per bush.

Generation	Peak number adults per bush	Number adults in suction trap	Ratio of peak No. adults per bush to total number in suction trap
1st Generation 1959	406	363	1 : 0.89
1st Generation 1960	556	60	1 : 0.11
1st Generation 1961	72	9	1 : 0.13
1st Generation 1962	195	58	1 : 0.30
1st Generation 1963	10	0	0

Table 24. Fraction of days in main dispersal period of *A. genistae* with different wind directions.

Year	Number of days in dispersal period	Fraction of days with wind blowing psyllids from study area away from suction trap	Fraction of days with light variable wind		Fraction of days with wind blowing from study area towards suction trap
				Calm Days	
1959	32	0.13	0.06	0.09	0.72
1960	13	0.46	0.31	-	0.23
1961	28	0.39	0.25	0.07	0.29
1962	18	0.28	-	0.06	0.66

(86% fall) while 90% of the recorded dispersal occurred. In 1961 when the density of the first generation adults was much lower, the fall off after the peak was less steep than in 1960 (65% of fall while all dispersal occurred). This suggests that dispersal had a smaller effect in 1961 which is contrary to the figures in Table 23. Winds blowing *A. genistae* from the study area to the suction trap were more frequent in 1961 (Table 24) so that the number of adults trapped may be relatively high in that year. In 1962 the slope of the fall off after the adult peak was again less steep than in 1960. While all of the recorded dispersal took place in 1962 the adult numbers fell from the peak of 5 to 3 per 100 grammes, a decrease of 43% taking place in 33 days. Dispersal seems to have had a much smaller effect on adult numbers than in 1960 or 1961. The available evidence then suggests that the highest proportion of adults dispersed in 1960, the next highest in 1961 and the least in 1962. In 1959 dispersal seems to have had an important effect while adult numbers were still rising. In 1963 flight appears to have been negligible. The second generation of 1960 was very small, producing a peak number of only 0.17 adults per 100 grammes and this was probably largely due to the dispersal of many of the first generation adults.

A few adults of the second generation were found in the suction trap in 1959 and 1961 (Figs. 26 and 28) but little dispersal occurs in this generation in spite of the fact that the weather may sometimes appear favourable. Adults of the second generation were never found in the suction trap in the following spring or early summer. This finding contradicts Heslop-Harrison (1951) who states that *A. genistae* normally migrates in fair numbers in autumn away from the food plant to hibernate on other shelter plants. Heslop-Harrison also mentions a return migration in spring. It may be that *A. genistae* does behave differently in Northern England where Heslop-Harrison made his observations. He believes that the flight of *A. genistae* is directed. The present study suggests, however, that flying *A. genistae* are at the mercy of the wind and unable to direct their flight. The present study also suggests that in Silwood Park all autumn *A. genistae* adults overwinter on the food plant, *Sarothamnus scoparius*, and that the observed decrease in autumn and winter is due to mortality on the food plant.

The adults produced by the second generation always live much longer than those of the first generation which lay all their eggs and die within two or three months. The second generation adults live 6 - 9 months and reach their peak in egg laying in the following spring. Their numbers fall relatively slowly and steadily from the peak in autumn throughout the winter until they die out early in the following summer. By the time the first nymphs hatch in the following spring 40% - 80% of the peak number of adults have died (Table 25). A smaller fraction of the adults died in the mild winter of 1960 - 1961 than in the very severe winter of 1962 - 1963, While the fraction dying in the 1961 - 1962 winter was intermediate. Death of overwintering adults appears then to depend on the coldness and length of the winter. Since the size of the first generation in any year depends on the number of adults surviving the winter, this could be important in determining

Table 25. Number of second generation *A. genistae* present in following spring.

Generation	Number adults present per 100 gm.at time of appearance of first nymphs in following spring	Fraction of peak number of adults in autumn dying before first nymphs appear in spring	Average daily mean temperature between peak of second generation adults and appearance of first nymphs in spring	Number days between peak of adults and appearance of nymphs in spring
2nd Generation 1960	0.09	0.47	4.87°C.	97
2nd Generation 1961	1.66	0.69	4.11°C.	106
2nd Generation 1962	0.56	0.75	2.52°C.	164

population fluctuations.

Egg mortality seems to have been higher in the first generation than in the second generation in each year. It was highest in the first generation of 1963 and lowest in the second generation of 1961. Unfavourable weather during winter and spring probably accounts for these variations. Nymphal mortality was probably lowest in the second generation of 1961; high in the second generation of 1962 and highest in 1963. These differences may be accounted for by variations in the intensity of predation. The results from the methods of data analysis support some but not all of these conclusions. However, more reliance can be put on the field observations than on the results from this analysis.

The Sex Ratio of *A. genistae*.

The numbers of males and females are about equal at the beginning of a generation of adults. The males, however, die out more quickly than the females and there is usually a steady decrease in the proportion of males as the adults get older. Copulation occurs early while the numbers of males and females are still equal. All females of the second generation have spermatozoa in their spermathecae in autumn. By the time the first nymphs appear in spring the males form between a half and a third of the population depending on the length and severity of the winter. In 1961 - 1963 the percentage of males present in spring was respectively 47%, 37% and 30%.

The numbers of males and females in the suction trap samples in 1961 - 1963 were equal and there was no tendency for either sex to predominate in any part of the dispersal period. This is in contrast to the situation in *A. spartii* already described.

The Reproductive State of Female *Arytaina genistae* in the Suction Trap (1959 - 1962).

Both immature females with small undeveloped ovaries and mature ones with variable numbers of fully developed eggs in their oviducts are found in suction trap samples. The fractions of immature females found in the suction trap was highest in 1959 when most of the recorded emigration occurred before the peak of adults had been reached in the study area (Table 26). In 1959 all the females dispersing in the first part of the dispersal period were mature. In the second maximum of adults in the suction trap, however (see Fig. 26), there was a fraction of immature adults varying between 50% and 86%. The few females in the suction trap (after the main dispersal period) were almost entirely immature. In 1960 only one immature female was recorded in the main dispersal period. The other two were from after the main dispersal period when A. genistae was found singly in the suction trap on occasional days. In 1961 the only immature female found was in a suction trap sample from the weekend 11, 12, 13 August when the second generation adults were beginning to appear. In 1962 only 1 immature female was found in the main dispersal period, the rest being trapped between 12 July and 1 August before second generation adults had begun to appear, and while fifth instar first generation nymphs were still present. In 1959 and 1961 then a few second generation adults flew out but probably none in 1960 or 1962.

Table 26. The fraction of immature female *Arytaina genistae* in the suction trap in different years.

Year	Total number of females dissected	Number of immature females	Fraction of immature females
1959	158	62	0.39
1960	33	3	0.09
1961	5	1	0.20
1962	31	8	0.26

Factors Affecting Hatching in *Arytaina spartii* and Egg-laying in *A. genistae* (See Figs. 7, 8 and 9).

(a) Hatching in *A. spartii*.

There was wide fluctuation in the daily numbers hatching during spring. This fluctuation appeared to be controlled by daily maximum temperatures. Frequently fluctuations were contrary to temperature changes, however, and this was most probably caused by the small numbers of branches used.

The winter of 1960 - 61 was mild and *A. spartii* started hatching about 10 February. Maximum daily temperatures were a little over 10°C. during the last four days of January and the average daily maximum temperature for February was 10°C. On only one night in February did the temperature drop below freezing point. This was the night of 3 February when the temperature fell to - 0.6°C.

In 1961 hatching of *A. spartii* on the twelve branches reached its peak of 575 on 6 - 7 March when there had been three consecutive days with maximum temperatures above 15°C., the first time in 1961 when temperatures rose as high as this. The minimum night temperatures at this time were - 3.3°C. to - 2.5°C. In spite of this hatching continued at a rate of between 261 and 401 nymphs per day on the twelve branches.

In 1961 it was apparent that maximum day temperatures above 10°C. were required to initiate and maintain a hatching rate above 100 nymphs per day for the 12 branches. A drop in maximum temperature from 13°C. on 18 and 19 February to 6°C. on 22 February brought the hatching rate down from 209 for the twelve branches on 19 February to 30 on 22 February, (Fig. 7). After the peak the daily numbers hatching continued fluctuating widely about a moderately constant level until 12 April when a steady fall began, reaching almost zero by 28 April.

In the spring of 1962 a single newly hatched nymph was found in the sample taken on 23 February, in a period when maximum day temperatures were between 0°C. and 7°C. Temperatures had been at 10°C. and a little above earlier in the month, however. This single nymph most probably hatched on 18 or 19 February when the maximum temperatures were 13°C. and 10°C. respectively. The first newly hatched nymphs were found on the hatching branches on March 9 after a day when the temperature had reached 12°C. Hatching continued at a low erratic rate until 27 March when maximum daily temperatures reached 13°C. (after 16 consecutive days with maximum temperatures below 10°C.) (Fig. 8).

The peak in the 1962 hatching was reached on 11 April when 778 nymphs were found on the branches and the maximum temperature was 15°C., the highest temperature so far that year, apart from one occasion on 29 March when it reached 15.7°C. After the peak, the hatching rate fluctuated at a lower level until hatching finished on 21 May. After 11 April the daily maximum temperature did not rise above 15°C. until 17 April.

In 1963 the first nymph was found in the samples on 5 April and on the hatching branches on 12 April, much later than in 1962 because of the very severe and prolonged winter. Maximum temperatures reached 10°C.

and over on many days in March, however, before hatching started (20 days above 10°C. and of these 4 days had maximum temperatures over 15.5°C.) The average daily mean temperature in March 1963 was 6°C. while that in March 1962 was 2°C. and hatching started early that month in 1962. In 1962 - 1963, however, the months September to February were colder than in 1961 - 62; January and February, 1963, being particularly cold with average daily mean temperatures of - 2.5°C. and - 1.1°C. respectively compared with 4°C. during the same period in 1962. It is probable that the eggs of _A. spartii_ required a certain amount of time in spring 1963 at higher temperatures in which to complete their development.

After hatching started in early April 1963 maximum daily temperatures were mostly above 13°C. (average maximum temperature for April = 14.6°C.). Hatching reached its highest level of 1,226 for all 24 hatching branches on 19 April when the temperature reached 18.5°C., the highest so far recorded that year. Hatching finished more quickly in 1963 than in either 1961 or 1962 (Table 27) because of higher temperatures.

From the above it is evident that _A. spartii_ will start hatching in spring when maximum day temperatures are around 10°C. even though there may be frost at night. Hatching does not start, however, on the first occasion in spring when temperatures do reach or exceed 10°C., but only after a certain time possibly required for physiological changes in the fully formed nymph inside the egg shell. This required time seems to be influenced by temperatures in preceding months. Hatching reaches its

Table 27. Effects of temperature on the time taken for hatching and nymphal development in *A. spartii*.

(Initial period when hatching was slow and nymphal numbers were low is excluded).

(a) Hatching.

Year	Dates of Hatching	Number of days	Average daily maximum temperature	Average daily mean temperature
1961	15/2 - 28/4	73	14.15	8.13
1962	16/3 - 21/5	67	13.18	7.02
1963	5/4 - 23/5	49	14.88	8.87

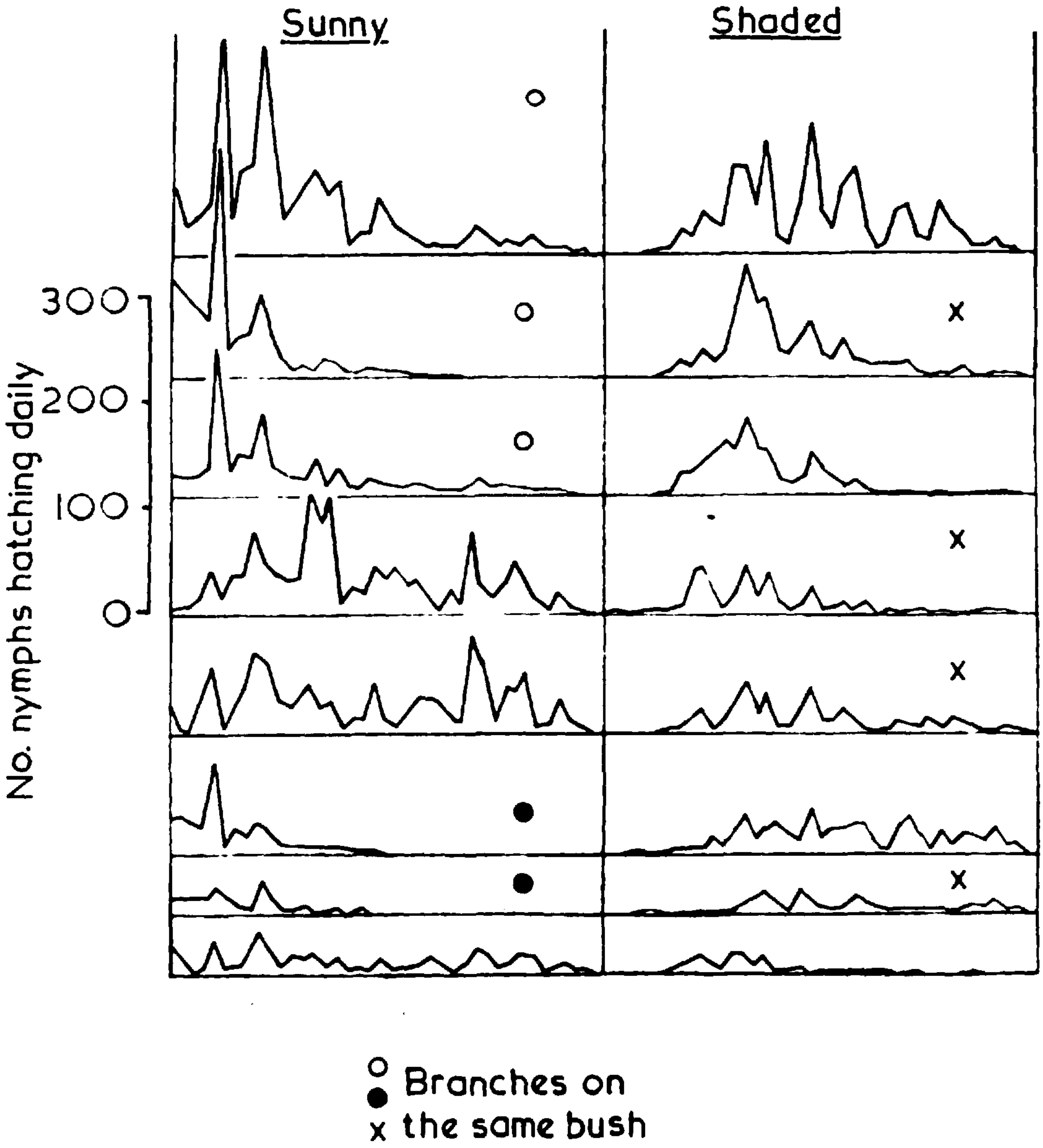
(b) Time taken for nymphal development.

(For all nymphs to moult to adults).

