# LIFE-HISTORIES OF SOME BRITISH *ANTHOCORIS* (HEMIPTERA:HETEROPTERA), WITH SPECIAL REFERENCE TO FOOD REQUIREMENTS AND FEEDING HABITS.

by

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## ABSTRACT

An account is given of the life-histories of six species of British *Anthocoris* studied by weekly collections from 10 species of trees and from *Urtica dioica* L.. Except in the case of the polyphagous *A. nemorum* (L.), the life-cycles are shown to be correlated with the life-cycles of preferred psyllids or aphids as prey. It was demonstrated that all species require animal food for development and although they suck plant juices these have little or no nutritive value. Honeydew and sugar solution were found to be maintenance diets but inadequate for growth or oviposition.

Emphasis is placed on the food requirements of *Anthocoris* in order to determine whether host plant restriction is due to the presence of suitable prey occurring only on these plants. A series of insects were compared as prey for larvae of the six species of *Anthocoris*, using growth rate as the chief criterion of suitability. Each species exhibited a different order of preference on the test insects. However, the prey preference of larvae determined by laboratory experiments, do not entirely explain the restricted host plant range of some species. Some prey that are suitable for larval development are unsuitable for immediate reproduction; instead of producing eggs, the females enter reproductive diapause. Therefore, the food requirements of adults may also be a factor determining host plant preference. It is suggested that the mechanism of host plant selection may be olfactory attraction to the plant and/or oviposition preference.

The wet weight of food required for normal development of *A. nemorum* larvae and for egg production by females was determined. Gross efficiency of food conversion by larvae ranged between 12 and 30 per cent when fed on different prey.

TABLE OF CONTENTS.


| | Page. |
|---|---|
| INTRODUCTION | 1. |
| LITERATURE REVIEW | 2. |
| MATERIALS AND METHODS | 6. |
| RESULTS: PART I. LIFE-HISTORIES OF SIX SPECIES OF ANTHOCORIS | 16. |
| 1. *Anthocoris nemorum* (L.) | 16. |
| Spring emergence and overwintered generation. | 16. |
| Spring and summer generations. | 25. |
| Pre-hibernation period. | 29. |
| Overwintering. | 32. |
| 2. *Anthocoris nemoralis* (Fab.) | 38. |
| Spring emergence and overwintered generation. | 38. |
| Spring and summer generations. | 46. |
| Pre-hibernation period. | 54. |
| Overwintering. | 55. |
| 3. *Anthocoris confusus* Reut. | 57. |
| Spring emergence and overwintered generation. | 57. |
| Summer generations. | 61. |
| Pre-hibernation period. | 66. |
| Overwintering. | 70. |
| 4. *Anthocoris sarothamni* D.& S. | 73. |
| Spring emergence and overwintered generation. | 73. |
| Spring and summer generations. | 76. |
| Pre-hibernation period. | 81. |
| Overwintering. | 83. |
| 5. *Anthocoris gallarum-ulmi* (DeG.) | 85. |
| Spring emergence and overwintered generation. | 85. |
| Summer generation. | 86. |
| Pre-hibernation period. | 87. |
| Overwintering. | 88. |

Page.

6. Anthocoris minki Dohrn. 90.

Spring emergence and overwintered generation. 90.

Summer generation. 91.

Pre-hibernation period. 93.

Overwintering. 94.

Summary of Life-Histories of Anthocoris spp. 95.

A. nemorum. 95.

A. nemoralis. 95.

A. confusus. 96.

A. sarothamni. 97.

A. gallarum-ulmi. 97.

A. minki. 98.

RESULTS: PART II. LABORATORY STUDIES OF ANTHOCORIS SPP. 101.

1. Breaking Reproductive Diapause. 101.

A. nemorum. 102.

A. confusus and A. nemoralis. 103.

A. sarothamni. 105.

2. Larval Rearing Studies. 106.

Mortality. 106.

Duration of instars. 109.

Growth rate. 111.

3. Basic Feeding Studies. 119.

Searching and attack. 119.

Influence of prey size on preference. 121.

Choice chamber experiments. 124.

Water intake and plant feeding. 128.

Maintenance diets. 134.

Influence of food on larval colour. 138.

4. Food Consumption. 142.

Minimal food requirements. 142.

Food consumption measured by weight. 147.

Gross efficiency of food utilization. 154.

Weight of food consumed by adults. 157.

Food consumption by A. nemorum throughout its lifetime. 162.

Page.

5. Food Value of Different Prey. 164.

A. nemorum. 166.

A. gallarum-ulmi. 168.

A. confusus. 170.

A. nemoralis. 173.

A. sarothamni. 175.

A. minki. 178.

6. Other Factors Affecting Host Plant Preference. 181.

Olfactometer studies. 181.

Ovipositon preference. 185.

DISCUSSION 187.

Food Consumption. 187.

Relative Value of Various Prey. 190.

Interrelationship Between the Host Plant and Anthocoris Spp. 196.

SUMMARY AND CONCLUSIONS 201.

SUGGESTIONS FOR FUTURE WORK 204.

ACKNOWLEDGEMENTS 206.

REFERENCES 208.

APPENDIX 213.

# LIFE-HISTORIES OF SOME BRITISH *ANTHOCORIS* (HEMIPTERA: HETEROPTERA, WITH SPECIAL REFERENCE TO FOOD REQUIREMENTS AND FEEDING HABITS.

## INTRODUCTION

Thompson, 1951, has pointed out that there is a scarcity of information pertaining to the prey preference of predacious insects. The genus *Anthocoris* Fallen is no exception. These predacious bugs are known to have marked differences in host-plant preference, but it is not known to what extent this is associated with the occurrence of preferred prey.

The present work is a comparative biological study of six *Anthocoris*: *A. minki* Dohrn, restricted to *Fraxinus*; *A.sarothamni* D. & S., restricted to *Sarothamnus*; *A. gallarum-ulmi* (DeG.), restricted to *Ulmus*; *A. nemoralis* (Fab.) and *A. confusus* Reut., semi-restricted to a group of deciduous trees; and *A. nemorum* (L.), which is widely distributed on herbaceous plants and deciduous trees. It will be shown that while all species can be reared on insects that do not occur in their usual habitat, each *Anthocoris* exhibits some prey preference and this is a factor in determining the host-plant range.

The investigation is divided into two parts: Part I, field studies of the life-histories of each species; Part II, laboratory investigations concerning the food requirements and kinds of prey suitable for *Anthocoris*.

This work was conducted at the Imperial College Field Station, Silwood Park, near Ascot, Berks., from the late summer of 1958 to autumn, 1960.

## LITERATURE REVIEW

Several authors (e.g. Steer, 1929; Peska, 1931; Collyer, 1953; Southwood and Scudder, 1956; Sands, 1957; Hill, 1957; Cobben, 1958; Southwood and Leston, 1959; and Dempster, 1960) have published information on the life-histories of *Anthocoris* in Britain and Continental Europe. All of these workers stressed the predacious habit of these bugs, and some have discussed the value of *Anthocoris* in the natural control of small insects and mites. On the other hand, Prohaska, 1923, and others have stated that they are partially phytophagous and Theobald, 1895, considered some *Anthocoris* to be a pest of hops. Carayon and Steffan, 1959, have suggested that *Anthocoris*, along with other members of the Anthocorinae, may feed on pollen. In addition, some species in Europe, North America and Africa, have been reported occasionally to bite humans and to suck blood (Butler, 1923; Essig, 1954; and Anderson, 1958).

Most of the detailed information concerning feeding habits is based on the common species, *A. nemorum*. Hill, 1957, records it as preying on 35 species of insects and mites, representing 10 orders. Collyer, 1953, stated that adults consume an average of 50 red spiders, *Panonychus ulmi* (Koch), per day, while small larvae consume about 20 per day and the older larvae from 35 to 40. Peska, 1931, estimated that *A. nemorum* consumed 500 to 600 aphids in a lifetime.

Some *Anthocoris* are associated with aphid galls and appear to exhibit a preference for these aphids. *A. gallarum-ulmi* is partial to the curled leaf-galls produced by *Eriosoma ulmi* (L.) on *Ulmus* (Reuter,

1884; Massee, 1954; Leston, 1954; Sands, 1957; and Cobben, 1958). It is not clear to what extent this bug feeds on the aphids; Reuter, 1884, stated that A. gallarum-ulmi fed on honeydew and Cobben, 1958, noted the same habit. Cobben only observed one successful kill of an aphid by A. gallarum-ulmi larvae. However, Sands, 1951, and Southwood and Leston, 1959, state that it feeds on the aphids.

Other species of Anthocoris also breed in aphid galls. Stichel, 1956-1960, reported that A. amplicollis Hv. is associated with the galls of Prociphilus bumeliae (Schrk.) on Fraxinus in Europe. Harper, 1959, recorded A. antevolens White from the galls of Pemphigus spp. on Populus spp. in Canada. Wagner, 1960, recently described A. pemphigi from Pemphigus galls on Populus in Egypt. Mr. R.H. Cobben (personal communication) has found an undescribed Anthocoris, related to A. minki, also in Pemphigus galls on Populus in Holland. He found the larvae of this species in the closed galls, which suggests that this Anthocoris is extremely specific and well synchronised with the biology of the aphid. Dunn, 1960, reports that in England A. nemorum and A. nemoralis are the most important predators of Pemphigus bursarius (L.) when the galls on Populus open at migration time.

The basic pattern of attack by A. nemorum on aphids and mites is given by Steer, 1929; Peska, 1931; Sands, 1951; Collyer, 1953; and Hill, 1957. The rostrum, which is normally carried against the venter, is extended horizontally; then it is applied to the integument and the stylets are quickly inserted. If the prey walks away, the predator follows with its stylets still inserted. Small aphids or mites offer

little resistance, but large aphids often drag the bug for some time before succumbing. Peska, 1931, stated that the prey is not paralysed, while Hill, 1957, noted that, although there is no clear evidence of paralysis, the movements of the prey become slower after a short period (death by exhaustion, according to Peska).

Steer, 1929, noted that the method of attack by A. nemorum was different for various types of prey. Aphids and mites were attacked in the manner described above, but when resorting to cannibalism, or when killing active prey such as Jassids or young capsids, then the anthocorid captures its prey. In these cases the predator climbs on the back of the victim and holds it firmly with all six legs whilst manoevering the proboscis until it can be inserted into a coxa. This position is maintained although the predator is dragged about. The victim is unhurt if it manages to escape quickly but more often it is rendered lame and a droplet of fluid exudes from the wound. Prolonged insertion results in death and the victim is then sucked.

It is interesting to compare these reports of attacks by A. nemorum with Cobben's, 1958, notes on A. gallarum-ulmi, and Carayon's, 1953, observations on the feeding behaviour of another species of Anthocorinae, Scoloposcellis obscurella (Zett.). Cobben stated that young larvae make a very cautious attack on Eriosoma ulmi; if the aphid makes an abrupt movement, then the bug retreats and flees. Older larvae are more persevering and one was seen to unsuccessfully attack an aphid seven times. Cobben only observed one instance of a larva overcoming an E. ulmi. Carayon found that the behaviour of

S. obscurella depended upon the size of the scolytid larva being attacked. If the prey is smaller or the same size as the predator, then the stylets are inserted and kept there until the prey is immobilised. If, on the other hand, the prey is large, then the predator inflicts a rapid puncture and retires some distance until the toxic juices effect paralysis. If the paralysis is slow then the bug renews the puncture and again retires until the immobilisation is complete.

Dunn, 1960, has recently advanced the theory that Anthocoris in Pemphigus galls may kill the aphids by the secretions of the scent glands acting as a fumigant in the gall. He found that if there was an Anthocoris larva or adult in a gall, which had only been open for a few days, then invariably all the aphids were dead. He suggested that it was improbable than an anthocorid could kill all the 50-200 aphids as quickly and efficiently except by a fumigant action.

Little is reported on the searching behaviour of Anthocoris. Steer, 1929, stated that the larvae may be observed systematically searching a leaf for red spider and their eggs. The larvae will walk the length of a vein with the proboscis extended and carefully probe on either side of the vein where mites and eggs are most numerous. Peska, 1931, made observations on the searching of A. nemorum adults on Salix catkins; he found that they run restlessly about searching with their rostrum and antennae. Once the bug finds a larva inside a catkin, then feeding begins and continues often for more than half an hour until the larva is completely sucked out.

## MATERIALS AND METHODS

The preliminary investigations by W.A. Sands on the biology of the Family Anthocoridae at Silwood Park in 1951 have been a useful basis for the present study. He described the egg and larval stages of all species under consideration, except *A. minki*, so this has not been repeated.

The host-plant range, prey preference, and seasonal life-histories of the *Anthocoris* spp. were studied in the field. Most of the tree species at Silwood Park were sampled by beating, and sweeping was carried out in all likely sites on herbaceous plants to determine the host-plant range. Intensive collections were made from *Salix*, *Malus*, *Tilia*, *Quercus*, *Crataegus*, *Fagus*, *Ulmus*, *Acer*, *Fraxinus*, *Betula*, and *Sarothamnus*. The trees selected for sampling were those with the largest populations of *Anthocoris* that could be found. These were either large, isolated trees, or else trees along the edge of a wood; in either case there were more low branches suitable for beating than there are on trees located in a wood. Occasional collections were made from trees growing under other conditions to determine the species of *Anthocoris* present and their relative abundance. Weekly collections from the trees and shrubs were made from March to mid-October in 1959, and from March until mid-September in 1960. Weekly sweeping of a patch of nettles, *Urtica dioica* (L.) was added to the routine in 1960. The total numbers of each species of *Anthocoris* collected on the various plants are given in Table 1.

No standard sampling area could be used in collecting from

shrubs, trees, hedges, and Urtica, so a time interval of 10 minutes collecting on a one metre square sheet was used for the beating samples. The samples from Urtica consisted of 100 sweeps per week and are not numerically comparable with the collections obtained by beating.

The method of sampling employed in the present study cannot be used for quantitative population studies of Anthocoris. For example, in the collections of A. confusus, instead of the expected decrease in numbers as the population ages, there were twice as many late-instar as early-instar larvae, and also twice as many adults as late-instar larvae. Some explanations for this anomalous result are: (a) under-sampling of young larvae because they are small, almost colourless, and extremely difficult to find amongst a seething mass of aphids; (b) the relative longevity of adults means that they will be sampled several times; (c) there can be an aggregation of adults moving in from outside the sample area; (d) it is possible, though not proven, that behavioural changes may cause over-sampling of the late-instar larvae — for example, they may be dislodged more easily, or could be concentrated on the lower branches (that are sampled) by dropping from the top part of the tree.

Since the present study is chiefly concerned with seasonal occurrence, relative abundance of Anthocoris spp., and with population differences, it is felt that the results are not greatly affected by the drawbacks of the sampling method. All trees were sampled in the same manner so comparisons may be made between the samples.

The abundance of potential host insects estimated at intervals throughout the season is given in Appendix I. Aphids were identified by Dr. V. Eastop and Mr. W.O.Steel, psyllids by Miss H. Walker and jassids by Dr. W.J.LeQuesne.

The life-history studies were a combination of field collecting and laboratory rearing. The seasonal life-cycle of all species was determined from the records of the larval instars and the sexing of adults in weekly samples. A sample of females of each species was dissected weekly in 1959 to determine the condition of the fat body, stage of ovarial development, and condition and colour of the gut. In addition, most of the adults collected in 1959 were weighed in an attempt to correlate the weight of Anthocoris with the size of the prey population on different plants.

It was desirable to obtain some data on the dispersal of adult Anthocoris to supplement the results obtained in the weekly samples. Sticky boards and water traps set up for this purpose were found to be unsatisfactory. However, examination of material obtained by Dr. T.R.E. Southwood from suction traps provided information on the flight periods of A. nemorum, A. nemoralis and A. confusus. The catches examined were from traps located in a meadow about 100 yards from the nearest trees (1959 and 1960), in an oat field (1959), and a third trap located on a headland a few yards from an oak tree (1959).

Most of the laboratory rearing was carried out in a heated cabinet at a temperature of 74°F. (range, 72-76°F.), with constant

illumination provided by a 15-watt light. Some supplementary tests were conducted on the laboratory bench. Additional temperature data are given in the text where pertinent.