Year	Dates between which nymphs present in samples	Number of days	Average daily maximum temperature	Average daily mean temperature
1961	15/2 - 2/6	108	15.36	8.94
1962	16/3 - 19/6	96	14.86	8.38
1963	5/4 - 7/6	64	16.42	11.45

Fig.42

Daily numbers of Arytaina spartii nymphs hatching on separate hatching branches in shaded and sunny positions



peak after maximum temperatures have been consistently between 13 and 15°C. or above for several days. After hatching has started it will continue at a low level when maximum day temperatures are as low as 7°C.

Hatching is delayed on branches in shady positions as was found with some of the branches used in 1963 (Fig. 42). Eight of the 24 branches used in 1963 were on the shady north side of a large oak tree and hatching on these branches started several days after it had begun on branches in sunny positions.

From the graphs in Fig. 42 it can be seen that hatching on the separate branches shows a coincidence of smaller peaks even though the main peaks may not occur at the same times. In three cases there was more than one branch on a single bush in 1963, but generally these did not show any closer similarity to one another than to branches on other bushes. In sunny positions the aspect and level of a branch did not affect the rate of hatching on it.

(b) Egg-laying in *Arytaina genistae*.

Arytaina genistae will lay eggs at any time of the year, the rate of laying being controlled by temperature (Figs. 43 and 44). During winter eggs will be laid whenever temperatures are above 7°C. even though severe frosts may occur at night. During the winter of 1961 - 1962 the rate of laying was lowest between 19 December and 15 January when the average daily maximum temperature was 4.4°C. (0.57 eggs laid per female per day during this period). The highest temperature recorded during

The relation between the number of eggs laid per female *Arytaina genistae* per day and average daily maximum temperature

Fig. 43

8 Dec. 1961 – 13 June 1962

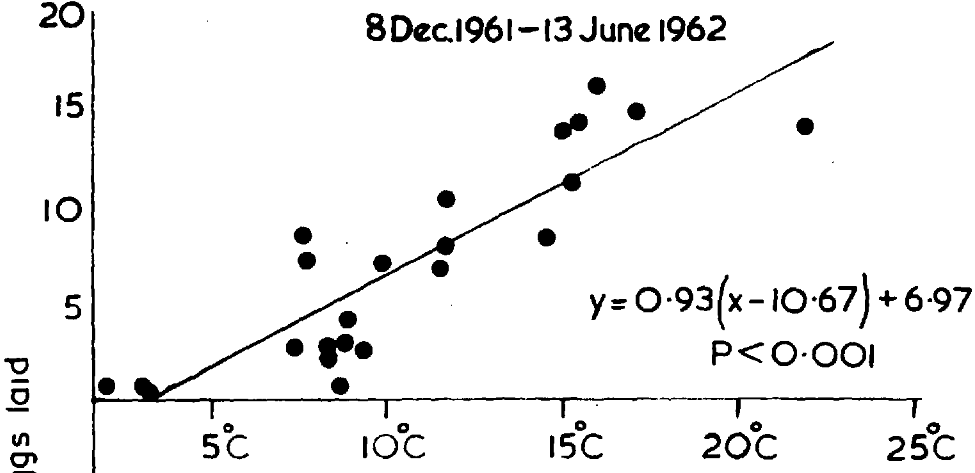
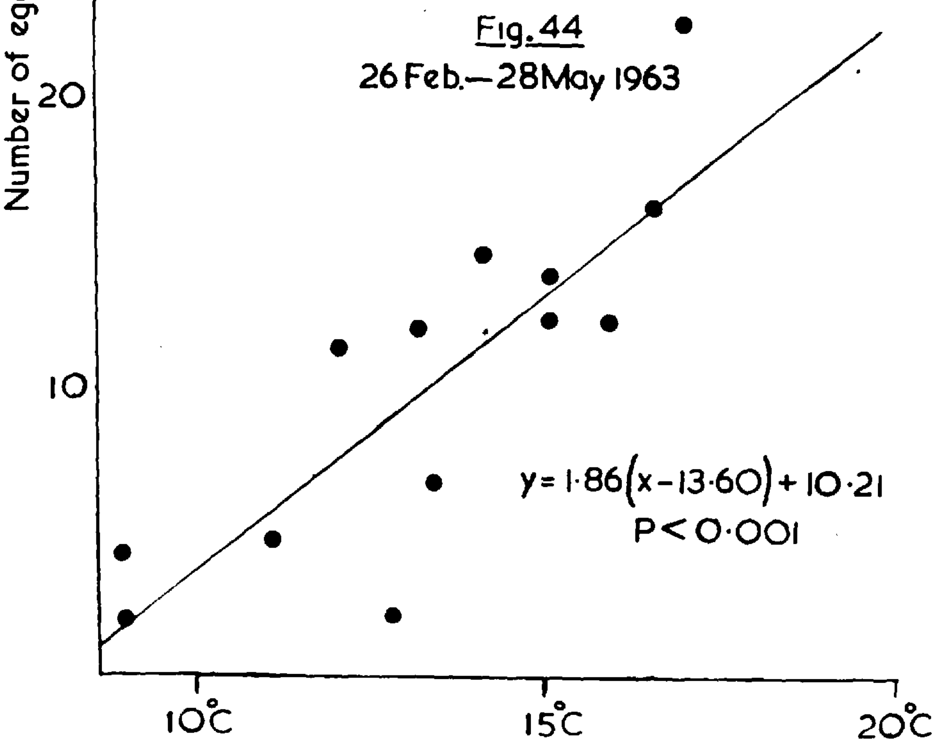


Fig. 44

26 Feb. – 28 May 1963



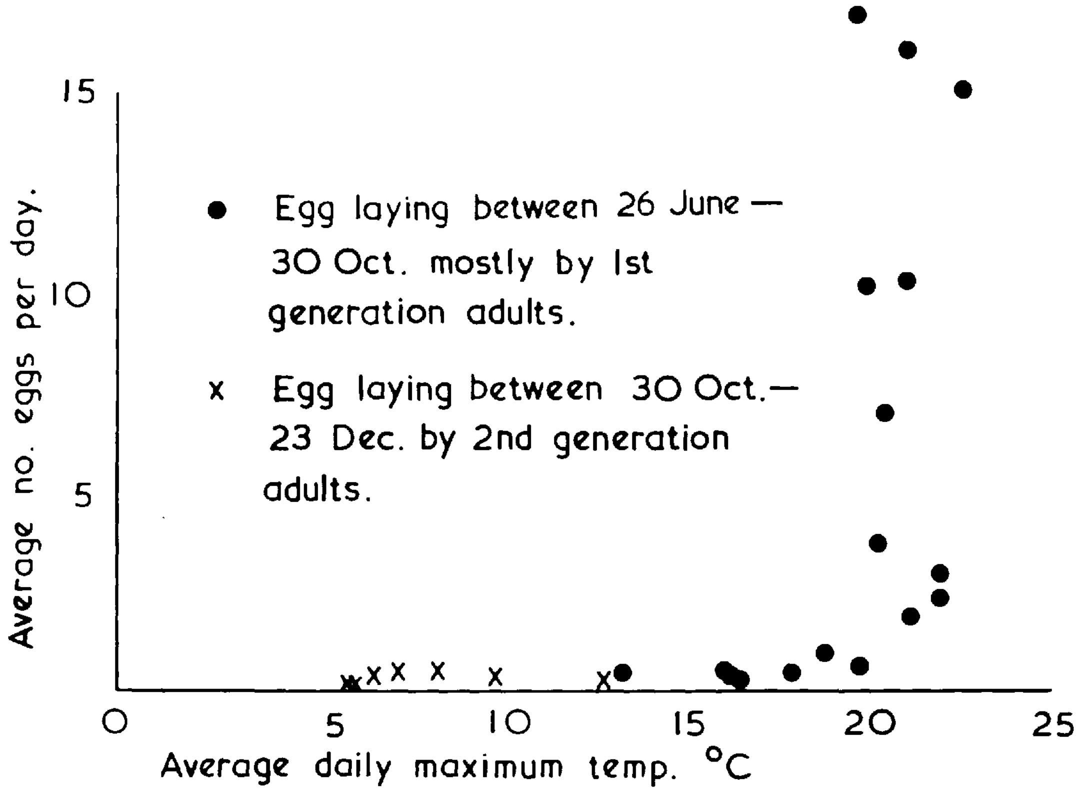
this period was 10.4°C. on 7 January and the broom area was covered by snow between 31 December and 7 January. After 15 January laying remained fairly constant at between 2.5 and 2.9 eggs per female per day until 15 February when it began rising steadily with one or two recessions caused by lower temperatures (Fig. 30). In the spring of 1962 the rate of egg laying rose with temperature according to the regression equation shown with Fig. 43 ($P < 0.001\%$ level).

During the winter of 1962 - 63 there was a long period between 23 December and 26 February when laying stopped completely. The average daily maximum temperatures for January and February 1963 were - 0.56 and 2.3°C. respectively and between 23 and 31 December temperatures were never above 1°C. Snow covered the broom area between 27 December and 26 February. During this period no adults could be found by beating exposed bushes. After 26 February day temperatures rose and the egg laying rate increased according to the regression equation shown with Fig. 44 ($P < 0.001\%$ level). This equation is not significantly different from the equation for the 1962 spring egg laying regression (Fig. 43) although the 1963 line has a somewhat steeper slope. The highest recorded number of eggs laid per female per day was 22.23 between 24 and 30 April, 1963 (Fig. 31).

Between 26 June and 23 December 1962 the egg laying rate was not clearly related to temperature (Fig. 45). The adults produced by the first generation of 1962 laid eggs at a rapid rate of between 9 and 19 eggs per female per day between 26 June shortly after they appeared

Fig. 45

The relation between the average daily no. of eggs laid per female *A. genistae* and average daily maximum temperature 1962



and 14 August when their numbers were decreasing rapidly. The solid circles on the graph (Fig. 45) indicate laying occurring while the first generation adults were present. The crosses indicate laying by second generation adults. After 14 August 1962 the egg laying rate fell to between 4 and 5 eggs per female per day in spite of average maximum temperatures around 21°C. The last fifth instar nymphs of the first generation were recorded on 13 July and no further new adults were added to the population until the adults of the next generation started to appear between 25 and 28 September. The rate of egg laying continued to fall until it was 0.80 eggs per female per day by 25 September (Fig. 30). It seems that the first generation adults were becoming senescent and were producing fewer eggs per female as the season progressed.

The appearance of new adults at the end of September did not cause a rise in the egg laying rate in spite of average daily maximum temperatures of over 15°C. continuing until 23 October. Dissections of females from the carbon dioxide samples showed that the percentage with fully developed eggs in their oviducts rose from 35% on 5 October to between 80 and 90% between 9 and 16 November. Between 18 and 24 October between 68 and 76% had fully developed eggs, but the number of eggs laid per female per day was still less than one.

Eggs were not laid at a high rate until the following spring.

Dissections of adults from the carbon dioxide samples between 18 June and 30 July showed that between 63 and 72% of the females had fully developed eggs. This was during a period when laying was at a maximum. It seems strange that the autumn adults did not lay eggs at a higher rate in October when the percentage of females with fully developed eggs reached about the same level.

IV. MORTALITY FACTORS OF BROOM PSYLLIDS.

The effects of unfavourable weather on psyllid populations have already been discussed. Other mortality factors investigated for *A. genistae* and *A. spartii* were competition and predation. The effect of the age of the food plant on the psyllid population was also studied.

The Effects of Competition.

(a) Methods of Studying Nymphal Mortality caused by Intraspecific Competition.

The psyllid nymphal populations were kept at various densities on small potted broom plants 10 to 60 cm. high. The movement of nymphs from one plant to another was prevented by isolating each plant in a water or paraffin filled petri dish. Care was also taken to ensure that the shoots of adjacent plants did not touch. Predators were excluded as far as possible, but spiders were a serious problem in some of the work.

For *A. genistae* the initial number of eggs present on a potted plant were counted and taken as the initial number per bud. This was corrected for the number of dead unhatched eggs present at the end of the experiment. Only buds which were opening were counted. The plant was cut down to five buds and one, two, or three mature females were caged on it for 24 or 48 hours. In this way egg densities from less than one to fifty or more per bud were obtained. The potted plants with eggs and nymphs were kept in a heated greenhouse (temperatures between 10 and 20°C.) or in an insectary at outdoor spring and summer temperatures. The amount of new growth made by the plant was measured at the end of the experiment in an attempt to determine the effect of this on the number of nymphs surviving and vice versa.

In experiments with <u>A. spartii</u> it was not possible to count the initial number of eggs. The small cavities left by hatching nymphs in the stems were therefore counted, at the end of the experiment. From the number of cavities the number of nymphs hatching per bud could be calculated. Again only buds which had developed leaves were counted. Plants used for <u>A. spartii</u> competition experiments were pruned to varying degrees to obtain different initial densities. With some plants pruning was also accompanied by the removal of some of the buds with a razor. In this way very high densities were obtained. <u>A. spartii</u> eggs were obtained by caging high densities of adults on suitable plants in the previous summer.

Experiments carried out in the greenhouse were interfered with by the presence of large numbers of spiders. The plants were cleared of spiders once or twice a day, but there were nearly always several more present on the following day. Because of this a further smaller experiment was carried out for each species in the insectary where spiders and other predators were absent.

Regressions were calculated using a logarithmic transformation

The effect of crowding on the mortality of *A. spartii* nymphs

Fig. 46

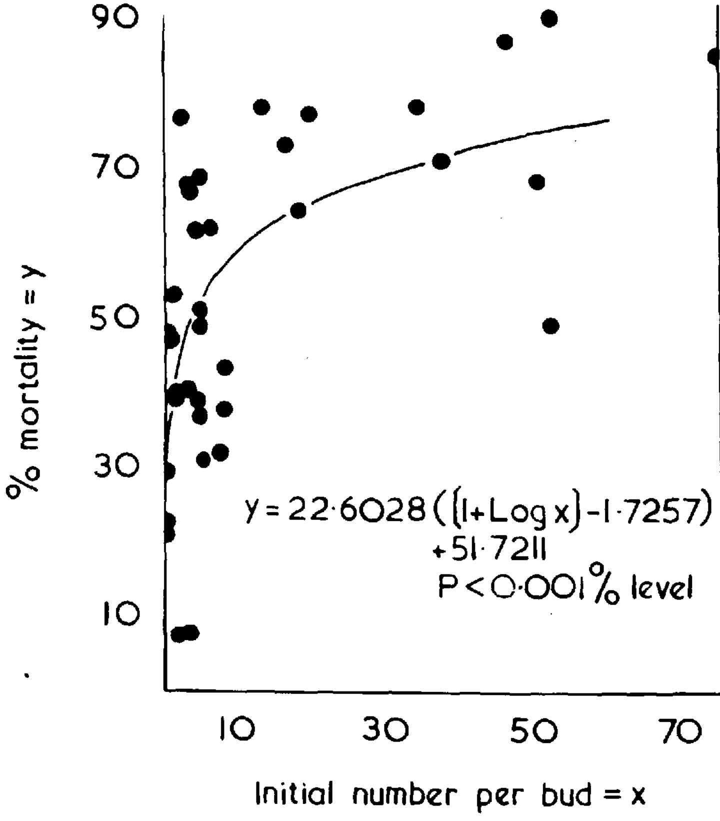
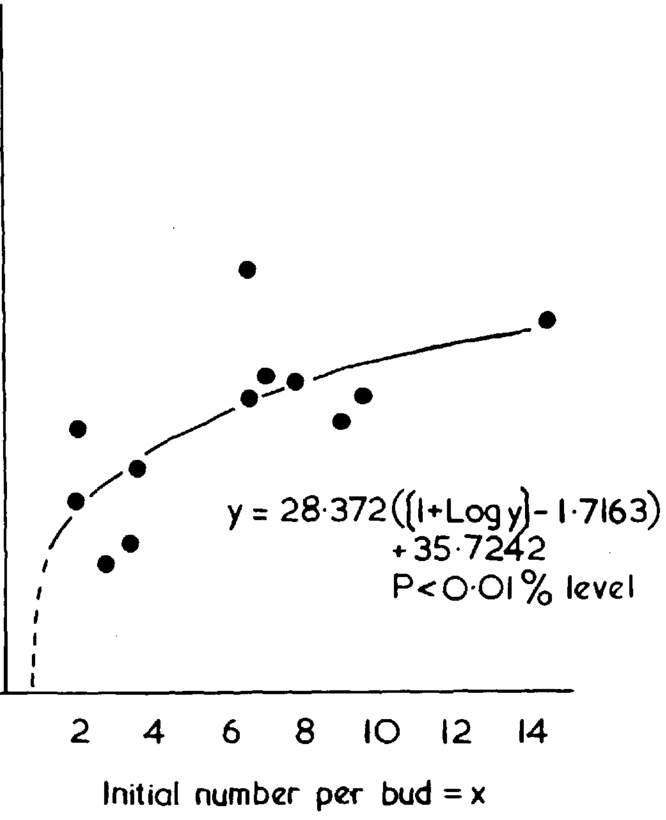


Fig. 47



of the values for the initial number per bud on the x axis and percentage mortality on the y axis (Figs. 46, 47, 48 and 49).

Results.

The results shown in Fig. 46 for *A. spartii* were obtained from plants kept in the greenhouse with spiders. Statistically they are not significantly different from the results in Fig. 47 obtained in the insectary free from predators. An examination of the curves will, however, show that mortality was about 20% higher in the greenhouse. In spite of the presence of spiders, however, the effects of competition were unaltered, the curves in Figs. 46 and 47 being similar. There are perhaps not enough data in Fig. 47 to prove any significant difference from Fig. 46. The equations for the two sets of *A. genistae* data in Figs. 48 and 49 are very similar and there is no statistically significant difference. The data in Fig. 48 were obtained in the greenhouse with spiders and those in Fig. 49 from the insectary without spiders. The *A. spartii* results were, however, significantly different from the *A. genistae* results ($P < 0.001\%$ level). *A. spartii* mortality was significantly lower at high densities than *A. genistae* mortality (compare Figs. 46 and 47 with Figs. 48 and 49). This might be connected with the larger size of *A. genistae* nymphs.

The percentage mortality for *A. genistae* shown in Fig. 49 was calculated from the numbers of adults produced. In all other experiments percentage mortality was calculated on the number of nymphs present when

The effect of crowding on the mortality of *Arytaina genistae* nymphs

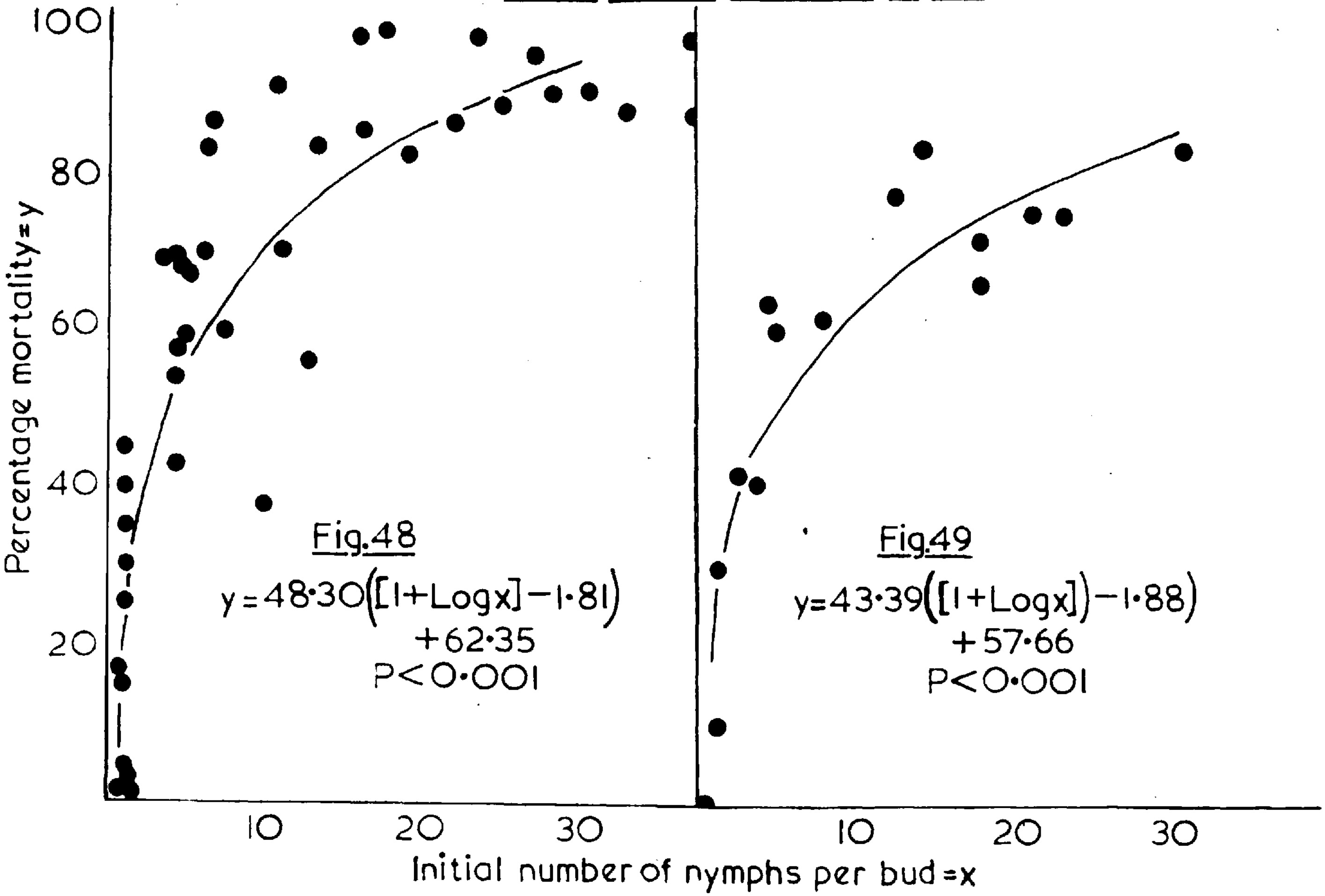


Fig.48

$y = 48{\cdot}30([1+\mathrm{Log}\,x]-1{\cdot}81)$
$+62{\cdot}35$
$P < 0{\cdot}001$

Fig.49

$y = 43{\cdot}39([1+\mathrm{Log}\,x])-1{\cdot}88)$
$+57{\cdot}66$
$P < 0{\cdot}001$

most had moulted to the fifth instar.

Nymphal mortality increases as density increases as is illustrated by the curves produced from the experimental data. There is much variability in the results caused partly by the different amounts of growth made by the plants. The plants with the largest amount of new shoot growth tended to have the lower psyllid mortalities. Plants with very high densities of psyllid nymphs were usually stunted with little new shoot growth and leaves and stems covered by honey dew and fungus. The final number of nymphs per bud was also variable but was proportional to the initial number. Plants with the highest initial numbers per bud tended to have the largest number of nymphs per bud at the end of the experiment. This suggests that the available space and food was more fully utilised at the higher densities. When densities were high many of the older nymphs spent much of their time sitting on exposed portions of stems away from buds and leaves.

Most of the mortality on plants with high concentrations of nymphs was through the movement of nymphs off the plants. Few nymphs were found dead on the plants and only about a fifth of the total loss of nymphs could be accounted for by counting the nymphs drowned in the paraffin or water filled petri dishes beneath the plants. Most of these drowned nymphs were in the third, fourth and fifth instars. There was obviously a large untraceable loss of younger nymphs which would probably be lost in or on the soil in the pots once they had left the plants. Few nymphs were found on the area around the pots. This suggests that not many dropped off the plants.

The Application of data from competition experiments to field populations.

It is likely that mortality in dense field populations follows the same pattern seen in the experimental work. A nymph on a large bush in the field would, however, have very much further to move before it was off the plant. First instar nymphs tend to move upwards in search of suitable buds after hatching. This was illustrated by the large numbers of first instar nymphs trapped on the lower edges of the sticky bands on the hatching branches in 1961. The possibility that nymphs displaced by crowding do not get off large bushes before dying was supported by the finding of fairly large numbers of dead first instar nymphs in samples in 1961. In field populations the movement of nymphs away from crowded buds would not result in much evening out in distribution since psyllid nymphs have relatively poor powers of locomotion. It is possible that the movement of nymphs out of buds in dense populations exposes them more to predation and weather.

In the experimental work the data appears most meaningful when population densities are expressed as the number per bud rather than as the number per 100 grammes. For the application of the experimental results to the field populations the number of buds in 100 grammes of green broom was obtained for 1961 - 1963 (Table 28). The buds were counted on cuttings taken for the estimation of _A. spartii_ eggs in spring when the buds were swelling. The numbers of swelling buds were kept separate from the numbers of small and dead buds. Swelling buds in spring were more or less spherical while small buds were flat and often

Table 28. Numbers of buds in 100 grammes green broom in different years.

Year	Swollen and opening live buds	Dead and small buds	Number live swollen buds not opening
1961	7,315	2,215	2,440
1962	7,460	2,497	-
1963	5,335	3,839	1,088

hidden in the cleft of the leaf axil. The number of live, swelling buds is the same in 1961 and 1962 but rather less in 1963, probably because the severe winter killed many. In 1961 and 1963 about a fifth to a third of the live swollen buds present in spring did not open. It is possible that about the same proportion did not open in 1962. Buds which do not open do not offer food or shelter to psyllid nymphs. The number of swollen buds not opening by the end of the A. spartii generation in 1961 and 1963 was estimated by examination of samples of green stems which had overwintered. It does not seem likely that buds which did not open were confused with small buds which might have swollen as these were present in the same numbers as in spring.

The number of A. spartii nymphs hatching per bud in 1961 - 1963 and the possible mortalities caused by crowding are shown in Table 29. The mortalities were obtained by substituting the field numbers per bud into the equation with Fig. 47. Only swelling, spherical buds are included in the calculations. The possible mortality caused by crowding

Table 29. Possible mortality in A. spartii caused by crowding in the study area. 1961 - 1963.

Year	Number hatching per bud (total number of buds)	Possible mortality caused with initial number per bud calculated from total number of buds	Number hatching per bud (total number of buds corrected for those not opening)	Possible mortality with initial number per bud calculated from total buds -those not opening
1961	2.98	28.85%	4.47	33.85%
1962	0.18	0%	0.24	0%
1963	0.30	0.57%	0.38	3.48%

in 1961 is 29%. In 1962 and 1963 crowding effects were virtually absent.

In *A. genistae* the density of nymphs was always very much less than in *A. spartii* and it is not likely that intraspecific competition ever had an appreciable effect. Buds with more than 5 - 10 *A. genistae* nymphs were relatively rare. The graphs show that *A. genistae* is affected by crowding in the same way as *A. spartii*, however.

The removal of *A. spartii* nymphs by predators and other factors in 1961 would have tended to reduce crowding effects. The percentage dying through crowding would therefore perhaps have been a little less than indicated by the figures in Table 29.

(b) Interspecific competition between *A. spartii* and *A. genistae*.

Potted broom plants 10 to 15 cm. high and cut down to five opening buds each were used in this experiment. The plants were caged from the start of the experiment to exclude predators. The cages were cellulose acetate cylinders (15 - 20 cm. high and 8 - 10 cm. diameter) with their lower ends sunk into plaster of paris covering the soil at the base of the plant. The upper ends were closed with gauze held in position by elastic and large gauze windows were set into the sides to improve ventilation.

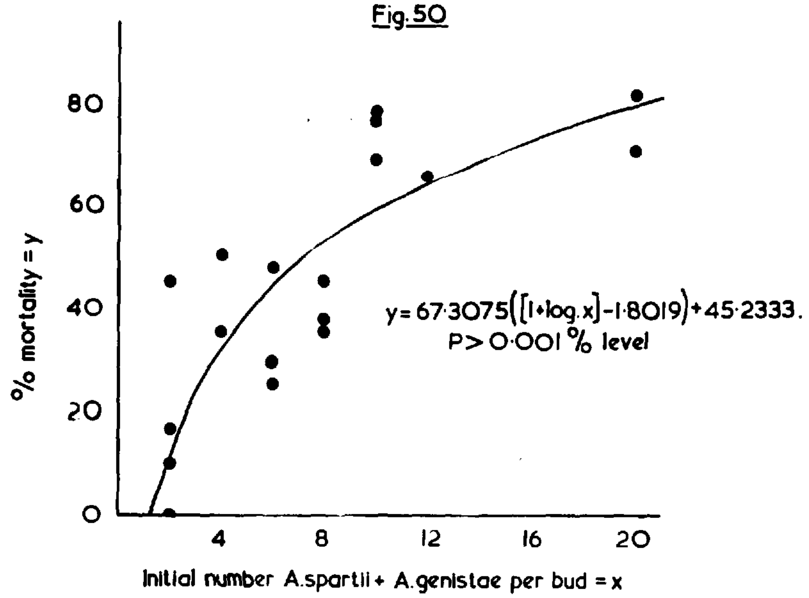
Equal numbers of first instar nymphs of both broom psyllids were placed in the buds with a soft brush. Densities varying from one to 13 nymphs of each species were placed in each bud and the plants were kept in the insectary at field temperatures. When it was found that there was not enough light in the insectary for caged plants the plants were moved outside into direct sunlight. They were brought into the insectary at night and when it rained. The experiment was set up between 29 April and 5 May at a time when first instar nymphs of both species were easily obtained.

Results.