The most practical rearing cage was a modified mite-rearing cell in which the insects could be observed under a stereoscopic microscope (Fig. 1). A wooden frame holds a 2 x $2\frac{1}{2}$ x $\frac{1}{4}$ inch lucite rectangle with a $\frac{3}{4}$-inch circular hole in the centre. A leaf is placed under the lucite on several thicknesses of filter paper. The leaf provides food for the prey and an oviposition site for the anthocorids. The filter paper serves two purposes: it provides an easy way in which to add moisture and permits the lucite to be firmly pressed over the leaf, thus preventing the escape of small specimens. The upper surface of the cell is closed with a one-inch glass square held in place by elastic bands. The humidity is high enough to provide good rearing conditions if the filter paper is kept moist. The leaves usually remain fresh for one to two weeks which is long enough for the inserted eggs to hatch. At high temperatures, when fungal growth is prevalent, it is necessary to change the leaves every few days and to remove all the dead prey daily to reduce the spread of fungi.

The cages were also used without the leaf to test feeding habits in the absence of plant material. Most of the anthocorids would oviposit in the filter paper, although the percentage of eggs that were laid loose was higher than when leaves were provided. If the loose eggs were not sucked, a large percentage hatched in the high humidity of the cages. The food supply was replenished daily and the filter

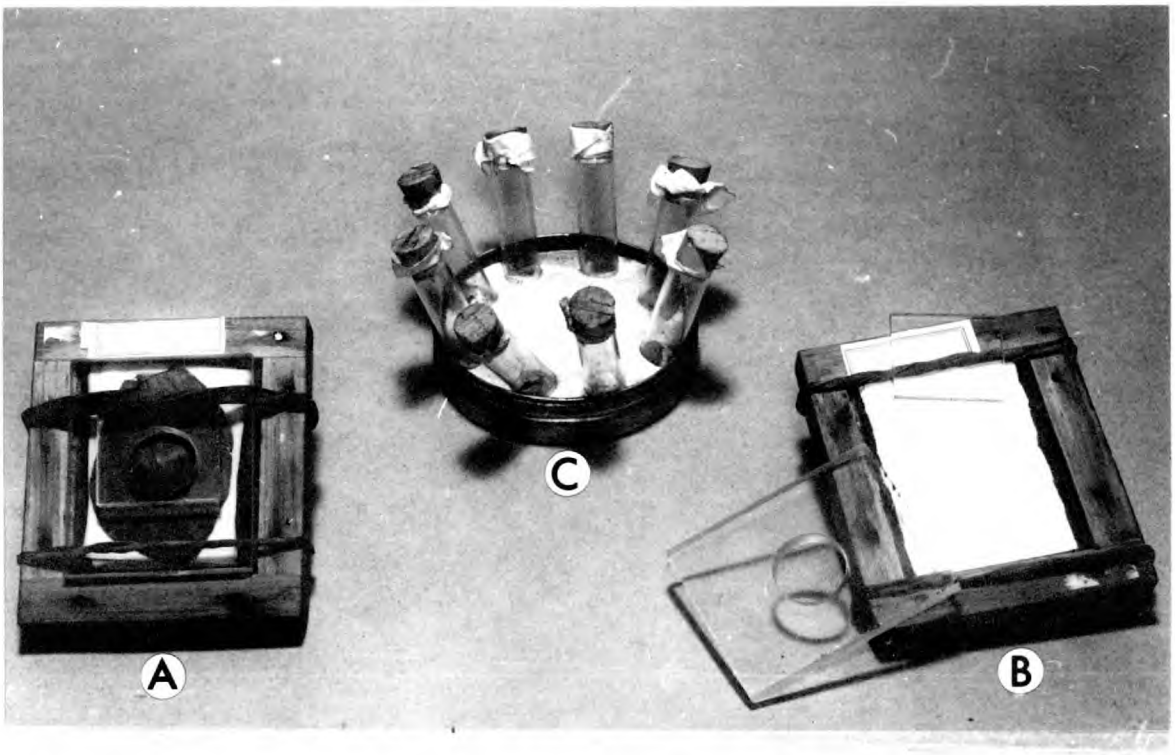



Fig. 1. Cages used for studying *Anthocoris:* A. Rearing cage, in use; B. Same, dismantled; C. Tubes embedded in plaster of Paris for artificial overwintering studies.

paper was changed frequently when no leaf was used.

Specimens were reared individually and the cages were examined daily in most experiments. The excessive labour of individual rearing, as compared with mass rearing, was justified because the results were more accurate and detailed, and could be analysed statistically. However, it did mean that most experiments could only be carried out on a small scale. Cannibalism was also prevented by individual rearing. Some mass rearing was done using petri dishes. Larger containers, such as Watkins and Doncaster cages containing a potted plant, were unsuitable because it was difficult to get lids tight enough to prevent the escape of specimens, and because the area of search was too large when collecting the specimens.

Several species and stages of insects and mites were tested as prey. The growth rate of each species of Anthocoris was determined for specimens fed on natural and unnatural prey. Most feeding tests were conducted using the aphids, Aphis fabae (Scop.) and Acyrthosiphon pisum (Harr.) reared on beans, and Aulacorthum circumflexum (Buckt.) reared on tulips or beans, and the psyllids, Psylla mali Schmid., P. spartiophilus (Foerster), and Arytaina genistae (Latr.), collected in the field.

All Anthocoris overwinter as adults. As this non-reproductive phase is a lengthy portion of each year it was an important facet of the life-history studies. The method of studying the overwintering habits consisted of: (a) determining the duration of the hibernation period; (b) studying the insects under natural winter conditions; and (c) laboratory studies under simulated winter conditions.

The duration of hibernation was calculated as the time between the autumnal decline of the population on the host plants and the date of re-emergence of adults in the spring. Hibernation sites, such as beneath bark-scales and litter, were examined in the autumn to try to show that the disappearance from plants resulted from the onset of hibernation but the number of specimens collected was too small to provide this information. Sack-bands were placed around tree trunks in July 1959 in an attempt to induce hibernation in sites that could be sampled. These were examined at intervals throughout the autumn and winter but very few Anthocoris were collected from them.

The overwintering habits and the effects of hibernation were studied by collecting specimens from their hibernacula and comparing them with specimens collected in the autumn and spring for: sex ratio, weight, and conditions of fat body, gut, and ovaries. Experiments were also conducted to determine the factors necessary to induce oviposition by hibernating females.

Artificial overwintering was attempted in order to study mortality, food requirements, and depletion of fat reserves. However, all specimens stored in a refrigerator and those placed outside in tubes (with small pieces of bark to simulate natural conditions) all died from desiccation within a few weeks. This problem was overcome by using tubes embedded in plaster of Paris (Fig. 1C). Bugs could be kept at 34°F. for at least six months if the plaster was kept saturated. It was more satisfactory to store Anthocoris singly in tubes rather than in groups. This facilitated handling when they

were brought out of the refrigerator and also reduced mortality by preventing the spread of saprophitic fungi.

A five-milligram torsion balance, calibrated in 0.01 mg. divisions, was used extensively to measure food consumption, growth rate, and depletion of fat reserves. Weighings were also useful for comparing the suitability of prey because weight is the ultimate parameter of growth. The bugs were usually anaesthetised with carbon dioxide prior to weighing. However, repeated anaesthetising was detrimental so in daily weighing experiments the bugs were weighed while still active.

It was necessary to standardise the weighing procedure because anthocorids desiccate rapidly. All insects collected in the field or taken from the refrigerator were given access to moisture for at least 30 minutes before they were weighed. Insects in the rearing cages could obtain moisture from the leaf or filter paper at all times. Dead prey also lose water rapidly even at the high humidity on leaves in the rearing cages. Sucked insects on moist filter paper remained at a steady weight so experiments on food consumption were carried out in cages without a leaf as a substrate. Insects that were killed, but not sucked, sometimes increased in weight due to osmosis.

Studies were carried out in an attempt to determine whether Anthocoris responded to olfactory stimuli from plants or from prey. The olfactometer was a circular choice chamber, using the charcoal-stablised diffusion gradient principle, and similar in design to one described by Pielou, 1954. The lucite arena is 40 mm. in diameter

and 3 mm. deep. The top is covered with a lucite lid while the bottom is closed with a false floor made of metal gauze, 150 mesh to the inch. A small petri dish 10 mm. deep, partitioned in the centre, containing the stimulus in one half and charcoal in the other is placed beneath the false floor and then the complete chamber is sealed with cellotape.

Test insects were placed in the arena and the numbers over charcoal and over the stimulus were counted at intervals. The possibility that attraction was due to colour differences was eliminated by using fine mesh in the false floor and by placing the stimulus on black filter paper. The bugs were given access to moisture immediately prior to each experiment and a control series was set up using water (instead of the stimulus) to determine the response of the bugs to the humidity gradient in the chamber. The experiments were conducted in a dark, constant temperature room; even illumination was provided by a bar-type lamp located directly above the choice chamber. The chamber was rotated through $180^{o}$ half way through each run to further eliminate the possibility of bias due to asymmetrical lighting.

TABLE 1. Total numbers of *Anthocoris* spp. collected in weekly samples of 10 minutes per tree, March to October, 1959, and March to September, 1960.

| | *A. nemorum* | *A. nemoralis* | *A. confusus* | *A. sarothamni* | *A. minki* | *A. gallarum-ulmi* |
|---|---|---|---|---|---|---|
| *Malus* | 1082 | 320 | 23 | 0 | 0 | 0 |
| *Sarothamnus* | 956 | 782 | 25 | 378 | 0 | 1 |
| *Salix* | 823 | 687 | 156 | 0 | 0 | 3 |
| *Tilia* | 721 | 780 | 1016 | 4 | 0 | 0 |
| *Acer* | 686 | 443 | 2916 | 51 | 0 | 4 |
| *Crataegus* | 489 | 1049 | 45 | 0 | 0 | 0 |
| *Ulmus* | 160 | 30 | 73 | 267 | 0 | 30 |
| *Quercus* | 109 | 25 | 1873 | | 0 | 3 |
| *Fagus* | 23 | 55 | 4294 | 0 | 0 | 1 |
| *Fraxinus* | 71 | 48 | 11 | 1 | 321 | 0 |
| *Betula* * | 34 | 5 | 20 | 0 | 0 | 0 |
| *Urtica dioica* ** | 1240 | 0 | 20 | 4 | 0 | 1 |

* Sampled only in 1959

** Sampled only in 1960; 100 sweeps per week.

## RESULTS : PART I. LIFE-HISTORIES OF SIX SPECIES OF ANTHOCORIS.

### 1. Anthocoris nemorum (L.)

#### Spring emergence and overwintered generation.

A. nemorum was first collected in mid-March in 1959 and 1960, but as Hill, 1957, has noted, the exact date of spring emergence depends on weather conditions. He found that the start of spring emergence in Scotland varied between March 23 and April 16. Sands, 1951, first collected A. nemorum at Silwood Park on April 18; weather records indicate that the spring of that year was exceptionally late.

Overwintered females greatly outnumber males in the spring; this has been reported by several other workers (Peska, 1931; Collyer, 1953; Southwood and Scudder, 1956; and Hill, 1957). However, Collyer, 1953, noted that in 1948 there was an exceptionally high proportion of males and Sands found a large number of males in the spring of 1951. In the present study, the ratio of overwintered males to females on Salix in 1959 was 0.18 : 1, and in 1960, 0.07 : 1. Males are very rare after the end of April.

The aggregation of A. nemorum on Salix has been discussed by several authors (Prohaska, 1923; Peska, 1931; Sands, 1951; Collyer, 1953; Hill, 1957; and Southwood and Leston, 1959). It is generally believed that they abound on this plant in early spring because of the availability of host insects. However, Prohaska, 1923, believed that they suck plant sap, and Sands, 1951, and Southwood and Leston, 1959, also state that they feed on the plant to some extent.

A detailed study was made of the occurrence of Anthocoris on five male and five female Salix spp. trees from March to May in 1960. The numbers of A. nemorum and A. nemoralis on male and female trees throughout the spring are compared in Fig. 2. The peak of spring emergence of A. nemorum is reached by April 20, one week later than the peak of A. nemoralis. By the time A. nemorum is abundant in the spring, buds have burst on both male and female trees so there is no obvious movement from male to female trees. The average population level is higher on the latter because some male trees have completed flowering and are past their most attractive phase by the time that A. nemorum is most abundant. There is a dispersal to other plants during late April and early May. Unlike A. nemoralis, some specimens remain and oviposit on male as well as on female Salix; there were three times as many A. nemorum larvae as A. nemoralis larvae on male trees (Fig. 2B). The attractiveness of Salix in the spring is attributed in part to an olfactory stimulus from the catkins (see p.182). Aggregation on Salix is also discussed in the following section on A. nemoralis.

Hill, 1957, reported that A. nemorum adults favoured Salix in early spring but they could be found at an equally early date on Sarothamnus, Mercurialis, Crataegus and Quercus. In the present study it was collected from Sarothamnus, Crataegus and Urtica in late March, but not from Quercus. Hill, 1957, found A. nemorum among the dead, unfallen leaves on Quercus long before bud burst; it seems probable that these specimens were still in their overwintering sites.

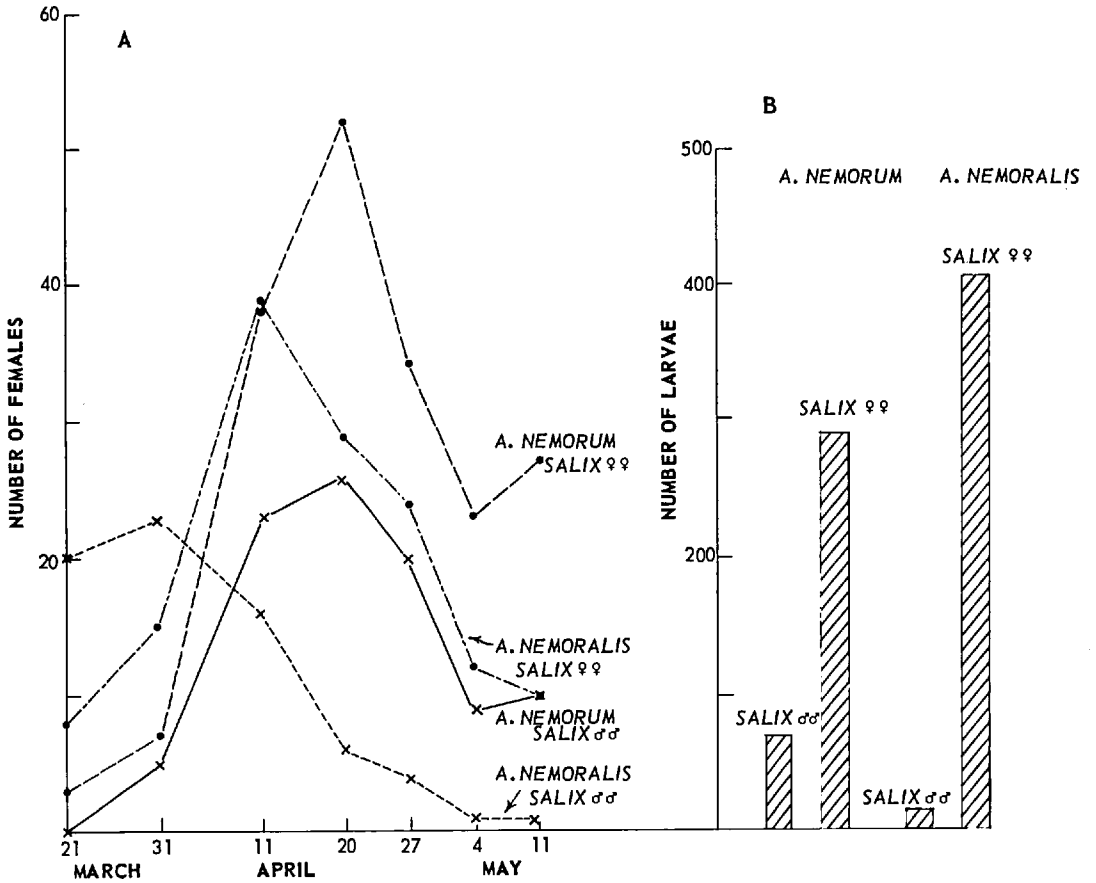



Fig. 2. A. Number of *Anthocoris nemorum* (L.) and *A. nemoralis* (Fab.) females collected from five male and five female *Salix* trees, March to May, 1960.