These are shown in Figs. 50 and 51. The curve for total mortality in the interspecific competition experiment is significantly different from the curves in Figs. 48 and 49 ($P < 0.05\%$ level). This is because total mortality at low densities was less in the interspecific competition experiment than in the *A. genistae* crowding experiments

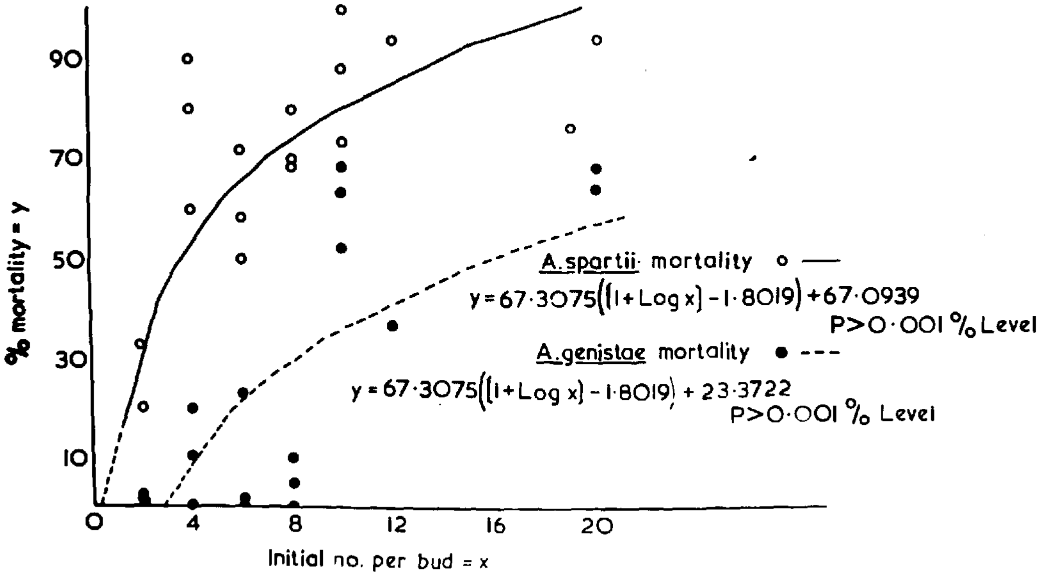
The effect of crowding on total mortality in interspecific competition between *A. spartii* and *A. genistae*.

Fig. 50



Separate mortalities of *Arytaina genistae* and *Arytaina spartii*

Fig. 51



shown in Figs. 48 and 49. The difference could have been caused partly by variation in the psyllid carrying capacity of the plants. Nymphs on caged plants frequently moved off the plants and became trapped in the gauze top of the cage. Some first instar nymphs of *A. spartii* wandered off the plants and died on the plaster of paris covering the soil in the pots.

Mortality was much greater in *A. spartii* than in *A. genistae* (Fig. 51). With two nymphs of each species in each bud the graph indicates no mortality for *A. genistae* and 45% mortality in *A. spartii*. This difference applied throughout the range of densities studied. Some of the plants with ten or more nymphs of each species per bud died before adults appeared and had to be discarded. The adults of *A. spartii* always appeared a week or two before those of *A. genistae*.

As *A. spartii* can develop at lower temperatures than *A. genistae* in spring competition with *A. genistae* is not likely to limit it in Britain. In 1961 - 1963 *A. spartii* reached its peak numbers before *A. genistae* and this might have given it an advantage. Even in 1961, however, when the overall density of *A. spartii* was about 4 per bud, mortality of *A. genistae* caused by interspecific competition is likely to have been small. The results of the experiment indicate a tendency towards better survival of *A. genistae* at the expense of *A. spartii*. This is probably more likely to be important in limiting *A. spartii* in a warmer climate where *A. genistae* can increase rapidly early in spring.

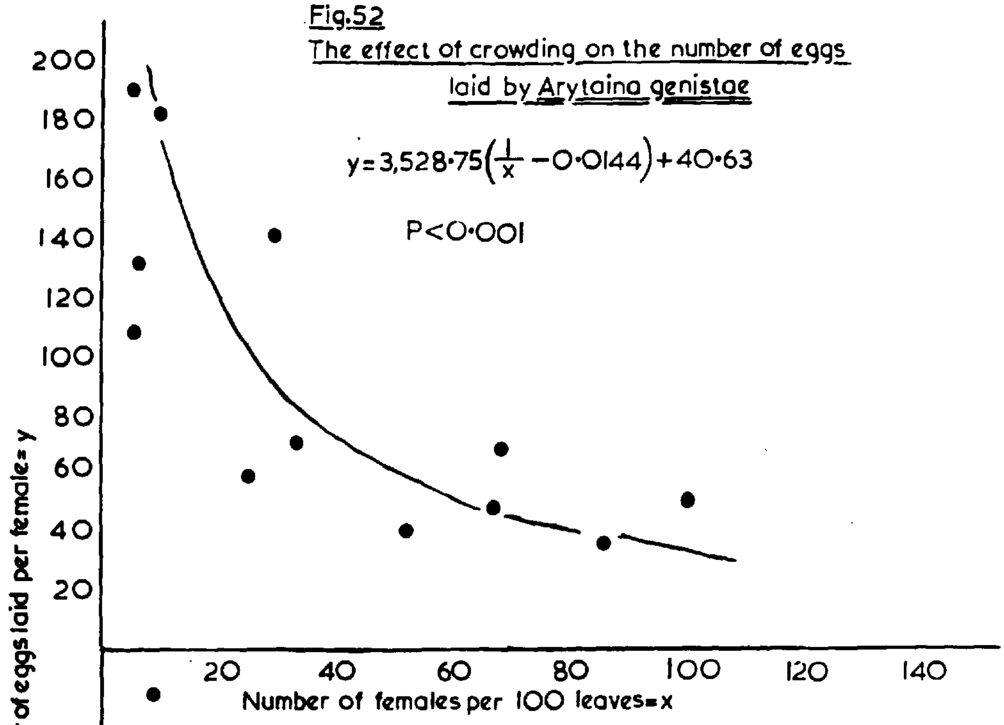


Fig.52

The effect of crowding on the number of eggs laid by *Arytaina genistae*

$$y = 3{,}528{\cdot}75\left(\frac{1}{x} - 0{\cdot}0144\right) + 40{\cdot}63$$

$P < 0{\cdot}001$

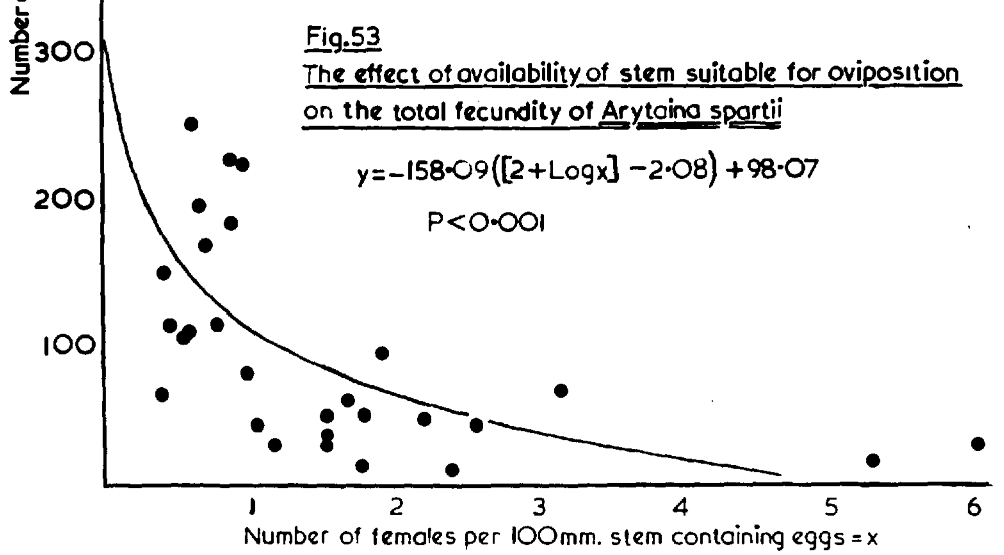


Fig.53

The effect of availability of stem suitable for oviposition on the total fecundity of *Arytaina spartii*

$$y = -158{\cdot}09\left([2 + \mathrm{Log}\,x] - 2{\cdot}08\right) + 98{\cdot}07$$

$P < 0{\cdot}001$

(c) Competition among Psyllid Adults.

The Effect of Crowding of Adults and the Availability of Suitable Oviposition Sites on the Number of Eggs Laid.

A. genistae.

Different numbers of A. genistae adults were caged on potted broom plants for seven days and the eggs that they laid were counted. Equal numbers of males and females were included. The plants were cut down to a single actively growing leafy shoot 8 to 14 cm. long. The density of psyllids was calculated as the number per 100 leaves rather than the number per unit of stem length since eggs are laid almost entirely on leaves and in leaf axils and buds. The cages were similar to those used in the interspecific competition experiment just described. The plants were kept in the insectary at summer field temperatures.

Results.

These are shown in Fig. 52 where only the female numbers are included. In A. genistae the average number of eggs laid by each female decreased markedly with increasing population density. The decrease in the number of eggs laid appears most rapid when the density of females is increased from 10 to about 30 per 100 leaves. Field densities of adults of both sexes are given in terms of the number per 100 mm. of stem and the number per 100 leaves in Table 30. The figures for peak densities of adults indicate that between 1959 and 1963 A. genistae adults were never dense enough to suffer from the effects of crowding on fecundity. The minimum number of females required before any effect on fecundity appears is about 8 per 100 leaves (Fig. 52). The figures in Table 30 are likely

Table 30. Peak numbers of *A. genistae* and *A. spartii* adults per 100 mm. of green broom stems and per 100 leaves (or buds) in the study area (1959 - 1963).

A. genistae			*A. spartii*
Year and Generation	Peak number of adults		Peak number of adults per 100 mm. stem
	per 100 mm.stem	per 100 leaves	
1959			
1st Generation	0.06	0.39	0.04
2nd Generation	0.05	0.33	
1960			
1st Generation	0.04	0.27	0.29
2nd Generation	0.0003	0.002	
1961			
1st Generation	0.004	0.03	0.40
2nd Generation	0.01	0.07	
1962			
1st Generation	0.01	0.07	0.01
2nd Generation	0.004	0.03	
1963			
1st Generation	0.0005	0.003	0.0004

N.B. Figures above include males and females.

to be too low in relation to the actual quantity of broom suitable for oviposition, but no effects on fecundity seem likely even when this is taken into account. The rapid emigration of adults as well as decrease for other reasons would have tended to minimise crowding effects on fecundity.

The Effect of the Availability of Suitable Oviposition Sites on the Fecundity of *Arytaina spartii*.

Single *A. spartii* females were caged on actively growing potted broom plants 8 to 15 cm. high in an attempt to determine their fecundity. A male was placed with each female and replaced whenever he died. The length of stem bearing oviposition scars and eggs was measured when the female psyllid died. The relative availability of stems suitable for oviposition was then expressed as the number of psyllids per 100 mm. of scarred stem for each plant and plotted against the number of eggs laid (Fig. 53). As there was only one male and female on each plant there were no effects due to interraction with other individuals.

Results.

The plants continued growing throughout the life of the psyllid, but the stems containing eggs and trial oviposition scars were localised. Since *A. spartii* will only lay eggs and make trial incisions in soft, actively growing stems the amount of stem suitable for oviposition at any time is limited. The faster the plant grows, the more oviposition sites will be available (caged females laid eggs on the young stems available during the earlier part of their adult life). Growth made while the females were in their senescent post-reproductive phase was untouched. The number of eggs laid showed little relation to the length of life and many females died after 20 - 60 days with the abdomen distended with eggs. No evidence of disease was seen. In a few cases eggs were found in leaf petioles when suitable stems were restricted. I have never observed eggs in this position in the field.

The effect of the availability of suitable oviposition sites on fecundity in *A. spartii* is shown in Fig. 53. There was a marked reduction in fecundity with the restriction of suitable stems for oviposition. The effect became conspicuous when there was less than 100 mm. of suitable stem per female. In 1961, when young growth was restricted it seems likely that the density of females exceeded the level of one per 100 mm. of suitable stem. The figure of 0.4 per 100 mm. of stem shown in Table 30, (0·2 females per 100mm.) is likely to be low compared with the actual amount of stem suitable for oviposition. The figures in Table 30 are calculated from the total length of green stem in 100 grammes of broom. The actual amount of young soft stem suitable for oviposition is not known.

As with *A. genistae* the rapid dispersal of *A. spartii* adults soon after their appearance was probably important in reducing loss of fecundity caused by excessive population density. The possible causes of reduction in *A. spartii* fecundity in 1961 have already been discussed. The available evidence seems to indicate a loss of fecundity through crowding of *A. spartii* adults in that year in spite of heavy losses through dispersal.

The Weight and Fecundity of Psyllid Adults.

The weight of newly emerged adults of both A. genistae and A. spartii reared at different densities was recorded (cf. Tables 31 and 32). There was wide variation and overlap of weights of individuals from different population densities. The mean weights, however, show that lighter adults tend to be produced at higher population densities.

No correlation between weight and population density was observed in numerous fifth instar A. spartii nymphs weighed, but this was probably because the differences in weight due to age were greater than differences due to population density.

In spite of the movement of many nymphs off crowded plants the remaining nymphs are probably deprived of a certain amount of food. Crowded plants are in an exhausted state which means that the food they offer psyllid nymphs is perhaps inferior.

The field populations of A. genistae never reached a level where crowding would have caused a significant loss in weight in the adults produced. It is possible, however, that the A. spartii adults of the 1961 generation were lighter because of crowding in nymphal life. The results indicate a 21% loss in weight of the adults when the nymphal density is increased from between 0.66 and 1.67 per bud to between 3.43 and 10 per bud.

Newly emerged females of both species were weighed and kept on potted plants in an attempt to study the relation between weight and

Table 31. Relation between weight of newly emerged *A. spartii* adults and population density in nymphal life.

A. spartii. Females only.			
Density at which reared	Average weight of adult at emergence in mg.	Weight range in mg.	Number of females weighed for each density
0.66 - 1.67 per bud	0.561	0.460 - 0.650	11
3.43 - 10.00 per bud	0.441	0.270 - 0.630	24
16.75 per bud	0.416	0.335 - 0.520	15
53.65 per bud	0.407	0.280 - 0.490	18

Table 32. Weight of newly emerged *A. genistae* adults and population density during nymphal life.

A. genistae. Males and females.						
Density at which reared	Average weight of adult at emergence in mg.		Number weighed for each density		Range in weight in mg.	
	♀	♂	♀	♂	♀	♂
1.20 - 7.80 per bud	1.071	0.869	11	6	0.845 -1.845	0.825 -0.945
14.40 per bud	0.975	0.773	4	7	0.820 -1.130	0.720 -0.845
19.60 - 21.60 per bud	0.983	0.761	8	17	0.820 -1.220	0.670 -1.080
31.20 per bud	0.945	0.723	18	8	0.760 -1.625	0.665 -0.775

fecundity. No differences in fecundity related to weight were detected, however, probably because of the interference of other factors (i.e. the availability of oviposition sites already discussed). *A. genistae* appears to have a higher fecundity than *A. spartii* (Table 33). This is also indicated by the total ovariole number, *A. genistae* having twice as many as *A. spartii*. The number of ovarioles present in mature and immature adults in the field is variable but does not appear to be related to weight.

A. genistae has a much higher egg mortality than *A. spartii* in the field. The higher fecundity of *A. genistae* would appear to be an adaptation reducing the effects of this high egg mortality.

Table 33. Fecundity of *A. spartii* and *A. genistae*.

Species	Average fecundity	Maximum fecundity	Number females taken	Average total number ovarioles in adults from field
A. spartii	93	354	27	50
A. genistae	435	962	12	105

Natural Enemies and Their Effects on the Psyllid Populations.

(a) Methods of Study.

Many predatory arthropods were present with the psyllids and they were obviously an important mortality factor. The effects exerted by predators are difficult to study since the many factors likely to be controlling the feeding of a predator in the field cannot be duplicated experimentally.

Predators of psyllids were studied by means of the precipitin test (Dempster, 1960). This test is based on the interaction of psyllid material in the gut of a predator with antibodies in the blood serum of rabbits which have been inoculated with psyllid extract. The test could only be used qualitatively to show which predators feed on psyllids. All estimates of mortality based on the precipitin test for psyllids were much lower than the observed losses, probably because the predators often take more than one psyllid per meal. Psyllid nymphs generally occur together so that a predator having found a psyllid is more likely to find another without much further searching.

For the preparation of the extract (antigen) required for injection into rabbits, psyllids were collected en masse by beating. They were then starved for 12 hours to remove broom from their guts and ground with 0.9% sodium chloride solution in a pestle and mortar. 5 Five ml. of saline were added to every 10 grammes of psyllid and the resulting psyllid solution was kept for about 24 hours at 4°C., centrifuged and then sterilised by passing it through a Seitz E.K. sterilising filter pad. The clear sterile antigen was then freeze-dried and stored until sufficient was accumulated for injection into rabbits. The antigen and anti-psyllid serum from the rabbits were prepared by Dr. Dempster.

For the preparation of antiserum the dry, sterile antigen was reconstituted with distilled water and the soluble proteins precipitated with 0.4% potassium alum. The pH of the resulting suspension was adjusted to 6.8 and 2.5 ml. was injected intramuscularly into each hind leg of a rabbit. Ten to 14 days after inoculation the rabbit was bled from the ear and its serum tested against a standard psyllid extract. Further injections were given to increase the sensitivity of the serum. The production of antibodies varies somewhat between rabbits, but usually reaches a peak after the fourth of fifth injection. 50 Fifty ml. of blood were taken from each rabbit after the fourth and fifth injections. All sera showing sufficient sensitivity were pooled, sterilised, freeze-dried and stored. Lipoids must be removed from serum before freeze drying or it becomes opaque on reconstitution with distilled water. The lipoids are extracted with ether at a temperature below -25°C.

The antisera were not specific enough to separate *A. genistae* from *A. spartii*. Because of this the antisera against both species were mixed in equal quantities for use in the precipitin tests.

Samples of possible predators were collected in the study area about once a week by beating. They were then identified to species and instar (Locket&Millidge 1953, Pope 1953, Sands 1957, Savory 1945, Southwood and Leston 1959, Waloff and Southwood 1960) and smears made on filter paper of either the whole animal or, in the case of larger coccinellids and Dermaptera, of the gut and its contents alone. The smears were then labelled and dried rapidly over phosphorus pentoxide. Once dry the smears can be stored indefinitely without deteriorating so long as they are kept dry.

For testing the predator smears were cut from the filter paper and placed in centrifuge tubes with either 0.1 or 0.2 ml. of normal saline solution according to the size of the smear. Smears of mites and first to third stage nymphs of Heteroptera were extracted with 0.1 ml. and all others with 0.2 ml. saline. The smears were allowed to soak overnight at 4°C. The supernatant fluid was then used for testing.

The test was done by drawing about 0.02 ml. of the smear extract into a small capillary tube, followed by an equal volume of the antiserum. As this is denser than the extract there is little mixing so that an interface is visible between the two liquids. Air was drawn into each tube so that the liquids rose to about the middle. The lower end of the tube was sealed by sinking it into plasticine. The tubes were filled twelve at a time using a multiple dispenser.

The capillary tubes were left at room temperature for two hours before being examined by an indirect light against a black background. The presence of psyllid material in the predator extract was shown by the formation of a white precipitate of antigen and antibody combining. This precipitate showed as a white ring at the junction of the liquids. It is essential that the liquids are perfectly clear and the capillary tubes clean for satisfactory results.

Results.

In 1961 - 1963 a total of 4,115 gut smears of predators were tested for the presence of psyllid material. Dr. Dempster carried out the 1961 testsas part of his work on mirid and anthocorid populations. The predators found to have fed on psyllids and the percentage of each reacting with psyllid antiserum are shown in Table 34.

The predaceous Heteroptera on broom feed on psyllids mostly in the third, fourth and fifth nymphal instars and the adult stage (Table 35). Only *Heterocordylus tibialis* Reuter and *Orthotylus virescens* Douglas and Scottwere found to have fed on psyllids in the second instar. Of 42 unidentified anthocorid nymphs in the first three instars none were found to have fed on psyllids. The percentages in Table 36 are corrected for the non-predatory early instars but this has made little difference because these were not well represented in tests.

The length of time for which a psyllid meal remains detectable in the gut of a predator was investigated by testing predators which had fed at a known time. Each predator was starved for 24 hours and then allowed to feed on an adult *A. spartii* until it had stopped feeding.

In the anthocorids a psyllid meal was still detectable 15 - 20 hours after feeding although in many cases it was no longer detectable after half an hour. In *Heterotoma merioptera* Scopoli a psyllid meal was still detectable after 9 hours while in *Heterocordylus* nothing was detected after 3 hours. *Anystis agilis* Banks did not give a reaction for a psyllid after 3 hours. The length of time for which a meal remains detectable would probably depend on the size of the meal and the predator species concerned. No other predators besides those mentioned above were tested for the persistence of a psyllid meal in their guts.

Dempster (1960) working on the predators of the broom beetle, *Phytodecta olivacea* Förster found that a beetle meal remained detectable far longer in a biting insect such as an earwig or coccinellid than in a sucking insect such as a mirid or anthocorid. Because of this a given percentage of mirid meals reacting with anti-psyllid serum would indicate a higher rate of predation than a similar percentage of positives in a number of earwig meals.

The heteropteran predators feeding most extensively on psyllids were *Deraecoris ruber* L. and *Nabis apterus* Fabricius followed by *Anthocoris nemoralis* Fabricius, *Asciodema obsoletum* Fieber, *Heterocordylus tibialis* Reuter, *Orthotylus concolor* Kirshbaum, *Anthocoris sarothamni* Douglas and Scott, *A. nemorum* L. and *Heterotoma merioptera* Scopoli. *Orthotylus virescens* Douglas and Scott and *O. adenocarpi* Perris appear to feed on psyllids less than any of the other heteroptera (Table 34).

The larvae of *Hemerobius* sp. appeared to prey as extensively on psyllids as *Deraecoris* and *Nabis apterus*. As *Hemerobius* larvae only suck the juices of their prey like the other Heteroptera, a psyllid meal taken by one of these is likely to remain detectable for a similar period.

Coccinellids and *Forficula auricularia*, particularly the latter, seem to take psyllids extensively. An adult *Coccinella septempunctata* L. was observed in 1961 pushing aside the leaves of a bud containing many *A. spartii* nymphs on which it was feeding. The coccinellids found on broom in 1961 - 1963 and reacting with anti-psyllid serum were larvae

Table 34. The percentage of predator meals reacting with anti-psyllid serum. Numbers in brackets are the numbers of each predator tested.

Predator	% of each predator giving reaction with anti-psyllid serum		
	1961	1962	1963
Heteroptera Miridae *Heterocordylus tibialis* Reuter	8.13 (160)	8.61 (244)	6.74 (193)
Asciodema obsoletum Fieber		13.16 (76)	-
Orthotylus adenocarpi Perris	2.88 (181)	3.90 (128)	-
O. virescens Douglas & Scott	2.37 (234)	0 (34)	-
O. concolor Kirschbaum	11.91 (117)	9.09 (122)	-
Heterotoma merioptera Scopoli		5.36 (68)	-
Deraecoris ruber L.		27.27 (11)	-
Heteroptera Anthocoridae *Anthocoris nemoralis* Fabricius	12.93 (116)	9.79 (327)	8.3 (12)
A. sarothamni Douglas & Scott	7.50 (232)	4.44 (140)	29.4 (21)
A. nemorum L.	2.70 (37)	5.22 (118)	16.7 (12)
Heteroptera Nabidae *Nabis apterus* Fabricius		31.25 (16)	-
Coleoptera Coccinellids		10.62 (226)	37.5 (8)
Neuroptera Hemerobiidae *Hemerobius* sp.		36.4 (11)	-
Dermaptera Forficulidae *Forficula auricularia* L.		55.32 (47)	-
Acarina *Anystis agilis* Banks		2.8 (575)	-
Spiders		14.57 (604)	-
Opiliones Phalangidae *Platybunus triangularis* Herbst.		6.67 (45)	-

Predator species	Instar I	Instar II	Instar III	Instar IV	Instar V	Adult
Heterocordylus	0 (21)	5.2 (156)	3.2 (248)	4.4 (205)	10.6 (207)	13.3 (45)
Asciodema	-	0 (1)	16.7 (6)	12.5 (16)	8.3 (36)	11.8 (17)
Orthotylus adenocarpi	0 (40)	0 (90)	5.7 (53)	0 (32)	3.0 (33)	3.1 (98)
O. virescens	0 (30)	5.6 (18)	0 (14)	0 (13)	7.7 (26)	1.2 (167)
O. concolor	0 (1)	0 (22)	16.7 (12)	4.3 (23)	10.0 (100)	10.0 (80)
Heterotoma	0 (6)	0 (6)	0 (4)	0 (7)	17.6 (17)	0 (25)
Anthocoris nemorum	0 (1)	0 (3)	1.11 (9)	25.0 (16)	1.9 (53)	15.6 (77)
A. sarothamni	-	0 (4)	0 (8)	0 (17)	16.8 (101)	4.2 (259)
A. nemoralis	-	-	0 (1)	7.7 (26)	10.5 (201)	10.6 (226)
Deraecoris	-	-	16.7 (6)	100.0 (1)	0 (2)	50.0 (2)
Nabis apterus	-	-	-	-	40.0 (10)	16.7 (6)

Table 35. The percentage of meals from Heteropteran predators of different instars reacting with anti-psyllid serum.

N.B. The numbers in brackets are the numbers of each instar tested.

Table 36. The percentage of coccinellid meals reacting with anti-psyllid serum in 1962. Figures in brackets refer to the actual numbers tested.

Coccinellid species	Percentage reacting with anti-psyllid serum
Adalia bipunctata (adults)	3.3 (61)
A. bipunctata (larvae)	10.6 (104)
A. decempunctata (adults)	11.1 (9)
A. decempunctata (larvae)	0 (15)
Coccinella septempunctata (adults)	44.4 (9)
C. septempunctata (larvae)	12.5 (8)
Propylea 14-punctata (adults)	28.6 (7)
Anatis ocellata (adults)	40.0 (5)

and adults of Adalia bipunctata L., A. decempunctata L., Coccinella septempunctata L., Propylea quatuordecempunctata L. and Anatis ocellata L. The percentage of each coccinellid species found to have fed on psyllids is shown in Table 36. Larval and adult coccinellids appeared to have been feeding to a roughly equal extent on psyllids.

The spiders, mites and harvestmen are comparable to the Heteroptera in their mode of feeding on the juices of insects. The red mite, Anystis agilis Banks will attack psyllid nymphs and adults readily on the beating tray and will take large numbers of A. genistae eggs in the laboratory. The precipitin test, however, suggested that it was feeding on psyllids less than the spiders and *Platybunus triangularis* Herbst.

The species of spiders on broom are numerous and many of them were shown in 1962 by Dr. Dempster to feed on psyllids. The spiders feeding on psyllids were the crab spiders *Xysticus cristatus* Clerck and *Philodromus aureolus* Clerck (Thomisidae), *Pisaura mirabilis* Clerck (Pisauridae) and *Evarcha* sp. (Salticidae). These spiders hunt their prey on foot. The web spinning spiders feeding on psyllids were *Theridion redimitum* L. (Theridiidae), *Linyphia triangularis* Clerck (Linyphiidae), *Meta segmentata* Clerck and *Araneus diadematus* Clerck (Argyopidae). *Linyphia triangularis*, spinning a sheet web, was perhaps the commonest species and fed more extensively on psyllids than most other species. *Theridion redimatum* fed on psyllids to about the same extent as *Linyphia*.

Arthropods tested but not reacting with anti-psyllid serum were 10 *Plagiognathus arbustorum* Fabricius (Heteroptera Miridae), 3 Syrphid larvae and 10 harvestmen, *Phalangium opilio* L. Two small syrphid larvae were, however, found in 1963 feeding on first instar *A. spartii* nymphs in samples.

The effect of birds as predators on psyllids is even more difficult to assess than that of predaceous arthropods. Flocks of sparrows and starlings were observed in the study area from time to time in the summer and they could have been feeding on psyllids as well as on other arthropods. Birds have been recorded as feeding on psyllids in

North America (Odell 1927). Odell records the black-capped chickadee, ruby throated and golden crowned kinglets and the red-breasted nuthatch feeding on the pear psyllid, *Psylla pyricola* Förster.

(b) Life Cycles of Predators of Broom Psyllids.