B. Number of larvae collected from the same trees, May 30 to 31, 1960.

The distribution of the overwintered generation on various types of plants is given in Table 2. There is a large or moderate generation of larvae produced on the Group 1 trees, on Salix and on Urtica. A minimum of oviposition occurs on the trees in Group 2. All of these trees, except Ulmus, are not at the bud burst stage until after the major period of post-hibernation dispersal. Ulmus is not a favoured host plant, apparently because of the absence of suitable prey. The Group 1 trees and Salix are all infested with psyllids but there are also some aphids present at that time of year. The numbers of A. nemorum on Urtica cannot be compared directly with the number on trees because of the difference in sampling methods. Urtica is included in Table 2 to indicate the time of occurrence of A. nemorum. The potential prey on this plant is abundant and varied; the aphid Microlophium evansi (Theobald) is by far the most abundant prey species, while the psyllid Trioza urticae (L.), is moderately common.

It should be emphasised that A. nemorum is more abundant on herbaceous plants than it is on trees (Southwood and Scudder, 1956). Its distribution on these plants has received only cursory attention because the chief object of this study is a comparative appraisal, and all the other Anthocoris occur chiefly on trees.

The condition of the ovaries at the time of spring emergence is compared with the other species in Fig. 3. The ovaries are more developed in A. nemorum than in any other species except A. sarothamni at spring emergence. The rate of ovarial maturation is slightly slower in A. nemorum than in A. nemoralis so both species begin to oviposit

TABLE 2. Numbers of overwintered Anthocoris nemorum (L.) adults collected on different types of plants, based on 100 minutes collecting for each group of trees and 500 sweeps for Urtica, 1959 and 1960.

| Interval | Salix ♂♂ and ♀♀ | | Group 1 Trees (Sarothamnus, Crataegus and Malus) | | Group 2 Trees (Tilia, Quercus, Fagus, Acer and Ulmus.) | | Urtica |
|---|---|---|---|---|---|---|---|
| | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 | 1960 |
| March 13-31 | 18 | 10 | 0 | 5 | 0 | 0 | 2 |
| April 1-22 | 88 | 81 | 44 | 22 | 10 | 6 | 16 |
| Apr.25 - May 6 | 97 | 47 | 75 | 34 | 10 | 1 | 28 |
| May 9 - 31 | 25 | 28 | 57 | 20 | 7 | 4 | 28 |
| June 1 - 23 | 7 | 7 | 20 | 9 | 4 | 2 | 0 |
| Total | 235 | 173 | 196 | 90 | 31 | 13 | 74 |

about the middle of April. Other workers report an earlier date for oviposition: late March (Collyer, 1953); April 3 (Peska, 1931); and 10 days after emergence = early April (Hill, 1957). Peska's record fs for oviposition in the laboratory in Poland. Oviposition in early April may be possible, considering yearly variability in weather, and the plasticity of A. nemorum. However, of 20 specimens dissected in both 1959 and 1960, between April 4 and 12, less than half contained ripe eggs.

The progressive weight increase of A. nemorum from spring emergence to the oviposition period is compared with other species in Fig. 4. The graph shows that there is a steady weight increase throughout the pre-oviposition period and then a slightly lower rate of increase after

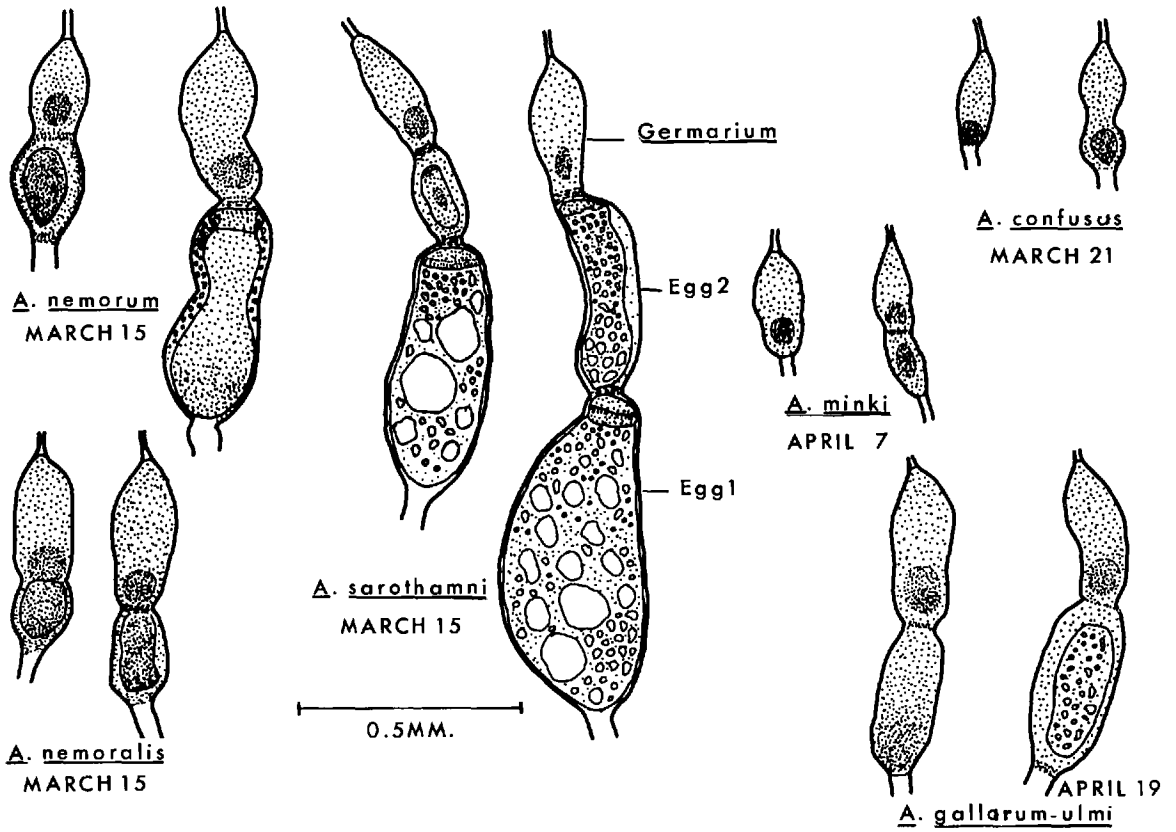



Fig. 3. Ovarioles of *Anthocoris* spp., illustrating degree of ovarial development at the time of spring emergence, 1960.

oviposition begins in mid-April. The initial weight increase is due to ovarial maturation; the continued increase after mid-April may be caused by smaller specimens dying first.

All workers agree that the oviposition period of overwintered females is an extended one. In Poland and in England it continues until June (Peska, 1931, and Collyer, 1953), while in Scotland, where A. nemorum is univoltine, females have been reported as late as July 6 (Hill, 1957). My records agree with the previous reports; overwintered females were present in small numbers until the latter part of June in both 1959 and 1960.

The incubation period at spring temperatures is between three and four weeks. Table 3 gives the incubation time for A. nemorum eggs at different temperatures.

TABLE 3. Incubation period of Anthocoris nemorum (L.) eggs at various temperatures.

| Number of eggs | Incubation at 74°F (hours) | Mean rearing temperature (°F.) | Total incubation period (days) | |
|---|---|---|---|---|
| | | | Range | Mean |
| 53 | 0 - 24 | 53 | 19 - 24 | 21.3 |
| 18 | 24 - 48 | 53 | 17 - 19 | 17.7 |
| 34 | 0 | 64 | 8 - 11 | 9.1 |
| 45 | Continuous | 74 | 5 - 6 | 5.6 |

The total numbers of A. nemorum collected from suction traps are given in Table 4. No overwintering adults were collected. The three

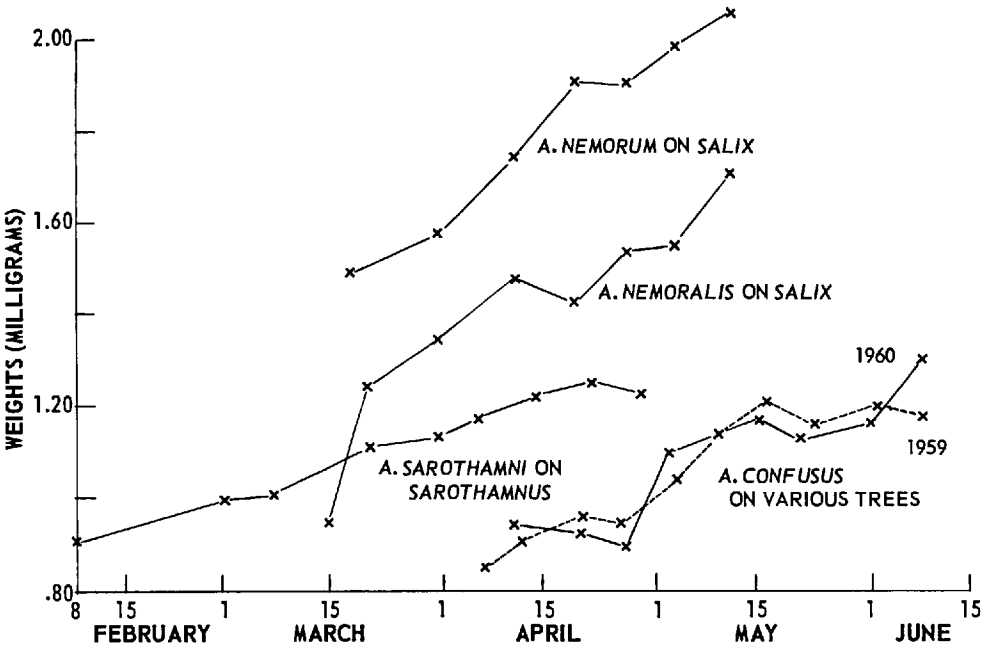



Fig. 4. Mean field weights of *Anthocoris* spp. females from the end of hibernation to the beginning of the spring generation, 1960. Minimum of 15 females per weighing.

traps used in 1959 were set up in May, which was too late to capture specimens during post-hibernation flights. The 1960 trap was run for a few days during March and continuously from April 1. Maximum numbers of A. nemorum adults appeared on most trees and on Urtica during late April and early May (Table 2), so this trap was operating during a period of some dispersal. The trap was located in a meadow, about 100 yards from the nearest trees or Urtica so there may not have been suitable breeding sites for A. nemorum near the trap during this period. A. nemorum was common in a field of oats near the trap later in the season. Southwood, 1960, only recorded one A. nemorum from March to June from four traps at Rothamsted in 1953. The limited data suggest that the flight range of A. nemorum during the spring is quite short.

TABLE 4. Total collections of Anthocoris nemorum (L.) from three suction traps in 1959 and one in 1960. All traps located in or near breeding areas.

| | Males | Females | Total | Remarks |
|---|---|---|---|---|
| May - June 18 | 0 | 0 | 0 | Overwintered generation |
| June 19 - 30 | 3 | 8 | 11 | First generation |
| July 1 - 31 | 29 | 40 | 69 | First generation |
| August 1 - 31 | 10 | 20 | 30 | First plus second generation |
| September 1 - 30 | 37 | 9 | 46 | Second generation |
| October 1 - 15 | 2 | 1 | 3 | Second generation |

Spring and Summer generations

The life-cycle of A. nemorum for two years on all plants sampled is illustrated in Fig. 5. No major differences were found between the life-history on Urtica in 1960 and that on trees, so the data are grouped for the purposes of Fig. 5.

The earliest spring-generation larvae emerge in the second week of May. The population on Salix develops slightly earlier than on other plants because the first eggs are laid there. Spring-generation adults begin to appear in mid-June, so the duration of the larval instars at that time of year is about five to six weeks. Hill, 1957, states that larval development takes six to seven weeks in Scotland, and Sands, 1951, gives a period of about four weeks in Berkshire. The latter record must be for development during the summer.

The first adults were collected from suction traps on June 19 (Table 4), which compares well with the first collection of spring-generation males on June 15 in the weekly samples. Dispersal of the spring generation, estimated from the suction trap catches, was twice as high during July as it was in the last half of June.

The spring generation is an extended one because of a long oviposition period and variation in the duration of larval development. Fifth-instar larvae of the spring generation are still present in mid-July. Collyer, 1953, stated that during June the eggs of the overwintered generation and the spring generation occur together. She found that the earliest laid eggs reach the imaginal stage in May, which is one

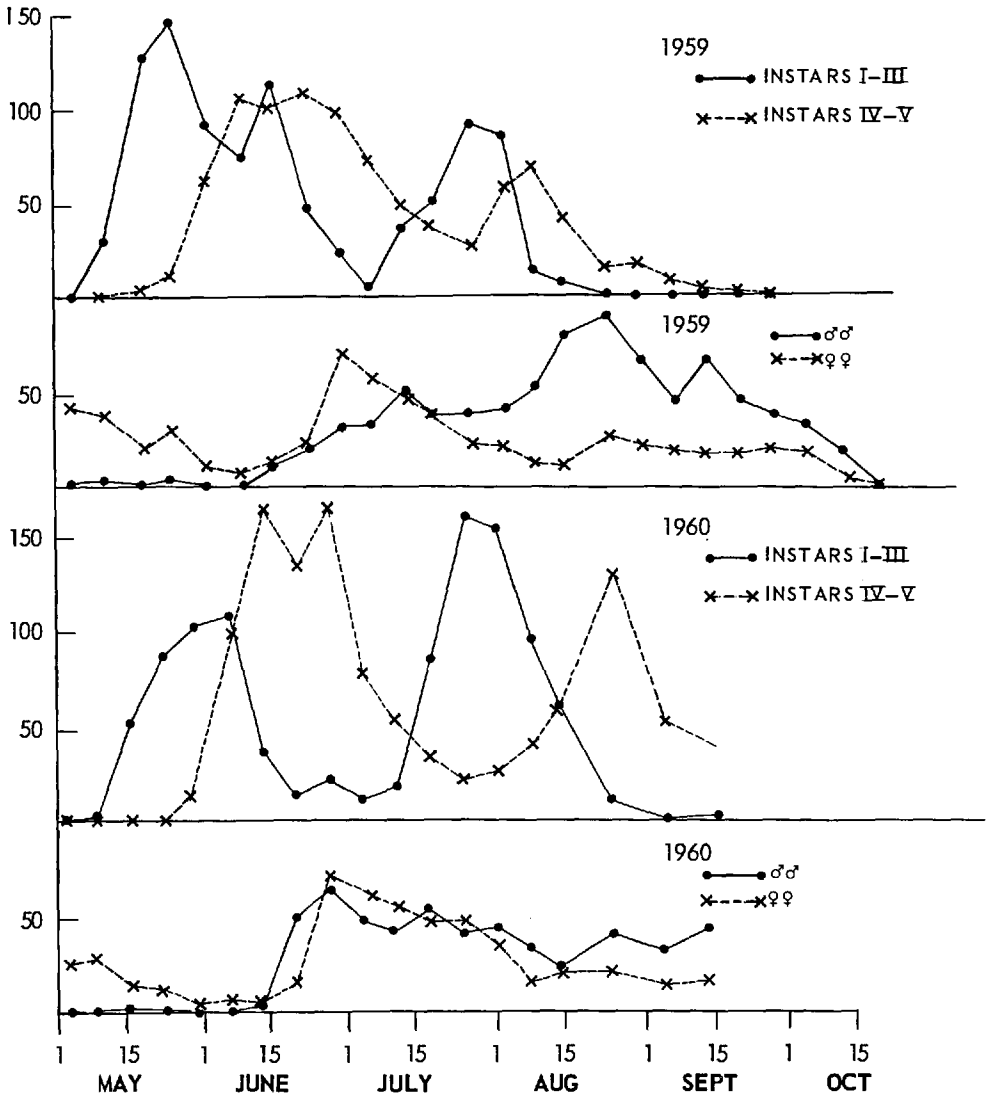



Fig. 5. Number of *Anthocoris nemorum* (L.), larvae and adults, in weekly collections, May to October, 1959, and May to September, 1960.

month earlier than my records. An overlap of imagines of the two generations was noted in the present study. Field observations were corroborated by dissections; overwintered females could be differentiated from spring-generation females by their mature ovaries and the off-white colour of the fat body. Sands, 1957, has pointed out that the pre-oviposition period is about three weeks so it is unlikely that there is much overlap in oviposition. The graphs in Fig. 5 indicate a clear demarkation of the spring and summer generations in 1959 and 1960.

There were only two generations of A. nemorum in both 1959 and 1960; the spring-generation larvae occurred from May to mid-July and a slightly smaller summer generation of larvae was present from early July until late September or October. Larvae of this species occur much later in the season than those of any other Anthocoris. No evidence was obtained of a partial third generation as is suggested by Southwood and Scudder, 1956. The summer of 1959 was the warmest of the century and if the occurrence of a third generation is dependent on temperature, then it should have been evident in that year.

A. nemorum does not show distinct host-plant preferences in different seasons except for the aggregation on Salix in early spring. In general, A. nemorum breeds on most plants where there is a fairly high population of small insects as prey. The size of the population on trees is usually rather low as compared with the numbers of A. confusus or A. nemoralis on their primary host plants. A. nemorum was the dominant species on Urtica, Malus, Salix, Ulmus, Betula and

sometimes on Sarothamnus (Table 1). The numbers on Fraxinus, Betula and Fagus were exceptionally low considering the density of prey on these plants. Evidently the ash psyllid, Psyllopsis fraxinicola (Foerster), the birch aphid, Euceraphis betulae (L.) and the beech aphid, Phyllaphis fagi (L.), are all undesirable prey for A. nemorum.

The life-cycle of A. nemorum does not closely follow that of any specific prey or groups of prey. For example, the spring generation is much longer than the duration of larval development of most psyllids, and the summer generation extends later into the autumn than the usual aphid season. Thus, on many trees at least, A. nemorum is more of a general predator than either A. nemoralis or A. confusus. In the autumn, after aphid and jassid populations have declined, psocids are probably an important part of the diet.

The mean weights of A. nemorum males and females obtained in weekly samples from various trees in 1959 are graphed in Fig. 6. The object of this work was to determine whether weight of adults could be associated with the occurrence of suitable prey, or with numbers of prey, on different plants. More than 1200 specimens were weighed individually during the season, but the results did not warrant the effort. There is no consistent trend between male and female weights or between weight and the size of the prey population (given in Appendix 1). This suggests that there were sufficient prey on all plants. The weight of adults is of little value in studying the relationship between predator and prey because it is not possible to determine whether the adults have moved in from some other location. Overwintered females are heavier than

summer females because a large portion of the latter were weighed before they were gravid. A comparison of weight of fifth-instar larvae on various plants would overcome variations due to dispersal. However, it would be difficult to obtain sufficient larvae from several of these plants and corrections would have to be made for age and sex of the larvae.

There was no evident peak of second-generation females that should have resulted from the peak of late-instar larvae in mid-August (Fig.5). This may result from short post-teneral flights to herbaceous plants, and hence out of the sample area. There was a peak of males in August and September, 1959, but none in 1960. Sampling was discontinued on September 14, 1960; most of the larvae had matured by that date so a peak could not be expected at a later date. I am unable to explain this variation between the two years.

Pre-hibernation period.

The onset of hibernation appears to be a gradual process with A. nemorum as there is no sudden disappearance from the host plants to mark the start of the period. Table 5 shows a gradual decline in numbers from mid-August to mid-October in 1959. However, the second generation was completed very early in 1959 because of the hot season. Table 6 shows that larvae were present for a month longer in 1958 than in 1959. Southwood and Scudder, 1956, found that the peak emergence of second generation adults in 1953 was in late September.

The predominance of males on the host plants in the autumn shows

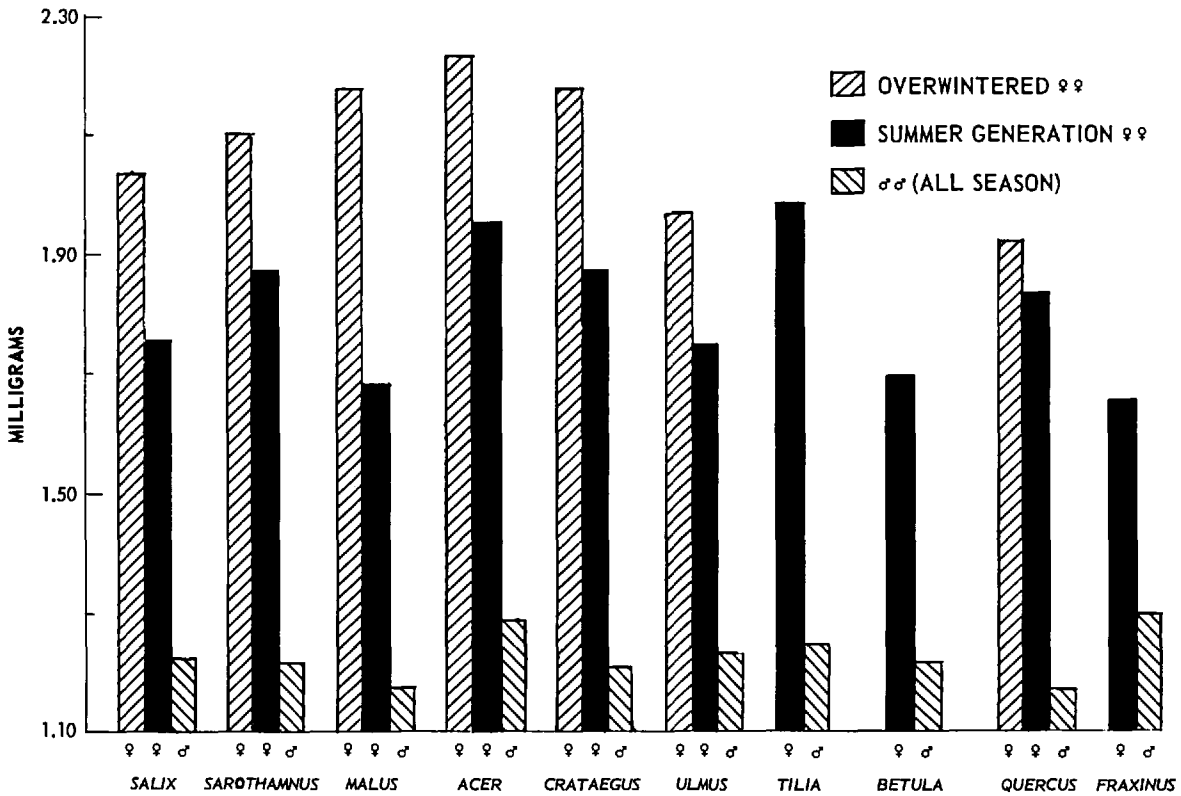



Fig.6. Mean weights of *Anthocoris nemorum* (L.) males and females on various trees, April to September, 1959.

TABLE 5. Total collections of Anthocoris nemorum (L.), August 15 to October 19, 1959.

| | Larvae | Males | Females | Total adults | Sex Ratio (♂♂ : ♀♀) |
|---|---|---|---|---|---|
| Aug. 15 | 33 | 52 | 9 | 61 | 5.78 : 1* |
| " 24 | 17 | 86 | 22 | 108 | 3.91 : 1 |
| " 31 | 13 | 59 | 17 | 76 | 3.47 : 1 |
| Sept. 7 | 8 | 41 | 17 | 58 | 2.41 : 1 |
| " 14 | 2 | 59 | 11 | 70 | 5.36 : 1 |
| " 21 | 1 | 30 | 11 | 41 | 2.73 : 1 |
| " 28 | 0 | 25 | 10 | 35 | 2.50 : 1 |
| Oct. 5 | 0 | 19 | 15 | 34 | 1.27 : 1 |
| " 12 | 0 | 11 | 3 | 14 | 3.67 : 1 |
| " 19 | 0 | 3 | 1 | 4 | 3.00 : 1 |

* Females mature slightly later than males, so late larvae may be largely females.

TABLE 6. Total collections of Anthocoris nemorum (L.), September and October, 1958.

| | Larvae | Males | Females | Sex Ratio (♂♂ : ♀♀) |
|---|---|---|---|---|
| Sept. 2 - 4 | 55 | 9 | 17 | 0.55 : 1 |
| " 9 -11 | 37 | 46 | 22 | 2.01 : 1 |
| " 16 | 13 | 29 | 16 | 1.81 : 1 |
| " 22 -24 | 7 | 41 | 27 | 1.52 : 1 |
| Oct. 5 - 7 | 13 | 72 | 22 | 3.27 : 1 |
| " 21 | 6 | 72 | 13 | 5.54 : 1 |
| " 27 | 0 | 8 | 3 | 2.67 : 1 |

that the females enter hibernation shortly after they are fertilized. Three times as many males as females were collected after the majority of the second generation had matured (Tables 5 and 6).

The suction trap records (Table 4) reveal an increased flight activity of males during September but a decreased activity of females. Southwood's, 1960, records also show that males outnumber females by 3 : 1 in suction traps in the autumn. These results suggest that females do not fly very far in seeking overwintering sites. Males remain active on the host plants for a longer period than the females.

Overwintering

A. nemorum hibernates in a wide variety of sites such as under bark scales, in litter, in plant stems and similar protected niches. The most successful methods of collecting overwintering specimens were searching under the bark scales of Acer, and warming litter collections in the laboratory.

Table 7 compares the sex ratio of A. nemorum in autumn, winter and spring for two seasons. The proportion of males does not decrease between winter and spring which indicates that mortality is equal for both sexes at least during the latter part of the winter. Thus the disproportionate sex ratio in the spring is due to males dying before they enter hibernation.

More than 20 hibernating females were dissected during February and March and only two had food in their crops. There were traces of food in the intestine or yellowish granules in the rectum of some others.

TABLE 7. Sex ratio of Anthocoris nemorum (L.) in autumn, winter and spring, 1958-59 and 1959-60.

| | | Males | Females | Ratio (♂♂ : ♀♀) |
|---|---|---|---|---|
| Autumn | (Sept. 22 - Oct. 27/58) | 193 | 65 | 2.97 : 1 |
| Winter | (1958-59) | 25 | 137 | 0.18 : 1 |
| Spring | (Mar. 13 - May 11/59) | 13 | 73 | 0.18 : 1 |
| Autumn | (Sept. 14 - Oct. 19/59) | 167 | 51 | 3.28 : 1 |
| Winter | (1959-60) | 2 | 28 | 0.07 : 1 |
| Spring | (Mar. 15 - May 4/60) | 18 | 261 | 0.07 : 1 |

Evidently there is a minimum of feeding during the winter. Most of the specimens dissected at this time (which is shortly before spring emergence) still had considerable fat reserves. Slight ovarial development occurs while the females are still in hibernation. The first noticeable development was found in specimens dissected in mid-February, when the first rudiment was slightly enlarged.

The results of experiments on artificial overwintering of A. nemorum are given in Table 8. Excellent survival was obtained by storing adults at 34°F. in individual tubes embedded in saturated plaster of Paris. Good survival of females (75 per cent) was also obtained by storing single pairs of males and females. There was a higher mortality, apparently caused by fungus, when five to ten individuals were stored together. The survival of males was much lower than the survival of females. Half of the males died by early November; under field conditions they would have died before winter.

TABLE 8. Survival of Anthocoris nemorum (L.) adults kept over winter at 34°F. 1959-1960.

Group 1: Males and females collected September 11-25, stored 5 to 10 per tube.

Group 2: Males and females collected September 17-28, stored as individual pairs.

Group 3: Females collected September 29 - October 12, stored in individual tubes.

| | Group 1 | | | | Group 2 | | | | Group 3 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 17 ♂♂ | | 33 ♀♀ | | 30 ♂♂ | | 30 ♀♀ | | 22 ♀♀ | |
| | No. dead | % survival | No. dead | % survival | No. dead | % survival | No. dead | % survival | No. dead | % survival |
| Oct. 9 | 2 | 88.23 | 0 | 100 | 2 | 93.33 | 2 | 93.33 | 0 | 100 |
| " 23 | 2 | 76.47 | 1 | 96.97 | 8 | 66.67 | 1 | 89.00 | 1 | 95.46 |
| " 29 | 2 | 64.70 | 1 | 93.94 | 1 | 63.34 | 0 | 89.00 | 0 | 95.46 |
| Nov. 9 | 3 | 52.94 | 1 | 90.91 | 3 | 53.34 | 1 | 85.67 | 0 | 95.46 |
| " 27 | 2 | 41.17 | 2 | 84.85 | 4 | 40.00 | 0 | 85.67 | 0 | 95.46 |
| Dec. 14 | 0 | 41.17 | 3 | 75.76 | 2 | 33.33 | 0 | 85.67 | 0 | 95.46 |
| Jan. 18 | 1 | 35.29 | 3 | 66.67 | 2 | 26.66 | 2 | 79.00 | 0 | 95.46 |
| Feb. 15 | removed for experiments | | | | 1 | 23.33 | 0 | 79.00 | 0 | 95.46 |
| Mar. 14 | | | | | 2 | 16.67 | 1 | 75.67 | 0 | 95.46 |
| " 28 | | | | | 0 | 16.67 | 0 | 75.67 | 0 | 95.46 |

The weight loss of A. nemorum females during the winter is shown in Fig. 7. These specimens were collected during September, before entering hibernation. Their fat bodies were probably not completely developed, which would explain why their weights were lower than those of specimens collected later in the season. Table 9 compares the weights of females collected in autumn, winter and spring, with the weights of specimens artificially overwintered. The percentage weight loss during the winter is very similar for the two groups.

Two-thirds of the total weight loss occurred within the first six weeks. The largest component of this would be the utilisation and elimination of the gut content. The remainder of the weight loss is due to depletion of fat, and possibly some dehydration of the body tissues. The increase in weight during March was unexpected. The insects had no access to food throughout the experiment but free water was available at all times. They were exposed to laboratory temperatures for 30 to 60 minutes prior to each weighing so they had an equal chance to obtain water on each occasion. Ovarial development commences in late winter even under the conditions of this experiment. Thus, it is concluded that the weight increase is the result of utilisation of the fat body for development of the ovaries and the increased absorbtion of water into the tissues. Lees, 1955, cites several cases of diapausing insects having to restore their water balance before becoming active. Overwintering box elder bugs, Leptocoris trivittatus (Say), remain inactive until their water balance is restored in the spring (Hodson, 1937, in Lees). However, this is not completely analogous with the situation in A.nemorum because the latter are very active during the winter when exposed to laboratory temperature.

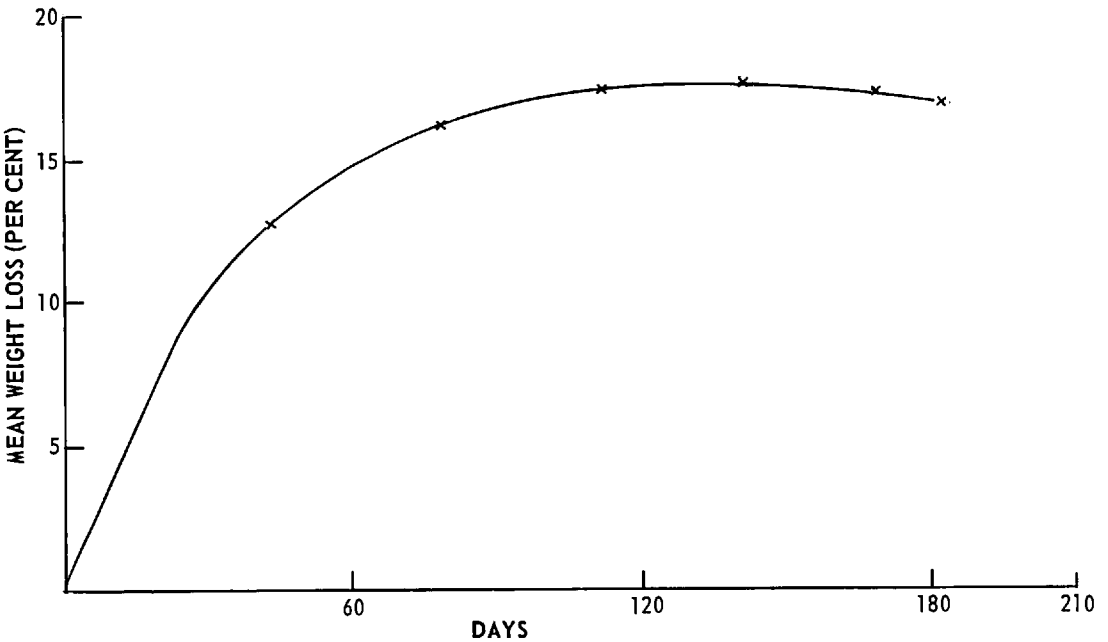



Fig. 7. Mean weight loss (%) of 49 *Anthocoris nemorum* (L.) females overwintered at 34° F.