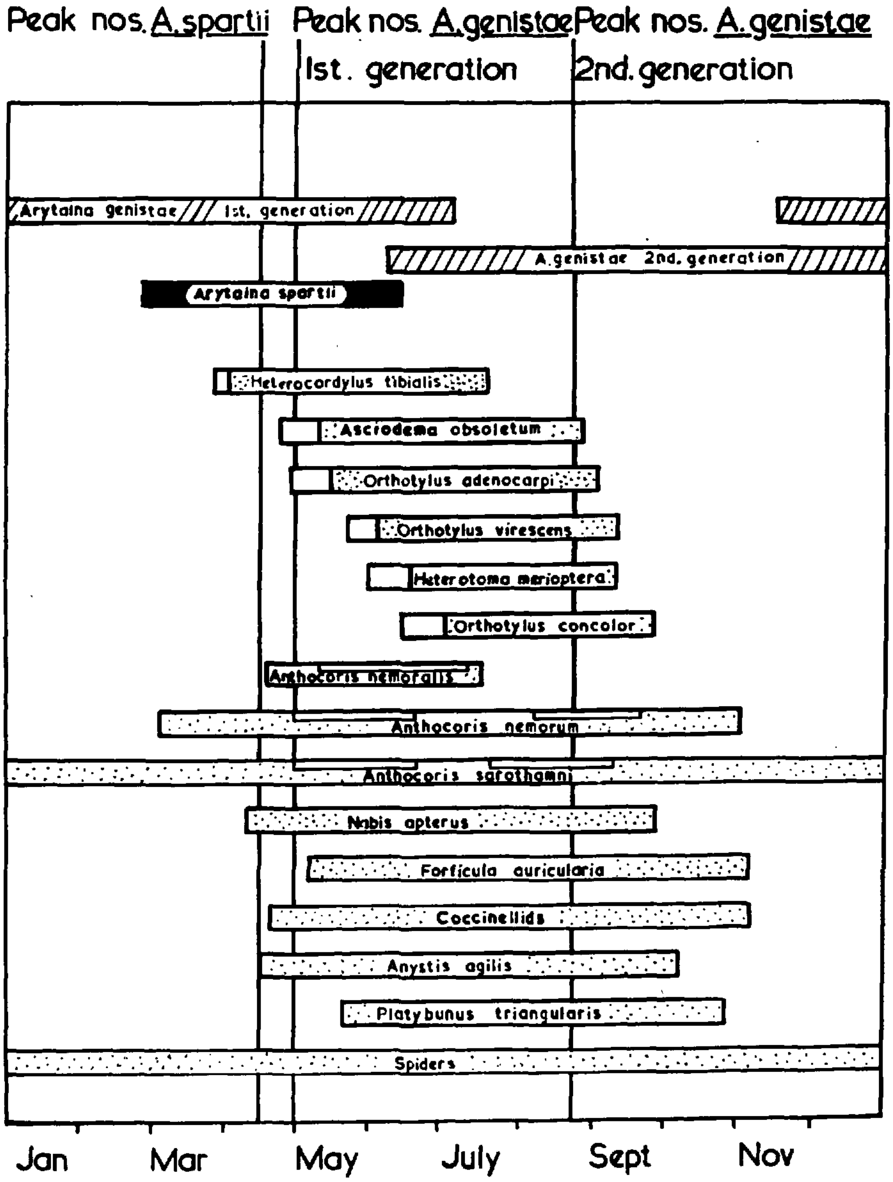
The dates of appearance of the various predators of broom psyllids are different so that their life cycles do not all overlap with *A. genistae* and *A. spartii* to the same extent. The result is a succession of predators occurring through most of the year with a maximum abundance in late spring and early summer (Fig. 54).

The three anthocorids found commonly on broom overwinter as adults. *Anthocoris sarothamni* lives only on broom and many adults hibernate inside old broom pods in winter. Some hibernate away from the broom plant and fly on to it in spring (Anderson 1962a, Hill 1961). It is the first predator to take psyllid nymphs and eggs in spring. This was shown by two out of 10 adult *A. sarothamni* collected on 16 March 1963 reacting with anti-psyllid serum. *A. spartii* only started hatching about 5 April in 1963 and these *A. sarothamni* were most probably feeding on *A. genistae* eggs. *A. sarothamni* is active and probably feeding whenever day temperatures are high enough in winter.

Anthocoris nemoralis and *A. nemorum* overwinter under bark and in other sheltered sites away from broom plants and move on to broom and a variety of other plants as soon as the weather is warm enough in spring (Anderson 1962). Both *A. nemorum* and *A. sarothamni* usually have two generations on broom each year but *A. nemoralis* disappears from broom

Fig. 54.

The times of occurrence of various predators compared with those of Arytaina spartii and Arytaina genistae.



Unshaded areas represent periods with non-predatory early instars present in June or July after a single generation.

In 1961 - 1963 the older nymphs of the anthocorids only appeared when the numbers of *A. spartii* were already rapidly falling (Fig. 54). Because the peak of *A. genistae* is later than that of *A. spartii* the anthocorid nymphs overlap better with this psyllid. The second generation of *A. nemorum* and *A. sarothamni* nymphs coincides well with the second generation of *A. genistae*. Anthocorid adults are likely to cause a steady mortality of psyllid nymphs throughout the season.

All the broom miridae overwinter as eggs in broom stems and hatch in spring and early summer. The first to start hatching is *Heterocordylus* in late March or early April as soon as temperatures are suitable and it dies out by mid-July. *Asciodema* and *Orthotylus adenocarpi* follow *Heterocordylus* in hatching and both die out in August or September. *Heterotoma* and *Orthotylus virescens* start hatching next at about the same time in May or early June. *Orthotylus concolor* is the last of the mirids to hatch in mid to late June. *Deraecoris* appears to start hatching at about the same time as *O. concolor*.

Heterocordylus overlaps the *Arytaina spartii* generation and the first generation of *A. genistae* better than any other mirid and for this reason is likely to be most important in reducing psyllid numbers in spring. The predatory stages (later instars) of the other mirids hatching later coincide with the end of the spring generation of psyllids and the first part of the second generation of *A. genistae*.

Nabis apterus hatches in early April and becomes adult by mid-July.

It therefore overlaps the same parts of the psyllid generations as most of the mirids.

Forficula is in low numbers on broom during the early part of the year but becomes more common from late July onwards. It therefore coincides best with the second generation of *A. genistae*. *Forficula* overwinters in the adult state among litter on the ground and under stones and logs.

Adult coccinellids move on to broom in spring and disappear in autumn. There is a generation of coccinellid larvae in May - August starting after the peak of psyllid numbers in spring and finishing after the peak in numbers in the second *A. genistae* generation. The adults probably cause a steady mortality of psyllid nymphs throughout the spring, summer and autumn.

Hemerobius larvae appear on broom in early summer and are present until August or September. They therefore prey almost entirely on the second *A. genistae* generation.

Spiders are present on broom throughout the year. They therefore prey on all psyllid generations. *Anystis* appears in April at about the time when the psyllids are at their peak numbers and disappears between August and November. The peak numbers of *Anystis* coincide with the end of the *A. spartii* generation and the first part of the second *A. genistae* generation.

Platybunus appears in May - July but only reaches peak numbers during the second generation of *A. genistae*.

Arytaina spartii is relatively free of predators in the early part of its development as it builds up to peak numbers before the mirids start hatching. The same applies to a lesser extent to the somewhat later first generation of *A. genistae*. Most of the predators coincide more with the second generation of *A. genistae* which probably suffers more predation as a result. Even after the mirids disappear in August the summed effect of the remaining predators is likely to be important.

The Size of Predator Populations.

The average numbers of predators present with each psyllid generation are shown in Tables 37 and 38. These figures are from population estimates made by Richards, Waloff and Dempster using the carbon dioxide sampler. There were more predators in 1961 than in 1962 or 1963. This was entirely due to the higher numbers of the mirids, *Heterocordylus*, *Asciodema* and *Orthotylus adenocarpi* and the anthocorids *Anthocoris nemoralis* and *A. sarothamni*. The numbers of other predators were similar in each of the years 1961 - 1963.

The mirids, except for the rather scarce *Heterotoma* and *Deraecoris* were always the most numerous predators. *Anystis* was frequently the next most numerous predator being most common in the early summer of 1963.

(c) The Relative Importance of the Different Predators.

The importance of a predator in reducing psyllid numbers is likely to depend on the extent to which it feeds on psyllids, its numbers and the extent to which it overlaps the period of psyllid occurrence.

A predator could be important even towards the end of a psyllid generation when psyllid numbers are low if it kills a high proportion of the older nymphs or adults.

The mirids are likely to be the most important single group of predators because of their large numbers and because many of them feed on psyllids extensively. The Anthocorids are perhaps the next most important group because they are collectively fairly numerous and also two of the species feed preferentially on psyllids (Dempster 1963).

(d) Alternative Prey of Predators on Broom.

Most of the predators taking broom psyllids are also known to feed on a wide variety of other prey (Dempster 1960). Dempster found that all the broom mirids also feed to about the same extent on the broom itself. The anthocorids feed to a somewhat lesser extent on broom, while *Nabis apterus* seems to be entirely carnivorous. Of the other predators besides Heteroptera only the omnivorous earwigs feed on broom and other plant material.

Anthocoris nemorum is the most widely distributed of the predators being found on very many plants besides broom. It appears to be mainly carnivorous and will feed on almost any small arthropod. A list of its recorded prey is given by Hill (1957). At Silwood Park alternative prey to psyllids are numerous. It has been seen feeding on the two broom aphids, *Aphis sarothamni* Franssen and *Acyrthosiphon spartii* Koch, *Phytodecta olivacea* larvae, small caterpillars and spiders and it

Table 37. Average numbers of predators per 100 grammes broom present with *A. spartii*. 1961 - 1963.

Predator	Average number of each predator present in whole psyllid generation (nymphal period only)		
	1961	1962	1963
Heterocordylus tibialis	11.36	1.30	0.53
Asciodema obsoletum	4.03	0.34	0.25
Orthotylus adenocarpi	6.30	1.33	1.79
O. virescens	0.79	0.22	0.40
O. concolor	-	0.007	-
Heterotoma merioptera	0.02	0.009	0.006
Deraecoris ruber	-	-	-
Anthocoris nemoralis	1.28	0.13	0.05
A. sarothamni	0.94	0.15	0.05
A. nemorum	0.18	0.09	0.17
Nabis apterus	-	-	-
Coccinellids	0.07	0.009	0.01
Hemerobius larvae	-	-	-
Forficula auricularia	0.01	0.01	0.006
Anystis agilis	0.14	0.35	0.87
Spiders	0.55	0.57	0.74
Platybunus triangularis	-	0.002	0.01
TOTAL	25.670	4.517	4.882
Acyrthosiphon pisum	23.30	4.41	4.14
Arytaina spartii	3,032	130	166

Table 38. Average numbers of Predators per 100 grammes broom present with *A. genistae*. 1961 - 1963.

Predator	Average number of each predator present in psyllid generation (nymphal period only)				
	1961		1962		1963
	1st Generation	2nd Generation	1st Generation	2nd Generation	1st Generation
Heterocordylus tibialis	10.04	1.03	0.91	0.02	0.68
Ascodema obsoletum	5.17	2.28	0.54	0.30	0.35
Orthotylus adenocarpi	8.68	4.27	1.99	1.08	2.63
O. virescens	0.10	0.85	0.47	1.58	0.20
O. concolor	0.06	0.33	0.33	0.67	0.08
Heterotoma merioptera	0.02	0.02	0.02	0.29	0.004
Deraecoris ruber	-	0.002	-	0.004	0.009
Anthocoris nemoralis	1.30	0.38	0.23	0.06	0.07
A. sarothamni	1.36	0.68	0.18	0.16	0.07
A. nemorum	0.24	0.12	0.19	0.12	0.20
Nabis apterus	-	0.002	0.005	0.006	-
Coccinellids	0.13	0.18	0.08	0.22	0.06
Hemerobius sp.	V.low	V.low	V.low	V.low	V.low
Forficula auricularia	0.02	0.14	0.02	0.12	0.02
Anystis agilis	0.18	0.41	0.49	0.58	1.06
Spiders	0.53	0.69	0.48	0.61	0.81
Platybunus triangularis	-	0.03	0.001	0.08	0.01
TOTAL	27.830	11.414	5.936	5.900	6.253
Acyrthosiphon sarothamni	29.91	14.52	14.13	9.80	5.64
A. genistae	51	39	243	137	180

undoubtedly will take Collembola, Psocoptera and Miridae (Dempster 1960).

The two anthocorids *Anthocoris sarothamni* and *Anthocoris nemoralis* feed on psyllids preferentially (Dempster, 1963). *A. sarothamni* females will enter reproductive diapause at the end of the first generation (Anderson 1962b) if psyllid prey are not available. The numbers of these two anthocorids reflect the numbers of psyllids present (Tables 37 and 38). In 1961 when *A. spartii* was very numerous the numbers of *A. nemoralis* and *A. sarothamni* were highest. In 1962 and 1963 the lower numbers of psyllids led to lower numbers of anthocorids. The numbers of psyllids in the spring and early summer of 1963 were lower than at a similar time in the previous two years and so also were the numbers of anthocorids. The second generation of *A. sarothamni* was larger in 1962 than in 1961 because the second generation of *A. genistae* was larger. This does not show in Table 38 because of the effect of the large first generation of 1961. The numbers of *Anthocoris nemorum* do not appear to be correlated with the numbers of any particular prey species.

All the mirids are omnivorous and will take aphids in the laboratory. Large nymphs of *Heterocordylus* and *Orthotylus adenocarpi* will feed on the young stages of other miridae in the laboratory. *Heterotoma merioptera* is a widespread mirid recorded from many plants (Butler 1923, Kullenburg 1946). It is omnivorous and is recorded by Kullenburg as feeding on lepidopterous eggs and larvae and on aphids. *Nabis apterus* occurs on many trees and shrubs. It will take a variety of prey but feeds particularly readily on mirids and psyllids in the laboratory. These probably make up much of its food on broom.

The coccinellids are well known as predators on other insects and they will attack a wide variety of prey including aphids, scale insects, immature stages of Lepidoptera, Hemiptera and many others. *Hemerobius* has been found feeding on aphids, mealybugs, white flies and diaspine scale insects (Clausen 1940). *Forficula* is omnivorous and feeds on a wide variety of plant and animal material. *Anystis*, spiders and *Platybunus* will also attack many different insects besides psyllids.

(e) The Availability of Psyllids to Predators on Broom.

Psyllids are the most abundant prey available to predators on broom and, for this reason, are likely to be an important food source. The next most abundant potential prey on broom is the aphid, *Acyrthosiphon pisum*. Other fairly numerous potential prey are psocids, and collembola.

The number of each species of psyllid taken by predators is likely to be related to the proportion in which each is available from the total population of potential prey. The numbers of predators in relation to the available prey is also important. Large numbers of one species of psyllid are likely to reduce the intensity of predation for the other species because the overall predator - prey ratio is reduced. The ratio of the number of predators to the number of psyllids for each year is shown in Table 39. The eggs of *A. spartii* are excluded from the figures in this table because they, being embedded in stems under a wax cap, are relatively safe from predators. The exposed eggs of *A. genistae* are however very vulnerable to predators.

Table 39. The relation of the numbers of A. spartii and A. genistae to one another and to the numbers of predators.

Year	Average number psyllids present in spring generations	Ratio of psyllid numbers to predator numbers	A. spartii: 1st generation A. genistae ratio	Average number second generation A. genistae present	Ratio of 2nd generation A. genistae numbers to predator numbers
1961	3090	1 : 0.008	1 : 0.02	39	1 : 0.29
1962	572	1 : 0.008	1 : 3.56	137	1 : 0.04
1963	400	1 : 0.012	1 : 1.41	-	-

The relation and extent of overlap of aphid and psyllid numbers are shown in Tables 40 and 41. The numbers of aphids present in 1961 were higher than in 1962 or 1963. The coincidence of aphids with the first generation of A. genistae is poorer than that with A. spartii because of the aphids miss the peak of A. genistae eggs. The occurrence of aphids is likely to have had its greatest effect in the second generation of A. genistae in 1961 when there was an average of 1 aphid to every 4 psyllids for 87% of the generation (see Tables 40 and 41).

(f) Predation on A. spartii.

The ratio of A. spartii to first generation A. genistae in each year is shown on Table 39. In 1961 the proportion of A. genistae with A. spartii was much lower than in the other two years. Predators

Table 40. Relation between Psyllid and Aphid numbers.