TABLE 9. Mean weights of field-collected Anthocoris nemorum (L.) females in two seasons compared with the weights of specimens overwintered in a refrigerator at 34°F., 1959-1960.

| | No. of specimens | Weight (mg.) | Weight loss (%) |
|---|---|---|---|
| Field-collected, 1958-59 | | | |
| Autumn (Oct. 21) | 15 | 1.915 | |
| Winter (Feb. - Mar.) | 45 | 1.585 | 17.2 |
| Spring (April 8) | 10 | 1.637 | |
| Field-collected, 1959-60 | | | |
| Autumn (Oct. 5) | 30 | 1.819 | |
| Winter (Feb. - Mar.) | 12 | 1.530 | 15.9 |
| Spring (Mar. 15-31) | 25 | 1.556 | |
| Overwintered in Refrigerator | | | |
| Autumn (Sept. 28 - Oct. 12) | 49 | 1.763 | |
| Winter (Mar. 28) | 49 | 1.464 | 17.0 |

## 2. Anthocoris nemoralis (Fab.)

Spring emergence and overwintered generation.

A. nemoralis leaves its winter hibernacula in mid- to late March; it was first collected in 1959 on March 27, and in 1960 on March 15. Only general records were obtained on the movements of A. nemoralis during its spring dispersal stage in 1959. In 1960, a more detailed picture of its movements was obtained because there was a large overwintered population and larger samples were taken than in 1959. The intensive collections from Salix in early spring provides a comparison between the life-cycles of A. nemoralis and A. nemorum.

Males leave hibernation slighly earlier than females. The sex ratio of males to females up to the end of March was 1.11 : 1. However, during the first week of April the ratio was reversed to 0.76 males : 1 female. The sex ratio for the entire overwintered generation is grouped in intervals of three weeks in Table 10. The table shows that most of the males die earlier than the females but there are some males present throughout the generation; there is a larger proportion of A. nemoralis males present near the end of the overwintered generation than of any other species of Anthocoris. The abrupt rise in the proportion of males from May 30 to June 5 is due to the early maturing males of the spring generation. Dissections showed that all the females in these collections had overwintered; on the other hand most of the males appeared to be freshly emerged specimens.

TABLE 10. Sex ratio of Anthocoris nemoralis (Fab.), spring, 1960.

| | Males | Females | Ratio (♂♂ : ♀♀) |
|---|---|---|---|
| Mar. 15 - Apr. 9 | 99 | 109 | 0.91 : 1 |
| Apr. 11 - May 3 | 188 | 264 | 0.71 : 1 |
| May 4 - May 22 | 58 | 108 | 0.54 : 1 |
| " 23 - June 5 | 13 * | 17 | 0.77 : 1 |

* Largely spring-generation males.

The period of spring emergence is relatively short; maximum numbers of A. nemoralis are present in mid-April, at least one week before the peak for A. nemorum. Most of the population aggregates on Salix after leaving the winter hibernacula. The majority of specimens collected during March were on male trees, but by the middle of April there was a preponderance on female trees (Fig. 2). Sands, 1951, noted the movements of overwintered A. nemoralis and A. nemorum from male to female Salix, followed by a further dispersal to other plants. The data in Fig. 2 does not indicate a mass movement of A. nemorum from male to female trees in 1960, but the trend is very obvious for A. nemoralis.

The occurrence of Anthocoris on individual Salix trees is closely associated with the stage of development of the plant. Maximum numbers occur on male trees when the catkins are fully mature. A. nemoralis leaves these trees at catkin-fall and the numbers on female trees then increase. At this time the stigmas are receptive and the leaf buds are bursting. Table 11 illustrates the association between numbers of

TABLE 11. Numbers of *Anthocoris nemoralis* (Fab.) on male and female *Salix* at different stages of development, spring 1960.

| *Salix* spp. | March 21 | March 31 | April 11 | April 20 | April 27 | May 4 | May 12 |
|---|---|---|---|---|---|---|---|
| *S. caprea* L. ♂ | 100% catkins mature; most pollen blown off. 17 | 50% catkin fall; leaf buds bursting. 9 | 95% catkin fall; leaves to 1". 0 | 0 | 0 | 0 | 0 |
| *S. atrocinerea* x *viminalis* ♂ (= *S.* x *geminata* Forbes) | No catkins open 0 | 5% catkins mature 1 | 20% catkin fall; leaf buds burst. 10 | 50% catkin fall; pollen all blown off. 3 | Leaves over 1". 5 | 1 | 0 |
| *S. atrocinerea* x *viminalis* ♀ | Stigmas receptive 8 | Leaf buds bursting 16 | Ovules maturing. Infertile flowers falling 8 | Leaves over 1" 9 | 6 | 0 | 1 adult + 3 larvae |
| *S. atrocinerea* ♀ Brot. ♀ | Flowers immature 0 | 10% stigmas receptive 2 | 100% stigmas receptive; leaf buds bursting 37 | Ovules maturing 36 | Leaves over 1" 30 | 19 | 15 adults + 7 larvae |

A. nemoralis and the stage of development of the earliest and latest male and female Salix trees that were sampled.

All possible aspects of why Anthocoris are attracted to Salix have not been investigated, but by combining the results obtained for A. nemoralis and A. nemorum, the following conclusions are obtained. Salix is practically the only tree whose buds have burst by the time Anthocoris have emerged from hibernation. The primary stimulus may be olfactory attraction to the catkins (see p. 182 ). There is a relative abundance of prey on Salix in early spring: psyllids (all stages), small lepidopterous larvae, thrips, mirid larvae, aphids, jassids, coleopterous eggs and larvae, dipterous larvae and small adult Hymenoptera and Diptera. No gross difference was noted in the fauna of male and female trees, but this aspect warrants further study in the light of the results obtained for differences in numbers of Anthocoris. As will be shown in a later section (p. 130 ), there is no evidence that Anthocoris feed on pollen or that they derive nourishment from the leaves of Salix. However, the length of life of A. nemoralis females is increased by one-third when fed on dilute sugar solution as compared to those only receiving water (p.134). Thus, nectar in the catkins can probably be used for food in the event that prey is scarce.

The distribution of the overwintered generation of A. nemoralis on Salix is compared with the distribution on other species of trees in Table 12. The trees are grouped according to the plan adopted for A. nemorum in Table 2, with the addition of Fraxinus to Group 1. Salix and the trees in Group 1 are infested with psyllids, which are considered to be the primary prey of A. nemoralis in the spring.

TABLE 12. Numbers of overwintered Anthocoris nemoralis (Fab.) adults collected on different types of trees, based on 100 minutes collecting per group, 1960.

| | Salix (♂♂ and ♀♀) | Group 1 trees (Crataegus, Sarothamnus, Malus and Fraxinus). | Group 2 trees (Ulmus, Quercus, Tilia, Acer and Fagus). |
|---|---|---|---|
| Mar. 15 - Mar. 31 | 72 | 13 | 0 |
| Apr. 4 - Apr. 21 | 100 | 130 | 5 |
| Apr. 25 - May 6 | 49 | 113 | 1 |
| May 9 - May 31 | 20 | 60 | 3 |

Although most of the population is attracted to Salix in the spring, a few A. nemoralis occur on Crataegus and Sarothamnus as early as the third week of March. There is a marked migration from Salix during April and a corresponding increase in the numbers on the Group 1 trees. The numbers on Malus and Fraxinus are much lower than on Crataegus or Sarothamnus; the reason is probably that the former pair have not leafed out sufficiently when A. nemoralis is at the peak of dispersal in mid-April. A similar explanation is suggested for the lack of A. nemoralis on the Group 2 trees; however, the lack of a preferred prey (psyllids) on these trees is probably a contributing factor. The drop in numbers during May indicates the decline of the overwintered generation.

Suction trap records for A. nemoralis from May to September are given in Table 13. Only two of the four traps were set up early enough to obtain data on dispersal of the overwintered generation. One trap that was running during April collected three females from April 1 to 7 that are not included in the table. The data in Table 13 shows that

there is considerable flight activity of A. nemoralis overwintered adults as late as the first half of May. This indicates that gravid females are flying; possibly A. nemoralis females do not oviposit all their eggs on one plant.

TABLE 13. Total collections of Anthocoris nemoralis (Fab.) from three suction traps in 1959 and one in 1960. All traps located at least 100 yards from breeding areas.

| | Males | Females | Total | Remarks |
|---|---|---|---|---|
| May 1 - May 16 | 2 | 13 | 15 | Overwintered Generation |
| " 17 - " 30 | 0 | 1 | 1 | " " |
| " 31 - June 30 | 14 | 15 | 29 | First Generation |
| July 1 - July 31 | 3 | 8 | 11 | " " |
| Aug. 1 - Aug. 31 | 0 | 0 | 0 | Second Generation |
| Sept.1 - Sept. 30 | 0 | 1 | 1 | " " |

The progress of overwintered females towards oviposition was studied by weighing samples at weekly intervals and dissecting a representative sample to determine the condition of the gut and stage of ovarial development. The condition of the ovaries at spring emergence and the progressive weight increase of females during the spring are compared with other Anthocoris in Figs. 3 and 4. Mean weights of males and females on Salix, Crataegus and Sarothamnus are compared in Fig. 8.

There was a sharp weight increase in both males and females between March 15 and 21 in 1960; this is due to increase in gut content because specimens collected on March 15 had not fed since emerging from hibernation. The weight of males then remains steady for five weeks, and then increases again when only the heaviest still survive (Fig. 8).

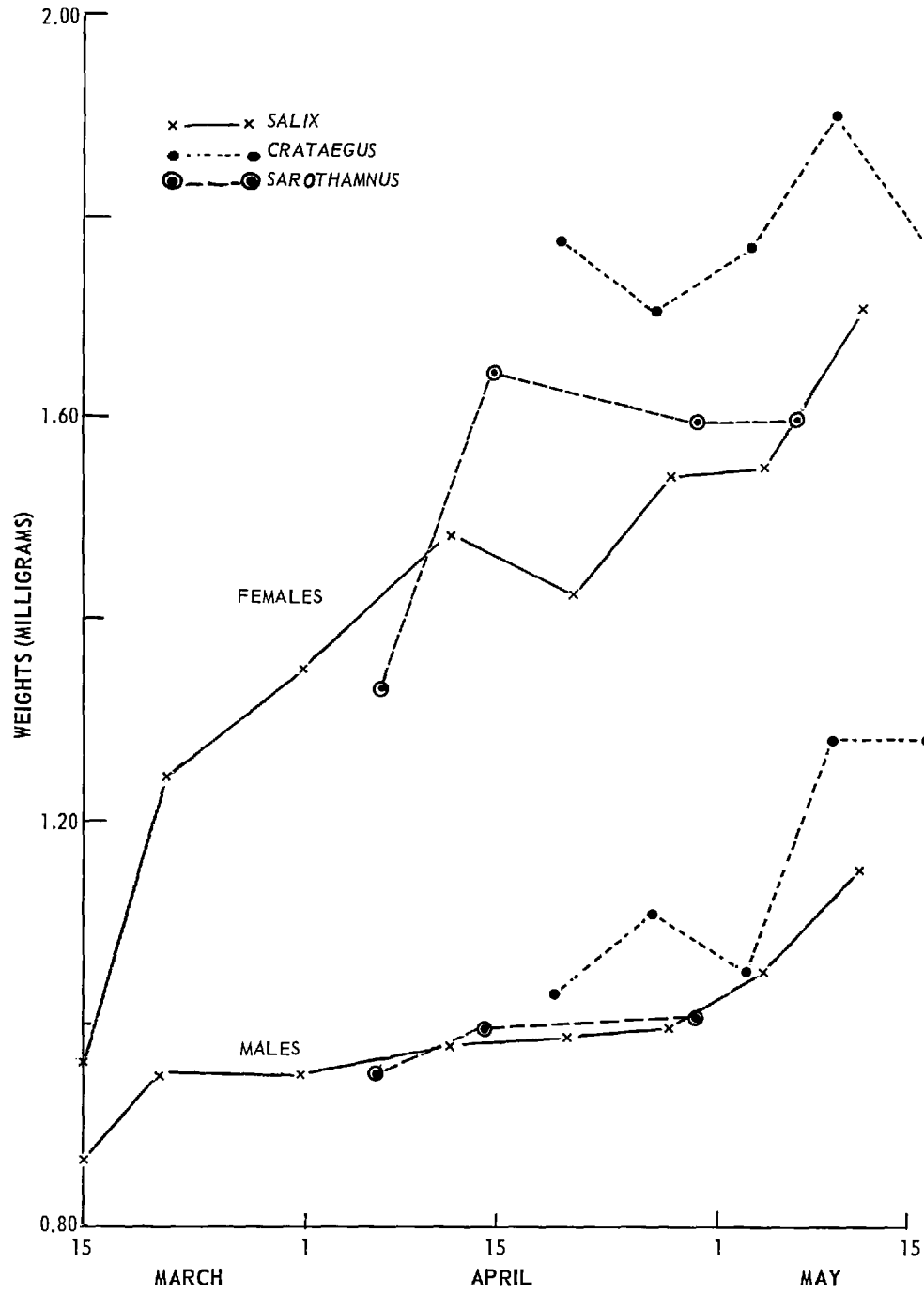



Fig. 8. Mean weights of *Anthocoris nemoralis* (Fab.) males and females on three host plants, March to May, 1960. Minimum of 15 specimens per weighing.

There is no difference between male weights on Salix and Sarothamnus but on Crataegus the males are markedly heavier.

The weight increase of females on Salix can be divided into four periods: (a) the sharp increase from March 15 to 21 attributed to increase in gut content; (b) a slower rate of increase from March 21 to April 11 due to ovarial development; (c) a decrease during the middle of April probably due to migration of the more mature females to other host plants; and (d) continued weight increase of females that remain and oviposit on Salix. The suction trap collections have indicated that mature females disperse, and mid-April is the period when most adults occur on Group 1 trees (Table 12), so it appears probable that the decreased weight of females on Salix at that time is due to dispersal of the most mature females. The weight of females on Crataegus is much greater than on either Salix or Sarothamnus. Apparently the psyllids on Crataegus, Psylla melanoneura (Foerster) and P. peregrina (Foerster) are very suitable prey for A. nemoralis.

Oviposition commences about the middle of April. Some females had mature ovaries by the first week of April in 1959, and on April 13, when the first eggs were found, all females had fully developed ovaries. Dissections were started in mid-March in 1960, so it was possible to follow ovarial development throughout its duration. All females dissected on March 31 showed some ovarial development, with most containing one or two rudiments per ovariole. The operculum was evident on some eggs by April 4, and on April 12 the first mature eggs were seen. No concentrated search was made for eggs in the field

but it is estimated that the first eggs were laid about the middle of April and that the peak of oviposition occurred towards the end of April and the beginning of May. As most of the population had left male Salix by April 20, it thus becomes apparent why the number of larvae is so much lower than on female Salix (Fig. 2B).

Spring and Summer generations.

Spring-generation larvae of A. nemoralis start to emerge about the second week of May. The life-cycle, based on collections from all host plants is illustrated in Fig. 9. As is to be expected from the distribution of the overwintered females (Table 12), most of the spring generation develops on the psyllid-infested plants, Crataegus, Salix, Sarothamnus and Malus. The earliest emergence of larvae is on Salix. Fig. 10 compares the number of larvae per instar of A. nemoralis and A. nemorum collected on male and female Salix on May 30-31, 1960. A. nemoralis larvae are considerably more advanced than those of A. nemorum even though the oviposition period of the two species commences about the same time.

Larval development is rapid; a few adults occur in late May and by mid-June most of the larvae have matured. The first spring-generation adults were collected in suction traps on May 31, in 1959. The life-cycle of the host psyllids runs a parallel course of development. For example, on June 6, 1960, over 90 per cent of Psylla mali on Malus were adults, while on Crataegus, 60 to 70 per cent of the psyllids were adult by this date. Southwood and Leston, 1960 state that A. nemoralis

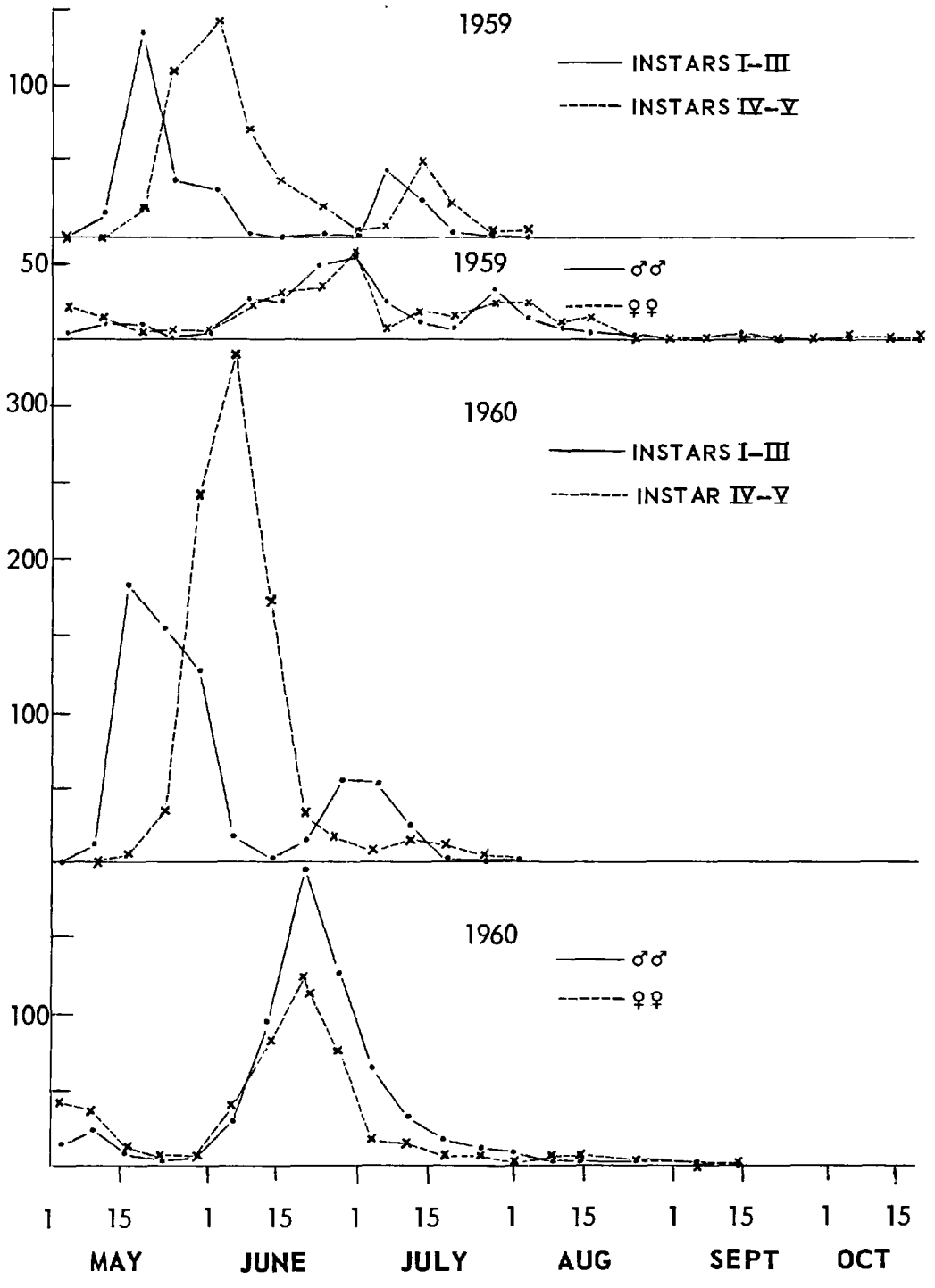



Fig. 9. Number of *Anthocoris nemoralis* (Fab.), larvae and adults, in weekly collections, May to October, 1959, and May to September, 1960.

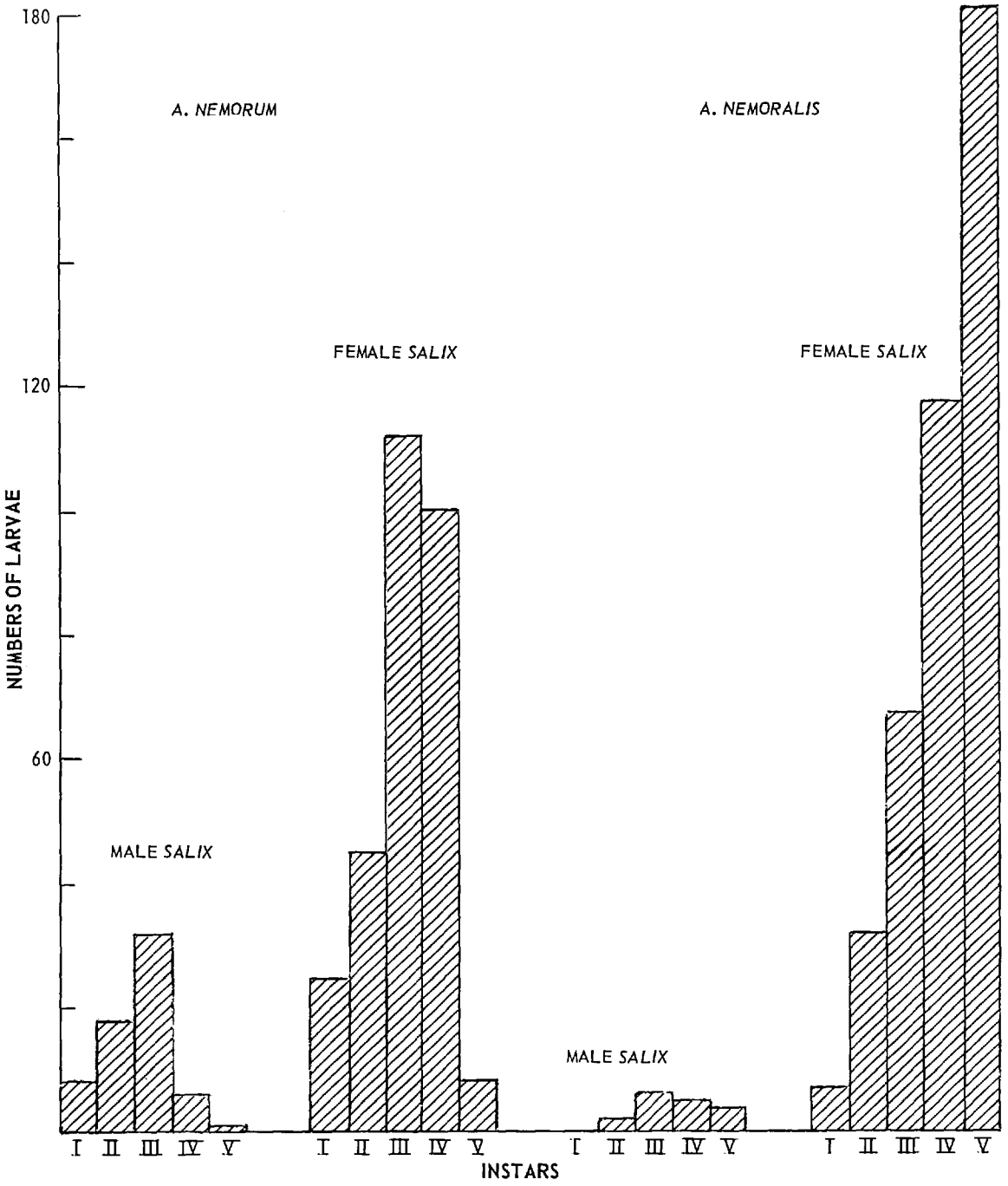



Fig.10. Number of larvae per instar of *Anthocoris nemorum* (L.) and *A. nemoralis* (Fab.) collected from five male and five female Salix trees, May 30 to 31, 1960.

first generation adults appear in July, but the present studies indicate that they actually appear a month earlier.

The post-teneral dispersion of A. nemoralis during June is very marked. Table 14 shows the decline in numbers of adults on the spring host plants and a corresponding increase in numbers on aphid-infested trees. Suction-trap records give further evidence of this dispersal period (Table 13).

TABLE 14. Total numbers of Anthocoris nemoralis (Fab.) collected on spring and summer host plants, showing the change in distribution during May and June. Forty minutes collecting in each block per week, 1960.

| | Spring Host plants | | Summer Host plants | |
|---|---|---|---|---|
| | Larvae | Adults | Larvae | Adults |
| May 30 | 362 | 9 | 3 | 3 |
| June 6 | 345 | 65 | 9 | 6 |
| " 13 | 165 | 111 | 13* | 76 |
| " 20 | 21* | 94 | 27 | 281 |
| " 27 | 1 | 45 | 89 | 190 |
| July 4 | 1 | 27 | 71 | 71 |
| " 11 | 1 | 9 | 51 | 44 |
| " 18 | 2 | 16 | 13 | 8 |
| " 25 | 2 | 11 | 1 | 5 |

* Occurrence of first-instar, summer-generation larvae.

A. nemoralis adults can be collected from a range of trees and herbaceous plants during June and July. The spring host plants are practically deserted, except for Crataegus, where a small but consistent population remains until autumn. Most of the adults aggregate on Acer and Tilia. A relatively large number were also collected on Fagus in

1960, associated with a heavy infestation of the aphid P. fagi.

A small, but distinct, second generation of A. nemoralis is evident from the graphs in Fig. 8. This generation is clearly differentiated from the spring generation because it occurs on different trees. Virtually the entire summer generation was found on Tilia in 1959. In 1960, when the population was greater, a trace of a second generation also occurred on Acer, Fagus and Sarothamnus. Table 15 compares the numbers of larvae collected from one Tilia tree with the numbers collected from nine trees of other species in both years.

TABLE 15. Numbers of summer-generation Anthocoris nemoralis (Fab.) larvae collected on Tilia in 10 minutes per sample, compared with the numbers collected on nine other species of trees in 90 minutes per sample. June to August, 1959 and 1960.

| | 1959 | | 1960 | |
|---|---|---|---|---|
| | Tilia | Others | Tilia | Others |
| June 20 - 22 | 0 | 21* | 17 | 27* |
| " 27 - 30 | 15 | 2 | 61 | 17 |
| July 4 - 5 | 49 | 2 | 49 | 12 |
| " 11 - 13 | 67 | 4 | 29 | 13 |
| " 18 - 19 | 23 | 1 | 10 | 2 |
| " 25 - 27 | 1 | 0 | 1 | 3 |
| Aug. 1 - 3 | 3 | 0 | 0 | 1 |
| Total summer-generation larvae | 158 | 9 | 167 | 48 |

* Late spring-generation larvae.

Sands, 1951, stated that A. nemoralis occurs on almost all trees infested with aphids. He recorded larvae from Salix, Crataegus, Malus,

Sarothamnus, Tilia, Populus, Quercus, Ulmus, Acer, Betula and from the herbaceous plant Urtica. Larvae were collected from all of these plants except Populus (which was not sampled) in the present study, but the numbers on Betula, Ulmus, Quercus and Urtica were extremely small. As has been shown in the present study, Sands' list of host plants is largely correct, but the association with aphids is erroneous; far more larvae are produced on psyllid-infested trees than on aphid-infested trees.

The summer generation of A. nemoralis was studied by additional collections, dissections of females, and a breeding experiment, in addition to the weekly field collections. Two other Tilia trees were checked in June and July in 1960, and found to harbour a similar size of population as the one on the sample tree.

Table 16 compares the ovarial development of females on various plants. Adults are found on Crataegus throughout the season but practically all of the females are univoltine. It has already been shown that a second generation of larvae is produced on Tilia. The dissection results show that ovaries are well developed in all females collected on this plant up to mid-July; at this time the second-generation adults begin to appear. More than half of the females collected from trees other than Crataegus and Tilia had developing or mature ovaries. There is no significant number of summer-generation larvae produced on these plants. Therefore, either the number of eggs per female is very low, or else the ovaries atrophy and the females enter reproductive diapause.

TABLE 16. Ovarial development of Anthocoris nemoralis (Fab.) females of the current year. June and July, 1959 and 1960.

| | Tilia | | Crataegus | | Other trees | |
|---|---|---|---|---|---|---|
| | Undeveloped | Developing or mature | Undeveloped | Developing or mature | Undeveloped | Developing or mature |
| 1959 | | | | | | |
| June 1 - 23 | 0 | 13 | 12 | 5 | 11 | 18 |
| June 30 - July 19 | 1 | 21 | 11 | 0 | 10 | 11 |
| 1960 | | | | | | |
| June 13 | 1 | 7 | 6 | 3 | 2 | 6 |
| " 27 | 0 | 10 | 10 | 0 | 1 | 9 |
| July 4 | 0 | 11 | 5 | 0 | 5 | 3 |
| " 12 | 7* | 8 | - | - | 3 | 8 |
| " 19 | 5 | 7 | 2 | 0 | 3 | 0 |

* Appearance of earliest second-generation females.

It is clear from the field data that although during the summer A. nemoralis preys on a variety of insects, especially aphids, the most suitable prey available at that time for reproduction is the lime aphid Eucallipterus tiliae (L.) An attempt was made to determine whether it could produce a second generation with the green broom aphid Acyrthosiphon spartii Koch, as the prey. Approximately 100 spring-generation adults were placed in a sleeve cage on Sarothamnus on June 10, 1960. Thirty females were collected and dissected two weeks later to determine the condition of the ovaries and fat body. Twenty-four had mature ovaries, while only three had entered reproductive diapause -- that is, had immature ovaries and fully-developed fat bodies. The cage was examined again on July 9, and larvae were numerous. Thus, A. nemoralis can produce a second generation on Sarothamnus with A. spartii as prey, but under natural conditions in both 1959 and 1960, no significant second generation occurred. This situation is analogous with Thompson's, 1951, results with attempts to control diaspine scale, Diaspis visci Schrk., in Bermuda by introducing 13 species of scale-feeding coccinellids. The coccinellids bred successfully in sleeve cages on trees with the scale insects as the only available host. When the cages were removed, the predators dispersed, and except for one species, failed to become established on the island, apparently because of a lack of a preferred prey.

The weights of A. nemoralis adults collected throughout the season on various plants in 1959 are illustrated in Fig. 11. The drawbacks to this type of data are discussed with regard to A. nemorum (p. 28), and

the results should be interpreted with this in mind. The weight of overwintered females on Crataegus is higher than on any other plants, as was also shown in Fig. 8. Summer-generation females on Crataegus are as heavy as those on any other plant, even though few of the former contained eggs. Summer-generation females on Salix and Sarothamnus are very small but most of these weighings are based on young adults collected before they had dispersed for feeding. The heaviest summer-generation males and females were collected from Acer, yet there was no appreciable second generation of larvae on this plant. Evidently the aphid, Drephanosiphon platanoides (Schrk.) provides suitable nourishment for building up the fat body but not for reproduction.

Pre-hibernation period.

The numbers of A. nemoralis decline very early in the summer. Table 17 compares the total number of adults collected, grouped in bi-monthly intervals, from the peak population in late June until the end of the season in 1959 and 1960. In both years there was a sharp decrease in numbers during the first half of July. There was a slight increase at the end of the second generation in late July and early August in 1959, but no corresponding increase in 1960. Suction trap records (Table 13) indicate that flight activity in July drops to one third of the level in June. Thus, it appears from the field data that pre-hibernation feeding occurs in late June and most of the univoltine population enters over-wintering quarters during July. Most of the second generation goes into hibernation in August.

TABLE 17. Total numbers of Anthocoris nemoralis (Fab.) adults collected on all trees from the end of the first generation until autumn, 1959 and 1960.

| | 1959 | 1960 |
|---|---|---|
| June 20 - 30 | 193 | 524 |
| July 4 - 13 | 61 | 132 |
| " 18 - 27 | 77 | 43 |
| Aug. 1 - 9 | 52 | 24 |
| " 14 - 25 | 26 | 19 |
| Sept. 5 - 14 | 7 | 3 |
| " 21 - 28 | 6 | - |
| Oct. 5 - 13 | 4 | - |

The sex ratio during the summer varied between the two seasons; the ratio of males to females in 1959 was 0.91 : 1, while in 1960 there was a predominance of males in the ratio of 1.76 : 1. Even in 1960 the proportion of males was less than the 3 : 1 ratio for A. nemorum so the males and females probably enter hibernation about the same time.

Overwintering.

No major hibernaculum of A. nemoralis was discovered during this study. Only four specimens were collected in two winters: two in Sarothamnus pods, and one each under bark-scales on Tilia and Crataegus. The numbers of A. nemoralis in the study area during the summers were of the same order of magnitude as those of A. nemorum, A. confusus and A. sarothamni, and over 100 of each of these were found in hibernation.

A. nemoralis has been reported hibernating in sack bands on Malus (Massee et al., 1935), under the bark of Platanus and other trees (Cobben, 1958), and in crevices in Populus bark (Dunn, 1960). Such habitats were searched at Silwood Park without success.