Year	Size of aphid generation Av. no./100 gm.	Dates of occurrence	Ratio of psyllid numbers to aphid numbers			
			a) For whole period of aphid occurrence	b) While *A. spartii* present	c) While 1st generation *A. genistae* nymphs present	d) While 2nd generation *A. genistae* present
1961	25	29/4–31/8 128 days	1 : 0.02	1 : 0.02	1 : 0.24	1 : 0.26
1962	19	14/4–28/8 140 days	1 : 0.06	1 : 0.02	1 : 0.07	1 : 0.19
1963	8	25/4–15/8 116 days	1 : 0.03	1 : 0.02	1 : 0.03	–

Table 41. The fraction of each psyllid generation when aphids were present.

(This fraction is derived by summing psyllid population estimates at regular intervals during the period of aphid occurrence and dividing by the sum of all the population estimates. In the first generation of *A. genistae* for each year only the period when nymphs are present is considered).

Year	Fraction of psyllid generation present with aphids		
	A. spartii	*A. genistae*	
		1st Generation	2nd Generation
1961	0.47	0.39	0.87
1962	0.94	0.33	0.40
1963	0.86	0.51	–

were also most numerous in 1961. Because of these two factors the proportion of the *A. spartii* nymphal population killed by predators in 1961 is likely to have been greater than in 1962 when the overall predator-psyllid ratio was the same, but much larger numbers of *A. genistae* were present. The results of the analysis of the sampling data suggest a higher nymphal mortality in 1961 than in 1962, although much of this increased mortality was due to competition.

In 1963 losses of *A. spartii* nymphs through predation are likely to have been greater than in 1962 because the overall predator-psyllid ratio was larger and the proportion of *A. genistae* was smaller. The proportion and time of occurrence of aphids with *A. spartii* in 1962 and 1963 are similar (see Tables 40 and 41). The sampling data does in fact suggest that nymphal mortality was greater in 1963 than in 1961 and 1962. The data on the number of dead nymphs present in 1963 also agrees with this.

(g) Predation on *A. genistae*.

The figures in Table 39 suggest that predation in the first generation is likely to have been smallest in 1961 because of the very large numbers of *A. spartii* present. The numbers of aphids were also high (Table 40). In 1962 the proportion of *A. genistae* was at its highest and this would have resulted in greater predation on this species than in 1961. In 1963 the numbers of *A. genistae* and *A. spartii* were nearer equality so that both may have suffered a more equal share of predation. The number of predators per psyllid was higher than in either the spring of 1962 or 1961 so that more psyllid nymphs would have been killed in 1963.

The egg-nymph and nymph-adult ratios for A. genistae shown in Table 22 suggest that mortality was lower in the first generation of 1961 than in the first generation of 1962 or 1963. The numbers of adults produced by the first generation of 1963 were lower than in any other generation in relation to the numbers of nymphs and eggs. This suggests that mortality in 1963 was greater than in any other generation. The agreement with the conclusions to be drawn from predator-psyllid ratios is therefore reasonable. It seems likely then that the different numbers of first generation adults produced in each of the three years are related to different intensities of predation.

Tables 38 and 39 show a higher number of predators in the second generation of 1961 than in the second generation of 1962. Table 22, however, indicates that a larger proportion of nymphs produced adults in the second generation of 1961 than in that of 1962.

The second generation of 1962 started about a month later than that of 1961 and developed more slowly because of lower temperatures. The 1961 generation was almost entirely adult at the onset of winter, while the 1962 generation had many nymphs which were killed by unfavourable winter weather. It is likely therefore that weather was responsible for the different mortalities in the second generations of the two years.

It is possible that A. genistae built up to high numbers in the study area when the bushes were young partly because mirid numbers were low at the time. Estimates of mirid numbers made by Richards, Waloff and Dempster in 1959 and 1960 showed that mirids increased substantially between

1959 and 1961. *Anthocoris sarothamni* was also present in low numbers in 1959 and only built up later because of its low mobility (Dempster 1963). *A. sarothamni* gradually increased until the spring of 1961 when *A. spartii* was most numerous. A crash in psyllid numbers then resulted in a great reduction of *A. sarothamni*. The other predators of psyllids which colonise the broom anew each year are likely to have had a similar effect in all years. The broom mirids and *A. sarothamni* breed on the broom so that their numbers in any year are partly dependent on the numbers present in the same place in the previous year.

(h) The Parasites of Psyllids.

No parasites were found in psyllids in the present study in 1961 - 63. Several Chalcids, Encyrtids, Eulophids and a Platygasterid (Hymenoptera) as well as a Cecidomyiid and a tachinid (Diptera) are, however, known to parasitise psyllid nymphs and adults (Clausen 1940, Lal 1934, Thompson 1950). Professor O.W. Richards has found two brown mummies of parasitised fifth instar *A. genistae* nymphs at Silwood Park, however. From these adults of the encyrtid, *Prionomitus mitratus* Dalm. emerged. This parasite has been reported from a number of psyllid species in Europe (Lal 1934). Parasites have been known to have an important effect on psyllid populations (Clark 1962) and it is perhaps surprising that no parasites were found in the broom psyllids during the present study.

The Distribution of Psyllids on Bushes of Different Ages.

An attempt was made to study the effects of the age of a broom bush on its psyllid population. Four different natural areas of broom were sampled, 100 cuttings being taken from bushes in each of the age groups shown in Table 42. Only one or two cuttings were taken from each bush so as to cover the whole area. Many bushes in all age groups except the 8 - 10 year old group were present in each broom area. In the Silwood Park "Old Broom" there were only six bushes 8 - 10 years old. The Camberley broom had numerous bushes in this age group, however. The 1 - 3 year age group was always the most numerous. The *A. spartii* populations in each of these areas were sampled in May 1963 when nymphs were reaching the fourth or fifth instar. *A. genistae* was present in only low numbers.

All the broom areas sampled except the Silwood Park "Old Broom" had stands of broom and scattered bushes extending over 10 - 20 acres. The Silwood Park "Old Broom" was the smallest area sampled covering only about two acres. Two separate broom areas about one mile apart were sampled on Chobham Common in Surrey (Chobham Common A and B in Table 42).

Classification of bushes in age groups.

The broom bushes in each area sampled were classified as follows:

1) 1 - 3 year age group: Plants up to 2 feet (0.6 metres) high., with erect stems and almost all buds with trifoliate leaves. Mostly with rapidly growing soft, hairy shoots. Few flower buds and flowers. Little or no dead wood.

Table 42. The Distribution of Psyllids on broom bushes of different ages.

Site	Age of bush in years and % of *A.spartii* population on each age group				Age of bush in years and % of *A.genistae* population on each age group				Number psyllids per 100 gm.	
	1-3 yr.	4-5 yr.	6-7 yr.	8-10 yr.	1-3 yr.	4-5 yr.	6-7 yr.	8-10 yr.	*A.spartii*	*A.genistae*
"Old Broom" Silwood Park.	51	32	11	6	18	14	55	13	1,901	49
Chobham Common (A)	73	18	9	-	83	14	3	-	383	49
Chobham Common (B)	28	36	36	-	21	79	0	-	148	19
Camberley	25	33	29	13	39	34	25	2	127	63

2) 4-5 year age group: Up to 4 feet (1.3 metres) high and branches spreading to produce a rounded crown. Many buds with simple leaves only and many flowers frequently present. Less soft young growth than in the 1-3 year age group. Little dead wood.

3) 6-7 year age group: Up to 6 feet (1.8 metres) high with much branched broad, rounded crown and variable amounts of dead wood in centre. Many buds with simple leaves only and flowers frequently numerous. Young growth less than in youngest plants.

4) 8-10 year age group: Up to 10 feet (3.0 metres) high. Often with much dead wood and thick woody stems up to 10-12 cm. in diameter. Crown often broken up through loss of much of the centre. Buds often rather small in comparison with younger bushes and young growth limited.

This classification only applied to plants in May - June during the period of occurrence of *A. spartii* nymphs. The classification is rather rough as bushes are variable.

Results.

There is a tendency for *A. spartii* to concentrate on younger bushes (Table 36). This concentration was most marked in the two areas with the densest populations. The cause of this distribution is most probably the large amount of new growth on the younger bushes. This would provide adults with the most favourable oviposition sites and food. It is likely that the nymphs would also obtain better quality food from a young actively growing plant.

In all the natural areas of broom sampled bushes of all ages were mixed together or situated in adjacent stands. This was different from the situation in the study area which consisted of a large isolated uniform stand of plants of the same age. In a natural mixed area of broom the younger bushes could be expected to be readily colonised from adjacent older ones.

Large uniform areas of crop plants or timber trees of the same age favour insect outbreaks because they supply favourable conditions for certain insects on a large scale. Generally diversification of a crop, either by species or age, results in a reduction of the danger of insect outbreaks. Because of its uniformity, therefore, the study area probably favoured the rapid build up of psyllid populations. Both psyllid species colonised the young broom quickly after it was planted in early 1957 and increased greatly in numbers. A. genistae reached maximum numbers when the bushes were 2-3 years old and A. spartii when they were four years old. It appears that A. spartii numbers were reduced by over-exploitation of the habitat. A. genistae might have been reduced more by predation (see preceding section on predators).

In a natural broom area containing bushes of different ages one could expect the dense psyllid population on younger bushes to exhaust them. These exhausted bushes would be unfavourable for further egg-laying and the adults would move to other young, actively growing bushes or to older bushes which had recovered. In the study area this could not happen as most of the bushes were exhausted by a dense population at the same time (i.e. A. spartii in 1961). A large reduction in psyllid numbers therefore occurred and numbers remained at a lower level in the following years.

The broom psyllids are well adapted to colonising new broom areas. They would therefore appear fairly early in the life of a broom plant and be able to utilise it when it is most favourable. The psyllids require adequate means of dispersal because of the fragmented nature of their habitat. Broom in England, although sometimes abundant locally, is a scattered plant having a relatively short life of 10 to 15 years. It is found especially on disturbed soils where the natural vegetation has been destroyed and is often replaced as the original plants reappear. Insects with the best developed powers of dispersal are often those from the more temporary habitats which must be found quickly after they appear if they are to be effectively colonised (Southwood 1962).

DISCUSSION.

During the years 1959 - 1963 the broom psyllid populations were determined by interspecific and intraspecific competition, predators and weather. Competition was density dependent tending to limit the peak of numbers while predation was imperfectly density dependent and weather was density independent. Only the anthocorids among the predators were seen to definitely respond to psyllid numbers. Although the number of some mirids appeared to follow psyllid numbers between 1961 and 1963 it appears that some factor other than changing psyllid numbers was responsible. A brief account of what appeared to be happening to the psyllid populations in the light of the available evidence is given below.

From the time when the broom was planted in 1957 the numbers of A. spartii increased until 1961 when a crash occurred. This crash in numbers was caused by intraspecific competition among the nymphs and the emigration of a large proportion of the adults, the latter having the greater effect. These factors also probably operated in previous years but not to the extent of preventing further population increase. There was also probably a reduction of fecundity of the remaining adults but this would have been minimised by the loss of many of the adults by emigration.

The nymphs dying through intraspecific competition were probably the younger ones which were at a disadvantage when competing with older and largerindividuals. This also applied to any interspecific competition which might have occurred between *A. genistae* and *A. spartii* since *A. spartii* develops quicker than *A. genistae* in spring so that young *A. genistae* nymphs must compete with older *A. spartii* nymphs. It is possible that some of the individuals eliminated by competition differed in their genetic constitution from the survivors. These perhaps inferior genotypes might have survived in the absence of competition. Competition greatly increases the action of selection in genetic differences. Mortality resulting from competition is often a selective mortality of genetic defects (Allee, Emerson, Park, O., Park, T., and Schmidt 1959).

In 1961 the *A. spartii* nymphal population was probably near the maximum which the habitat could support. The bushes were exhausted by the nymphs and stunted in their growth so that suitable oviposition sites for the adults were restricted.

In 1962 and 1963 when *A. spartii* populations were much smaller competition was unimportant and predation was probably the most important factor causing nymphal mortality. The presence of *A. genistae* nymphs and eggs in the same habitat may have tended to protect *A. spartii* nymphs from predation, since *A. genistae* constituted an alternative prey species. This was probably most important in 1962 when a larger number of *A. genistae* eggs and nymphs were present. In 1963 *A. genistae* and *A. spartii* numbers were more equal and the numbers of predators per psyllid was higher than in the previous two years. Nymphal mortality was highest in 1963 because of increased predation.

In all years emigration was important in reducing the density of adults. The amount of emigration in 1961 - 63 seems to have been density dependent, but in 1959 - 1960 less emigration apparently occurred. This was probably because the broom bushes were young and growing rapidly. They provided very favourable conditions for feeding and egg-laying adults. Emigration is a regular feature of the life cycle of *A. spartii* and occurs even when the density of adults is low.

Arytaina genistae colonised the study area after it had been planted in 1957 as rapidly as *A. spartii* but failed to reach the high density achieved by *A. spartii*. This was probably because of predation and competition with *A. spartii* which is better adapted to British spring conditions. The numbers of *A. genistae* reached a peak in 1959 when predator numbers were low (Richards, Waloff and Dempster). High *A. genistae* numbers were maintained until the summer of 1960 when a crash occurred. This crash was caused by the emigration of adults and possibly predation on the second generation.

During 1961 - 1963 the numbers of *A. genistae* were much lower than in 1958 - 1960 and fluctuated with variations in predation and weather.

A. genistae appears to be more vulnerable to both predation and weather than *A. spartii*. The first generation of *A. genistae* is possibly protected from predation to a certain extent by the presence of *A. spartii*. The first generation of 1961 suffered less predation than the first generation of 1962 or 1963 because of the high numbers of *A. spartii* present in 1961. In 1962 the first generation suffered more predation than in 1961 because

A. genistae eggs and nymphs were more numerous than *A. spartii* nymphs. In 1963 the numbers of predators were highest in relation to the numbers of psyllids so that the first generation of *A. genistae* suffered more predation than in the previous two years. Because of its later development the first generation of *A. genistae* coincides better than *A. spartii* with maximum predator numbers. The second generation of *A. genistae* also occurs while predator numbers are still high.

Weather was important in restricting *A. genistae* in autumn, winter and spring. The mortality of overwintering adults is greatest in severe winters while frosts in spring and autumn kill young nymphs. The numbers of overwintered adults decrease steadily in spring so that a prolonged delay of the first generation by late frosts could reduce the size of the generation. Mortality caused by unfavourable weather was also large at the end of the second *A. genistae* generation of 1962. In *A. spartii* mortality caused by frost was only detected in 1961 and even then it appeared unimportant. In 1962 *A. spartii* started hatching later than *A. genistae* so that it avoided more of the frost early in spring.

In *A. genistae*, as in *A. spartii*, emigration of the adults is important in reducing adult population density. Because of emigration the adults of *A. genistae* probably rarely suffer any marked reduction of fecundity caused by crowding. The proportion of *A. genistae* adults emigrating is probably density dependent. The presence of large numbers of *A. spartii* adults with the peak in numbers of *A. genistae* adults in 1960 was probably responsible for the rapid dispersal of *A. genistae* adults.