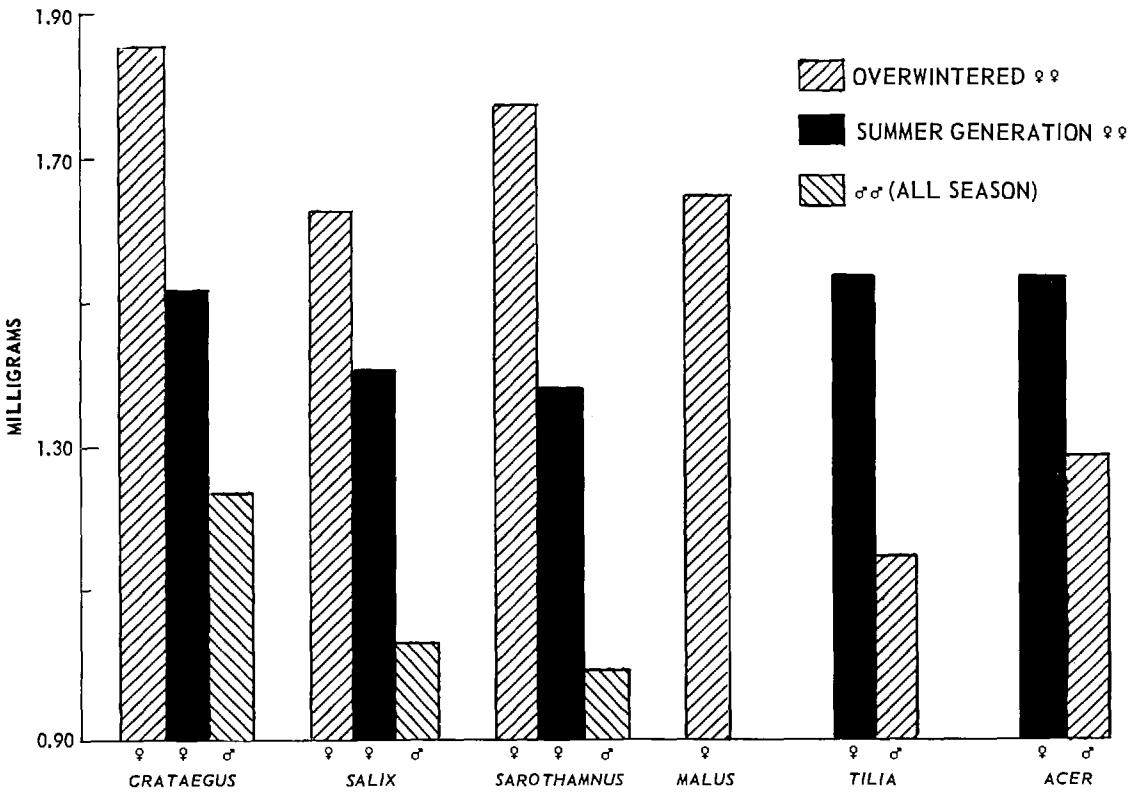



Fig. 11 Mean weights of *Anthocoris nemoralis* (Fab.) males and females on various trees, April to September, 1959.

## 3. Anthocoris confusus Reut.

Spring emergence and overwintered generation.

A. confusus was first collected in the spring on March 27 in 1959 and on March 22 in 1960. It appears slightly later than A. nemorum or A. nemoralis, and peak numbers do not appear on Salix until the latter half of April. As with A. nemoralis, the males are found slightly before the females in the spring. Table 18 gives the sex ratio for the overwintered generation in 1959 and 1960. Most of the males die within four to six weeks. The males that occur in late June are spring generation, but the numbers for females given in the table are overwintered generation.

TABLE 18. Sex ratio of overwintered Anthocoris confusus Reut., spring 1959 and 1960.

| | 1959 | | | 1960 | | |
|---|---|---|---|---|---|---|
| | ♂♂ | ♀♀ | Ratio (♂♂:♀♀) | ♂♂ | ♀♀ | Ratio (♂♂:♀♀) |
| Mar. 21 - Apr. 10 | 12 | 8 | 1.50 : 1 | 24 | 12 | 2.00 : 1 |
| Apr. 12 - Apr. 27 | 24 | 61 | 0.36 : 1 | 14 | 44 | 0.32 : 1 |
| May 3 - May 19 | 11 | 21 | 0.52 : 1 | 8 | 33 | 0.24 : 1 |
| May 23 - June 9 | 14 | 59 | 0.24 : 1 | 1 | 102 | 0.01 : 1 |
| June 13 - June 30 | 6* | 63 | 0.10 : 1 | | | |

* Some spring-generation males.

The distribution of A. confusus on different groups of trees during the springs of 1959 and 1960 is given in Table 19. The trees are divided into three groups: Salix; Early trees, those which burst their buds early in the spring; and Primary host trees, Fagus, Tilia, Quercus and Acer. There is an aggregation on Salix, but it is not always as marked as with A. nemorum or A. nemoralis, probably because A. confusus emerges later and by this time more plants have burst their buds. There is a dispersive phase in April and May in which A. confusus is found in small numbers on the early trees. This species finally begins to aggregate on the primary host trees for oviposition in mid- to late May.

TABLE 19. Numbers of overwintered Anthocoris confusus Reut. adults collected on three groups of trees, based on 100 minutes collecting per group, 1959 and 1960.

| | Salix ♂♂ and ♀♀ | | Early trees (Crataegus, Sarothamnus, Malus, Betula and Ulmus). | | Primary host trees (Fagus, Quercus, Tilia and Acer). | |
|---|---|---|---|---|---|---|
| | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 |
| Mar. 21 - Apr. 10 | 30 | 7 | 4 | 4 | 0 | 0 |
| Apr. 11 - Apr. 27 | 160 | 19 | 16 | 23 | 11 | 0 |
| May 3 - May 19 | 7 | 3 | 18 | 13 | 23 | 18 |
| May 23 - June 10 | 7 | 4 | 13 | 2 | 48 | 85 |
| June 13 - June 30 | 0 | 0 | 1 | 0 | 58 | 90 |
| Totals | 204 | 33 | 52 | 42 | 140 | 193 |

Table 20 gives the total numbers of A. confusus collected in the four suction traps. The majority of the specimens were collected in one trap that was located a few yards from a Quercus tree. The table indicates considerable flight activity of overwintered adults in late May. Thirty-eight of the 63 bugs were caught in a three-day period, May 22 to 24, in the trap near the Quercus. Ten females from this collection were dissected and all had fully mature ovaries. The suction-trap data thus supports the statement that A. confusus aggregates on its primary host trees for oviposition in mid- to late May.

TABLE 20. Total collections of Anthocoris confusus Reut. from three suction traps in 1959 and one in 1960. Most specimens collected in a trap located a few yards from a Quercus tree.

| | Males | Females | Total | Remarks |
|---|---|---|---|---|
| May 13 - May 31 | 6 | 57 | 63 | Overwintered generation |
| June 1 - June 30 | 5 | 17 | 22 | Overwintered plus first " |
| July 1 - July 31 | 19 | 13 | 32 | First generation |
| Aug. 1 - Aug. 31 | 3 | 6 | 9 | " " |
| Sept.1 - Sept.30 | 5 | 5 | 10 | Second generation |
| Oct. 1 - Oct. 10 | 2 | 1 | 3 | " " |

The four primary host trees are all infested with aphids of the Family Callaphididae that appear to be the major prey of A. confusus: Fagus, Phyllaphis fagi; Quercus, Tubercoloides annulatus (Hart.); Tilia, Eucallipterus tiliae; and Acer, Drephanosiphum platanoides. However, they are not partial to all callaphidids; for example, Betula supports a large population of Euceraphis betulae but A. confusus rarely breeds on this tree. Although the aphids are relatively numerous on the primary trees soon after the trees are in leaf, large numbers of A. confusus were not collected until the aphid population was so high that the leaves were sticky with honeydew.

The numbers of A. confusus adults collected on the primary host trees during May and June of both years are given in Table 21. There was an exceptionally heavy infestation of P. fagi on Fagus in 1960; it was so numerous that large numbers of alates could be collected from any trees in the vicinity of Fagus. P. fagi was recorded in early May in 1960, while in 1959 the much lower population was not noticed until June. This infestation in 1960 concentrated large numbers of A. confusus on Fagus.

TABLE 21. Numbers of overwintered Anthocoris confusus Reut. adults collected on the primary host trees in May and June, 1959 and 1960.

| | | Fagus | | Quercus | | Tilia | | Acer | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 |
| May | 3 - 4 | 3 | 0 | 5 | 3 | 2 | 4 | 2 | 2 |
| " | 9 - 11 | 2 | 3 | 2 | 1 | 0 | 0 | 2 | 0 |
| " | 16 - 18 | 0 | 5 | 7 | 2 | 0 | 1 | - | 0 |
| " | 23 - 25 | 0 | 12 | 9 | 1 | 1 | 0 | 0 | 2 |
| " | 31 - June 2 | 0 | 22 | 15 | 3 | 2 | 1 | 3 | 1 |
| June | 6 - 9 | 2 | 46 | 9 | 10 | 5 | 1 | 11 | 0 |
| " | 13 - 15 | 1 | 22 | 3 | 3 | 5 | 2 | 11 | 6 |
| " | 20 - 23 | 12 | 38 | 2 | 4 | 8 | 25 | 2 | 4 |
| " | 27 - 30 | 15 | 9 | * | 2 | 2 | 3 | * | 1 |
| Totals | | 35 | 157 | 52 | 29 | 25 | 37 | 31 | 16 |

* Spring-generation females only.

The progressive weight increase and ovarial development of A. confusus were studied in both 1959 and 1960. The condition of the ovaries at the time of spring emergence is given in Fig. 3 and the weight increase during the spring period is compared with other Anthocoris in Fig. 4. Ovarial maturation occurs later in the spring than with any other species. A. confusus and A. minki are the only species that have completely undeveloped ovaries at the time of spring emergence. The rate of development within the species is irregular; an occasional female has mature ovaries by the end of April, but there is still a range from undeveloped to fully mature ovaries in early May. Over half of the specimens dissected on May 4, 1959, were mature; this stage was reached about one week later in 1960. Practically all females have mature ovaries by the end of May.

No search was made for eggs in the field, but the start of oviposition can be estimated from the incubation period and the first occurrence of larvae. Table 22 gives the incubation period of A. confusus eggs at 53° and 74°F. Mean temperatures for May were 54°F. in 1959, and 55°F in 1960; at this temperature the eggs would hatch in about four weeks. The first larvae were found in early June of both years. Therefore, the data suggests that oviposition commences in early May, which also agrees with the dissection results and coincides with the occurrence of females on the primary host trees. The peak of oviposition occurs in late May and early June, and continues until the end of June. Most of the overwintered females have died by this time, but there is an overlap of generations in late June and early July.

TABLE 22. Incubation period of Anthocoris confusus Reut. eggs laid in a constant temperature cabinet, then subjected to normal diurnal temperature fluctuations. Mean temperatures, 53°F. April to May, 1960.

| Number of eggs | Incubation at 74°F. (hours) | Total incubation (days) Range | Mean |
|---|---|---|---|
| 6 | 0 - 24 | 27 - 29 | 28.3 |
| 6 | 24 - 48 | 26 - 27 | 26.3 |
| 24 | Continuous | 5 - 7 | 6.0 |

Summer generations.

The data concerning the summer generations of A. confusus for 1959 and 1960 are graphed in Fig. 12. The total numbers collected on all 10 species of trees are combined to give a comprehensive picture of the number of generations and the progression of instars. More than 90 per cent of the specimens were collected from the four primary host trees.

A. confusus larvae occurred in both years from late May or early June until mid-August. The late-maturing larvae are thus present after the major period of aphid abundance. Larval development takes slightly less than one month, so the oviposition period of overwintered females is an extended one. The graphs in Fig. 12 show only a single generation of A. confusus per annum. However, dissections of females in late June and July prove that a small portion of the population produces a second generation. Table 23 gives the condition of ovaries in females dissected during June and July. There is an overlap of overwintered- and first-generation adults during this period. Overwintered females can usually be separated from first-generation by:

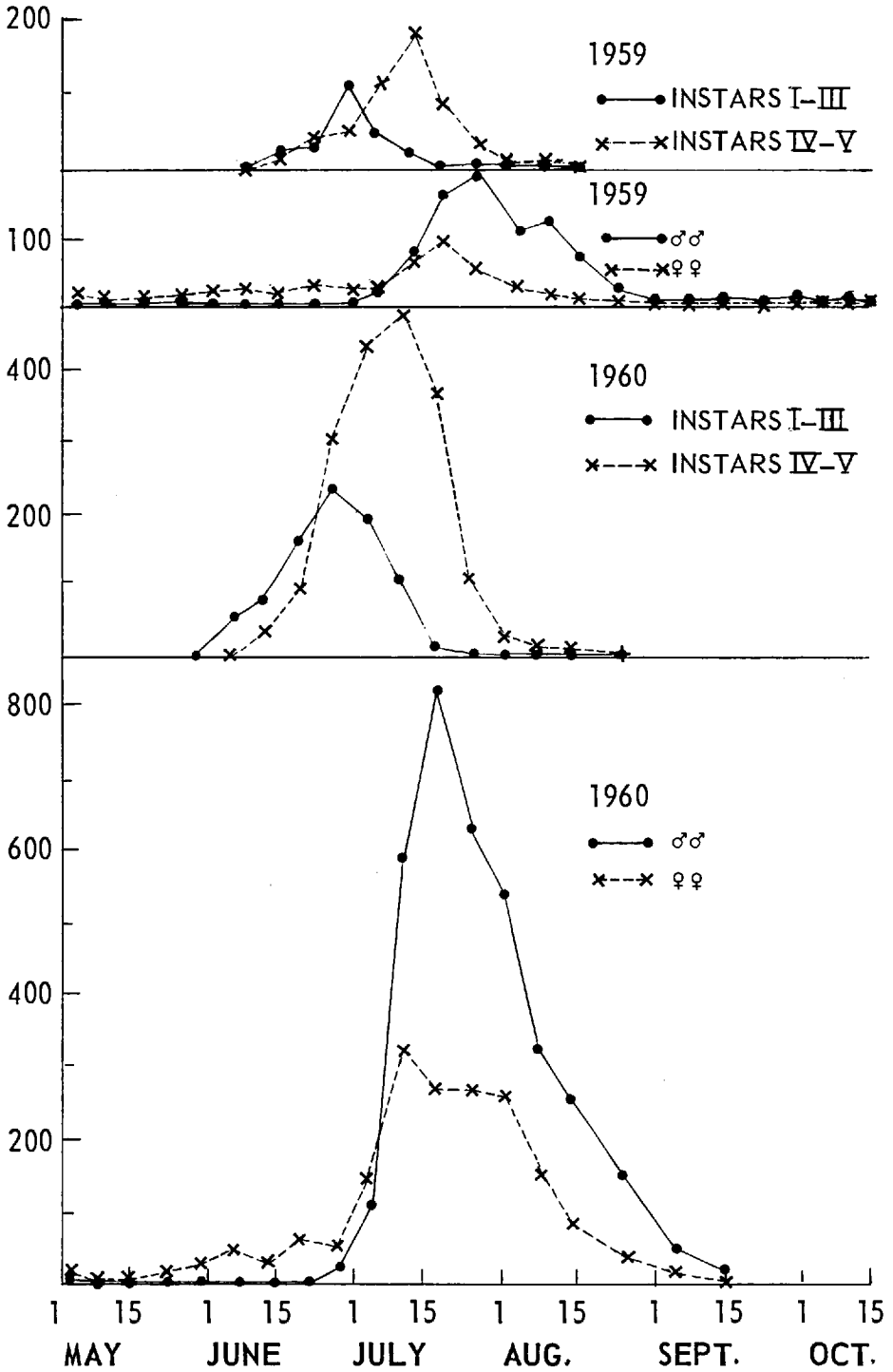



Fig.12.Number of *Anthocoris confusus* Reut., larvae and adults, in weekly collections, May to October, 1959, and May to September, 1960.

darker colour; depleted, off-white fat body; a large and sometimes discoloured sperm reservoir; and general appearance of senility of the gut and ovaries. First-generation females, with immature ovaries, varied from teneral females to some with fully-developed fat bodies. All of the distinguishing characters are subjective; there are many intermediate conditions, so the separation is not entirely reliable.

The most conclusive evidence that a portion of the females produce a second generation was the discovery of females with developing ovaries. Thus, although there is a partial second generation, maturing in late July and August, it is obscured by the predominant first generation.