In both broom psyllids mortality is highest in the early stages. In *A. spartii* mortality is low in the egg stage and highest in the earlier nymphal stages. In *A. genistae* mortality is highest in the egg stage and next highest in the earlier nymphal stages. The difference in egg mortality in the two species is related to the degree of protection enjoyed by the egg. *A, genistae* compensates for a high egg mortality with a high fecundity, but this is still apparently not as effective as the protected egg of *A. spartii*.

The presence of two closely related psyllids in the same habitat then results in advantages and disadvantages for both. The presence of the two species together has already been shown to result in a probable mutual protection from predation. *A. spartii*, however, is likely to be at an advantage should any interspecific competition occur because it is better adapted to the British climate. *A. genistae* could have the advantage in a warmer climate such as occurs in Southern Europe. The life cycle of *A. genistae* with two or more generations each year provides more opportunity for colonisation and utilisation of temporary favourable conditions. *A. spartii* is likely to be less flexible in utilising favourable conditions because of its single annual generation. In spite of this *A. spartii* seems to be able to build up larger populations than *A. genistae* in Southern Britain.

In Britain a bivoltine life cycle is imposed on *A. genistae* by the climate. In the warmer climates of Southern Europe this species is probably multivoltine with generations following one another throughout the year. In warm years in Britain three *A. genistae* generations do occur.

In Britain the diapause in the egg of *A. spartii* is obligatory so that there can only be one generation each year. Heslop-Harrison (1951) suggests that *A. spartii* may be bivoltine or even multivoltine in Southern Europe. Diapause in the egg stage would have to be reduced or eliminated before this could occur. In a number of other insects strains with facultative and obligatory diapause occur; in others additional strains are entirely free of diapause (Lees 1955). This could happen in *A. spartii*, but the matter requires investigation. Diapause is an adaptation for preserving a species in regions where seasonal climatic conditions are unfavourable for continuous multiplication. The occurrence of diapause in *A. spartii* suggests that this species has been influenced more by cold climates than *A. genistae* which is more plastic with no diapause in any stage.

Clark (1962, 1963a, b) has studied the biology and population dynamics of *Cardiaspina albitextura* Taylor, a test-forming psyllid inhabiting the foliage of redgums, particularly *Eucalyptus blakelyi* Maiden, in inland south eastern Australia. In certain respects Clark's findings agree with the conclusions to be drawn from the present work on broom psyllids. The test of *Cardiaspina* is a flat, scale-like structure completely covering the nymph and made of excreted wax. Clark's work is the only other existing work on psyllid populations.

Clark considers that *C. albitextura* numbers are determined, like those of the broom psyllids, by intraspecific and interspecific competition, predators and the condition of the food plant. An additional factor not present in the broom psyllids is the attack of *C. albitextura* by parasites. Weather is an additional factor but its effects are indirect operating by interfering with the relationship of the psyllid and its parasites.

C. albitextura, three other psyllids on the same genus, and the psyllid *Lasiopsylla subrotundipennis* Frogatt have all increased to a level causing severe foliage damage on gum trees in the last 10 years. Other psyllids on eucalypts have remained at low levels. The increase of psyllid populations has been associated with cooler than average weather and above normal rainfall, temperature being the most important in its effects. *C. albitextura* has maintained high numbers mostly in the cooler areas. Clark suggests that low temperatures have affected psyllid abundance by causing a breakdown of the synchronisation of psyllid parasites with their host. Cool weather also probably interfered with the searching behaviour of egg-laying parasites. The two important parasites of *C. albitextura* are the encyrtids *Psyllaephagus gemitus* Riek and *Psyllaephagus xenus* Riek. These attack *C. albitextura* at all population densities, but at high densities hyperparasites destroy a high proportion of the primary parasites. This tends to ensure a maintenance of high psyllid numbers once they have built up.

The increase of *C. albitextura* is limited by the damage inflicted on the food plant. The nymphs are relatively immobile and normally spend most of their life on a single leaf. The portion of the leaf on which a nymph is feeding becomes discoloured and eventually dies. In heavy psyllid nymph infestations most of the foliage on a tree may be destroyed. Under these conditions there is competition for food and nymphs migrate in search of it. Many drop off the tree or are lost on leaves which are shed by the tree. This is similar to what was observed in *Arytaina spartii* which prevents normal growth of the food plant at high densities and then moves in search of food.

Clark found that the *C. albitextura* nymphs could not reach undamaged leaves a few feet away and had difficulty in retaining a foothold on foliage after leaving their test.

As in the broom psyllids *C. albitextura* showed a slight loss in weight of females reared at higher population densities but males showed no weight change. *C. albitextura* nymphs living at extremely high population densities, however, were markedly reduced in size, but few of these ever became adult because of the shedding of damaged leaves by the host tree. A great reduction of the psyllid population is also sometimes achieved by seasonal leaf shedding associated with normal leaf renewal.

In *C. albitextura*, as in the broom psyllids there is a reduction of fecundity of adults under crowded conditions caused by restriction of food and oviposition sites. In *C. albitextura* heavy feeding by nymphs and adults greatly reduces the attractiveness of leaves as oviposition sites. On the other hand, the presence of eggs increases the attractiveness of leaves in proportion to the number laid on them. This leads to the concentration of *Cardiaspina* eggs on a limited proportion of suitable leaves. Males of *Cardiaspina* feed less than the females and do not appear to limit the fecundity of females much when present in large numbers. This may also be so on broom psyllids.

A. spartii is restricted in its requirement for young, soft broom shoots. *A. genistae* is not so obviously restricted as its eggs can be found at different times of the year on and in buds at all stages of development on old and young stems.

Cardiaspina often had to compete with defoliating beetles for suitable foliage on which to feed and lay. Clark found that beetles sometimes destroyed nearly all new foliage on some or all trees in a stand. In addition Clark recorded *Cardiaspina retator* Taylor on the same tree species as *C. albitextura*. *C. retator* was one of the other psyllids achieving heavy infestations so that interspecific competition between the two *Cardiaspina* species is possible.

When the numbers of *C. albitextura* were low parasites and predators exerted a decisive influence so long as temperatures were normal. The end of an outbreak period was marked by a crash in psyllid numbers caused often by leaf shedding by the host plant. Broom psyllid numbers were determined at low levels by predators and in *A. genistae* by weather as well in most years. As in *C. albitextura* the rise in broom psyllid numbers possibly occurs when some factor interferes with the normal mechanism of control. The crash in numbers of *Arytaina spartii* was similar to the population crashes of *Cardiaspina* in that they were caused partly by the limited capacity of the food plant.

The conclusions drawn from the work on psyllids can now be compared with existing theories of population control. If a population is to remain in being, two conditions must be fulfilled (Milne 1957):

1) The highest densities must always be below the level that would result in collective suicide resulting from destruction of the habitat by over-exploitation.

2) The lowest densities must always be above zero.

Control, as it is used here means the unfailing arrest of increase and decrease somewhat short of these two extinction levels.

The most generally accepted theory of population control is probably that of Nicholson (Nicholson 1933, 1954, 1957, 1958; Nicholson and Bailey 1935). Nicholson states that populations are maintained in a state of balance with the environment by density dependent (or density governing factors). Populations fluctuate about the equilibrium density, but are prevented from becoming extinct or from increasing indefinitely (controlled) by inter- and intra-specific competition for some natural requirement and by the density dependent action of a natural enemy.

The upper limit of psyllid numbers is controlled by density dependent competition, movement and deterioration of the food plant. A density dependent (or density governing) factor is one which reacts to density change so as to hold population densities in relation to environmental conditions (Nicholson 1954). Nicholson states that it is more usual for reaction to oppose change in density for increase in numbers must sooner or later lead to a significant reduction in quantity, quality or accessability of one or more requisites and this inevitably slows down population growth and eventually stops it. Nicholson's theory adequately accounts for the control of psyllid populations at high densities.

The control of psyllid populations at low densities when intraspecific competition becomes unimportant or even absent does not, however, appear to be described well by Nicholson's theory. Most predators are not capable of adjusting their attack immediately to changes in prey numbers. Most of the predators of broom psyllids are not specific in their attack and their numbers are therefore not determined by psyllid numbers. The action of predators on broom psyllids is then probably not density dependent. The anthocorids, *Anthocoris sarothamni* and *A. nemoralis* are possible exceptions to this as their numbers are dependent on the numbers of psyllids. The anthocorids, however, are unlikely to be capable of reversing increases in psyllid numbers alone.

Nicholson (1957) states that a population is a self-governing system which regulates its density in relation to its environment. He goes on to say that populations do this by depleting and impairing essential things to the threshold of favourability or by maintaining inimical factors, such as attack of natural enemies at the limit of tolerance. The psyllid populations, however, appear very different from a "self-governing system". There is no apparent reason why *A. genistae* numbers should not fall to zero should unfavourable weather continue for long enough. It appears that *A. genistae* numbers rise when temperatures are favourable and fall when temperatures are unfavourable. The psyllid population is unable to regulate itself and appears to be at the mercy of the environment. The psyllid populations do not alone maintain their predators which feed on a wide variety of other prey. _A. spartii_ did deplete essential things to the threshold of favourability on one occasion but this was due to the limited capacity of the environment, not due to any regulation on the part of the psyllid population. Nicholson's theory is therefore only partly true when applied to broom psyllid populations.

Nicholson's theory does seem to be partly supported by the fact that an animal population tends to persist rather than become extinct. Even after the most spectacular crashes in numbers there are likely to be some individuals left so long as the habitat has not been destroyed. This characteristic enables small-isolated populations to persist for long periods apparently in a state of balance with the environment. Small oceanic islands and isolated habitats on continents support small populations in a state of balance.

The population theory of Andrewartha and Birch (1954) attaches no importance to the idea of density dependence. This theory states that populations are controlled by the shortage of time when their rate of increase is positive, that is when natality is greater than mortality. Many factors, such as weather, natural enemies and shortage of material resources affect the rate of increase, but favourable and unfavourable conditions never last long so that populations do not increase indefinitely and rarely become extinct. This theory was formulated on the findings of Andrewartha and Birch in connection with the ecology of the South

Australian grasshopper, Austriocetes cruciata. This grasshopper which reaches high numbers in favourable years is confined by climatic conditions to a defined area. Birch (1957) suggests how the numbers of the grasshopper could be regulated by weather alone. He points out that populations near the edge of the distribution of the species become extinct in years when weather is unfavourable only to be re-established by the spread of individuals from the permanently inhabited regions in more favourable years. Birch assumes that weather governs both distribution and abundance of Austriocetes without any density dependent effects. Weather limits the distribution of the grasshopper, but probably only partially controls its numbers in permanently inhabited areas. In favourable years numbers are high and spread is likely to be caused by high population density. The theory of Andrewartha and Birch is incomplete because it ignores density dependent factors which certainly exist.

It is possible to visualise the limitations placed by climatic factors on broom psyllid distribution. These factors are unlikely to limit psyllid numbers within the area of distribution for long enough to cause extinction. At the edges of the distribution area, however, climatic conditions could lead to extinction from time to time. In A. genistae the edges of the area of distribution are likely to be marked by a critical increase in the severity and length of the winter. A.genistae extends into Spain and Italy which are much warmer than Britain. It also extends into Scotland and Scandinavia which have colder winters than Southern Britain. The range of conditions under which A. genistae can exist permanently are obviously rather wide. A. spartii appears to be better adapted to a cold climate than A. genistae and it is perhaps surprising that it has its northerly limit of distribution in Britain.

The population theory of Andrewartha and Birch is similar to that of Thompson (1929, 1956) which also attaches too little importance to the concept of density dependence. This is an important feature which makes the theory incomplete.

Milne's theory of natural control (Milne 1957, 1958, 1959 and 1962) is closest to the known facts and evidence concerning psyllid population dynamics. Milne states that, for the most part, control of population increase is due to the combined action of density independent and imperfectly density dependent environmental factors. In the comparatively rare cases where this combined action fails, increase to the point of collective suicide is prevented by competition between individuals of the population. Decrease in numbers to zero is prevented ultimately by density independent factors alone. Unless the latter begin at the appropriate time to favour increase instead of decrease, the remnant of individuals left by the imperfectly density dependent factors must perish. Milne adds that the fact that competition between individuals of a population may very occasionally play a part in control of increase does not contradict his proposition that the environment rules. A property of the environment, the limit to its capacity, makes competition possible, and so the environment ultimately rules.

Milne (1957, 1961) defines his terms as follows:

The Density Dependent Factor is one in which the intensity of action is determined solely by the density of the population. Milne adopts Smith's (1935) idea of density dependence. Smith was a supporter of the population theory of Nicholson. Milne says that there is only one perfectly density dependent factor namely intraspecific competition.

The Imperfectly Density Dependent Factor is one in which the intensity of action is determined partly by the population density and partly by other variables which vary independently of this. Imperfectly Density Dependent Factors are predators, parasites, pathogens and other species competing for the same resources.

The Density Independent Factor is one in which the intensity of action is entirely independent of population density. Density Independent factors are weather (and other physical factors included in the environment) many predators and browsing animals, which can, in certain circumstances kill many insects in the vegetation they eat.

Milne goes on to say that only a perfectly density dependent factor can, by itself, unfailingly arrest increase in numbers. For control the perfect density dependence must be geared to environmental capacity so that arrest occurs at or below the limit of capacity. Enemies and weather cannot control by themselves since they are affected by factors not connected with population density. This does not, however, prevent these factors from having important effects on population density.

Milne (1961) defines competition as follows:

Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all).

It is this concept of competition that has been adopted in the present work.

Milne's theory seems to fit the psyllid populations well. The numbers of broom psyllids are apparently determined at low densities such as occurred after the spring of 1961 by imperfectly density dependent predation. *A. genistae* is also affected at low densities by weather, a density independent factor. The emigration of adults, which was important in reducing numbers of both broom psyllids, was probably imperfectly density dependent. In *Cardiaspina*, the Australian redgum psyllid, parasites are an important imperfectly density dependent factor. Predators and, or parasites, would tend to damp the peaks of population fluctuations. In high density populations of *Arytaina* species and *Cardiaspina* the only perfectly density dependent factor, intraspecific competition, limits population growth. At lower population densities intraspecific competition is absent or unimportant. It is likely that the rise of the psyllid population towards a level where intraspecific competition stops further increase is started by the failure of predation and or parasitism or by favourable weather or increased favourability of the food plant. These factors could operate separately or together.

Clark produces evidence showing that weather interfered with parasitism in *Cardiaspina*. It is possible that the numbers of broom psyllids rose to high levels because predator numbers were low when the broom in the study area was young.

Another feature connected with intraspecific competition in A. spartii and Cardiaspina was the reduction in adult fecundity which affected the size of the succeeding generation. The loss of adult fecundity probably constitutes an important controlling mechanism when intraspecific competition among the nymphs and adult emigration fails to reduce the population sufficiently for adjustment to the exhausted state of the habitat. The fall in numbers caused by competition is always likely to be violent. The numbers of psyllids after such a crash are likely to remain low until the food plant recovers and its capacity to support psyllids is restored.

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