TABLE 23. Condition of ovaries of Anthocoris confusus Reut. females dissected in June and July, 1959 and 1960.

| | Number dissected | Overwintered Generation (Mature or atrophied ovaries). | First Generation | | |
|---|---|---|---|---|---|
| | | | Undeveloped ovaries | Developing ovaries | Mature ovaries |
| 1959 | | | | | |
| June 23 | 14 | 10 | 0 | 4 | 0 |
| " 29 | 15 | 7 | 2 | 3 | 3 |
| July 5 | 19 | 4 | 11 | 3 | 1 |
| " 13 | 35 | 0 | 21 | 6 | 8 |
| " 19 | 25 | 0 | 19 | 3 | 3 |
| " 27 | 25 | 0 | 20 | 4 | 1 |
| Totals | 133 | 21 | 73 | 23 | 16 |
| 1960 | | | | | |
| June 22 | 16 | 12 | 4 | 0 | 0 |
| " 27 | 60 | 15 | 21 | 9 | 15 |
| July 4 | 65 | 5 | 45 | 8 | 7 |
| " 12 | 75 | 0 | 73 | 0 | 2 |
| " 19 | 75 | 0 | 74 | 0 | 1 |
| Totals | 291 | 32 | 217 | 17 | 25 |

The trend of A. confusus populations was similar on all trees in both years, but in 1960 the level was four times as great as in 1959. This difference was due chiefly to the epidemic of P. fagi on Fagus and the resultant exceptionally high population of A. confusus on this plant. Over 70 per cent of all larvae were collected from Fagus in 1960. A. confusus was collected in greater numbers than any other Anthocoris during this study (Table 1).

Table 24 gives the numbers of larvae and adults collected in June, July and August, 1960, on various trees and on herbs. It is apparent from the table that, except for Fagus, insufficient larvae occurred on the sampled plants to account for the number of adults collected. It has been pointed out previously that there is a high degree of error associated with the sampling method, but this is insufficient to account for a six-fold increase of adults on plants other than Fagus. The explanation for the increase in adults is the post-teneral dispersive flights, particularly from Fagus, into the sample plots. The increase in numbers of adults on herbs and trees, other than the primary host plants, in July and August is a significant indication of dispersal. Although a few larvae were collected from Urtica, it is probable that they had dropped from overhanging trees, and that they did not develop from eggs laid on Urtica. The suction trap collections (Table 20) also indicate flight activity of the first-generation adults, particularly during July.

There is an evident crash in aphid numbers in late June and early July, coinciding with the peak appearance of A. confusus adults. The

TABLE 24. Numbers of Anthocoris confusus Reut. larvae (L) and adults (A) collected from June to August, 1960.

| | *Fagus | | *Quercus | | *Tilia | | *Acer | | **Other trees | | +Urtica and grasses | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L | A | L | A | L | A | L | A | L | A | L | A |
| June | 744 | 153 | 125 | 19 | 65 | 48 | 45 | 24 | 5 | 1 | 7 | 0 |
| July | 1379 | 1066 | 152 | 256 | 38 | 329 | 105 | 1552 | 2 | 35 | 7 | 47 |
| Aug. | 41 | 293 | 8 | 561 | 3 | 65 | 2 | 873 | 0 | 59 | 0 | 5 |
| Total | 2164 | 1512 | 285 | 836 | 106 | 442 | 152 | 2449 | 7 | 95 | 14 | 52 |

* Four 10-minute collections per month.

** Four 60-minute collections per month.

\+ Samples obtained by sweeping - not comparable with tree-collections.

aphid decline apparently results from the normal decrease in the reproductive rate and increased dispersal, plus the influence of natural enemies. The late-maturing larvae, and adults that remain on Fagus, Quercus and Tilia probably feed on jassids and psocids which far outnumber the aphids from July to the end of the season (Appendix 1).

Fig. 13 compares the mean weights of A. confusus adults collected on six species of trees in 1959. The low weight of overwintered females on Salix is due to the fact that they were chiefly collected in April (Table 19) before the ovaries were mature. Sands, 1951, stated that Crataegus was the most frequent alternative to Quercus as a host plant for A. confusus; however, in the present study it was only collected from Crataegus during the spring, so weights are not available for summer females. The only difference in weights of adults collected on the primary host trees is the larger size of summer-generation adults on Tilia. The data suggests that feeding on the lime aphid, E. tiliae,

produces the heaviest adults, but further work is necessary to determine whether the relationship is consistent from year to year.

Pre-hibernation period.

The post-teneral flights of first-generation A. confusus result in dispersal, but also in aggregation; the latter is evident on Acer. The aphid population on this tree remains fairly high until autumn and A. confusus is attracted to the aphids for pre-hibernation feeding. The excessive numbers of adults collected on Acer in 1960 (Table 24) are chiefly due to the location of the tree. Several adjacent Fagus trees were probably the origin of most of the specimens that migrated to Acer. As indicated in Table 24, there appears to be some aggregation on Quercus during August. A Salix tree, heavily infested with Cavariella archangelicae (Scop.), was also noted to harbour large numbers of A. confusus in early August.

A. confusus can be collected from most trees and also from herbaceous plants during July and early August (Table 24). The sex ratio of A. confusus on the primary host trees and on other plants during the summer and autumn of 1960 is compared in Table 25. There is a significantly larger proportion of males on the primary hosts than on the miscellaneous plants. Although the proportion of females on the latter is slightly greater than the males (1 : 0.89), there is not a significant difference in the sex ratio. Mating takes place prior to overwintering and apparently, as is the case with A. nemorum, the females enter hibernation first while the males remain active on the host plants.

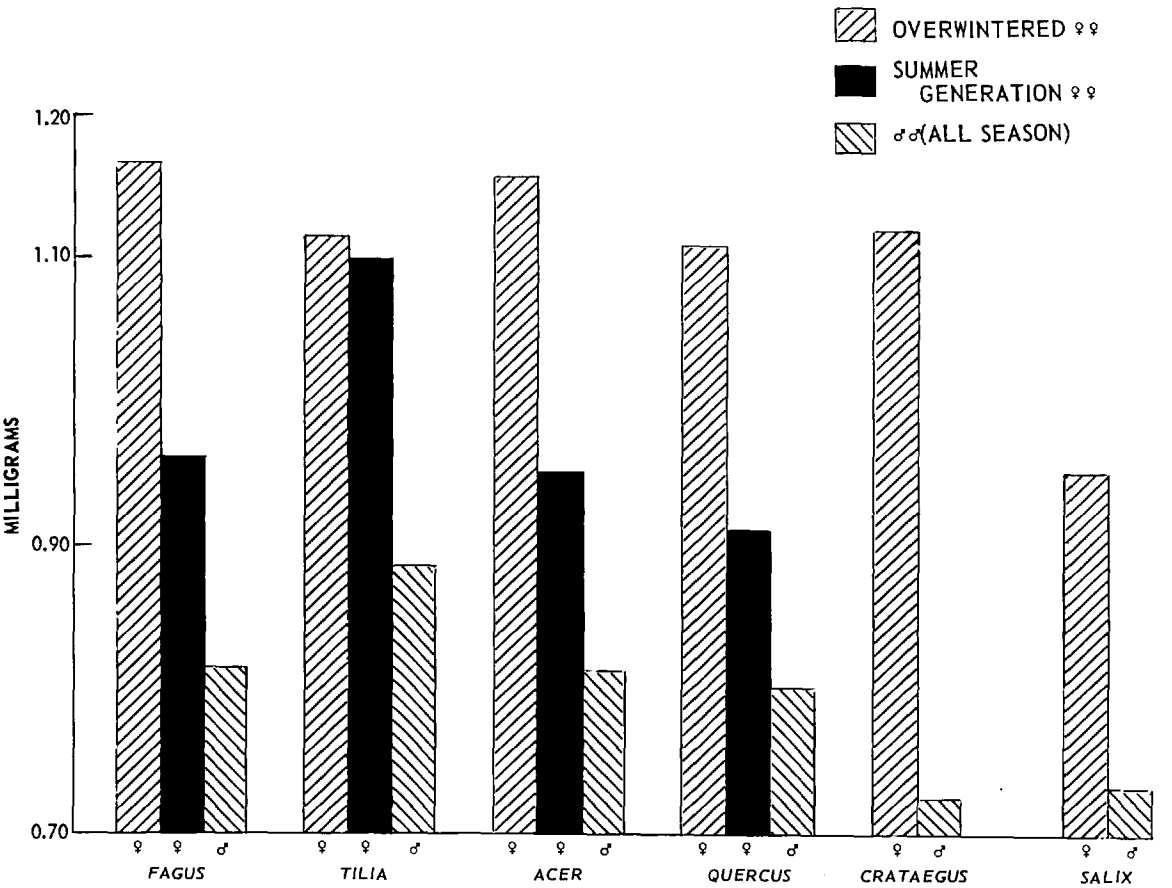



Fig. 13 Mean weights of *Anthocoris confusus* Reut. males and females on various tree, April to September, 1959.

TABLE 25. Sex ratio of Anthocoris confusus Reut. on the four primary host plants compared with other trees and herbs, July to September, 1960.

| | Males | Females | Ratio (♂♂ : ♀♀) |
|---|---|---|---|
| Primary trees | 3502 | 1605 | 2.18 : 1 |
| Other trees and herbs | 127 | 142 | 0.89 : 1 |

Table 26 gives the numbers of A. confusus and the sex ratio of adults in the weekly collections on the primary host plants from mid-July until the end of the season in both 1959 and 1960. About two-thirds of the population leaves the trees by mid-August. Judging by the scarcity of A. confusus on other plants after this time, it is concluded that most of these specimens have entered overwintering quarters.

TABLE 26. Total collections of Anthocoris confusus Reut. from the primary host trees. July to October, 1959 and 1960.

| | Larvae | | Males | | Females | | Total adults | | Sex ratio (♂♂ : ♀♀) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 | 1959 | 1960 |
| July 18 - 19 | 98 | 389 | 151 | 814 | 87 | 270 | 238 | 1084 | 1.74 : 1 | 3.01 : 1 |
| " 25 - 27 | 27 | 124 | 183 | 627 | 71 | 270 | 254 | 897 | 2.58 : 1 | 2.32 : 1 |
| Aug. 1 - 3 | 4 | 31 | 101 | 534 | 40 | 243 | 141 | 777 | 2.53 : 1 | 2.20 : 1 |
| " 8 - 9 | 6 | 13 | 115 | 319 | 17 | 158 | 132 | 477 | 6.76 : 1 | 2.02 : 1 |
| " 14 - 15 | 2 | 7 | 69 | 254 | 13 | 89 | 82 | 343 | 5.31 : 1 | 2.85 : 1 |
| " 24 - 25 | 0 | 3 | 23 | 154 | 4 | 39 | 27 | 193 | 5.75 : 1 | 3.95 : 1 |
| " 31 | 0 | - | 14 | - | 4 | - | 18 | - | 3.50 : 1 | - |
| Sept. 5 - 7 | 0 | 0 | 6 | 51 | 3 | 18 | 9 | 69 | 2.00 : 1 | 2.83 : 1 |
| " 14 | 0 | 0 | 13 | 22 | 2 | 6 | 15 | 28 | - | 3.67 : 1 |
| " 21 | 0 | - | 10 | - | 3 | - | 13 | - | | |
| " 28 | 0 | - | 10 | - | 1 | - | 11 | - | | |
| Oct. 5 | 0 | - | 2 | - | 2 | - | 4 | - | | |
| " 13 | 0 | - | 4 | - | 0 | - | 4 | - | | |
| " 19 | 0 | - | 0 | - | 1 | - | 1 | - | | |

Mean sex ratio after most of the larvae were mature: (August 15 to end of season), 1959 = 4.08 : 1; 1960 = 2.41 : 1.

Overwintering.

A major overwintering site of A. confusus is beneath the bark scales of Acer. More than 200 specimens were collected from this hibernaculum during two winters. Most of these were collected singly, but groups of two to four beneath a bark scale were quite common. Acer bark can be flaked off easily and a larger area can thus be searched than on other trees, hence the search for specimens was concentrated on Acer. Minor numbers were collected beneath bark scales on Malus, Fagus, and Aesculus, but none from Tilia, Quercus or Crataegus. None was collected in litter, dehisced Sarothamnus pods, or from sackbands on tree trunks.

Specimens collected and dissected during the winter had no food in the crop; the intestine and rectum were usually empty, but in some there were traces of a yellowish, granular material. Thus, apparently there is little or no feeding during the winter. Under artificial overwintering conditions, A. confusus can live for a considerable time on fat reserves. The mortality in a group of nine males and eleven females in a refrigerator for five months was four and one, respectively. Some of the females were starved for seven months without detriment.

The fat reserves in overwintered specimens are lowered but not exhausted by spring. Table 27 compares the weights of males and females in autumn, winter and at spring emergence. The table shows a significant weight decrease from autumn to late winter but this reflects a difference in gut content rather than a depletion of fat body because spring feeding again brings the weights almost to the autumn level. The spring

weight increase cannot be attributed to ovarial development because this does not start for some time after spring emergence.

TABLE 27. Mean weights of Anthocoris confusus Reut. adults in autumn, winter and spring.

| | Males | | Females | |
|---|---|---|---|---|
| | No. of specimens | Mean weight (mg.) | No. of specimens | Mean weight (mg.) |
| Autumn (Sept. 5, 1958) | 40 | 0.793 | 40 | 0.943 |
| Winter (Feb. 25, 1959) | 25 | 0.722 | 30 | 0.821 |
| Spring (Mar.27 - Apr. 27, 1959) | 30 | 0.777 | 30 | 0.932 |
| " (Mar. 24 - Apr. 28, 1960) | 30 | 0.771 | 33 | 0.929 |

The effects of depletion of the fat body are indicated by comparing the longevity of starved females in autumn and spring in Table 28. The fact that the overwintered specimens only lived half as long as the autumn specimens is attributed to lack of food reserves and not to senility because overwintered specimens that are feeding live two to three months after spring emergence. The females on leaves, as compared with those on filter paper, derived no nourishment from the plant substrate. Temperature records were not available for the autumn series, but the temperature would be at least as high as, if not higher than, the temperature in the spring.

If the autumn decline in early August is the commencement of overwintering (and not some unexplained mortality factor) then the duration of overwintering is seven to eight months, because the majority of adults do not appear in the field again until mid-April the following spring.

TABLE 28. Length of life of Anthocoris confusus Reut. females starved in autumn and spring, 1958-59.

| Date collected | Rearing temperature | Rearing conditions | No of specimens | Mean days lived |
|---|---|---|---|---|
| Sept. 5 | Lab. temperature | On filter paper | 8 | 32.8 |
| Sept. 5 | " " | On leaf | 9 | 33.2 |
| Late Feb., then kept at 34°F. until Apr. 7. | Mean = 62°F., Range = 48°-73°F. | On filter paper | 20 | 15.5 |
| " " " | " " " | On leaf | 20 | 15.7 |

## 4. Anthocoris sarothamni D.& S.

Douglas and Scott, 1865, separated this species from A. nemoralis on the basis of its small size, dark colour, and because it was confined to a single host plant, Sarothamnus scoparius (L.). A. sarothamni has been studied in conjunction with the rest of the insect complex on Sarothamnus by previous workers at Silwood Park (Sands, 1951; Smith, 1957; and Dempster, 1960), but the present work is the first detailed study dealing with the life-history of A. sarothamni. This species does not have a discrete hibernation period as do the other Anthocoris. The life-cycle is discussed in four intervals, but these intervals are not clearly demarkated in the field.

### Spring emergence and overwintered generation.

As A. sarothamni can be collected from its host plant at all seasons of the year, the exact date of spring emergence is difficult to determine. However, in 1960 the adults were observed to be numerous and active on the plants during the third week of March, and this period is, somewhat arbitrarily, designated as the termination of hibernation. The leaf buds on Sarothamnus were bursting, and psyllid and aphid eggs were hatching by this time.

Ovarial development at spring emergence and the progressive weight increase of females in the early part of the year are compared with other Anthocoris in Figs. 3 and 4. It is necessary to discuss the progress of ovarial development and weight increase starting in the overwintering period because both of these events commence long before the bugs become fully active in the spring. Dissections showed that

the majority of specimens collected on February 8 were fully fed and that ovarial development was surprisingly well advanced at that time. A few females contained one mature egg, while development in most females had progressed to the stage of opercular formation. Eighteen of twenty-two females dissected during February had some ovarial development.

The steady increase in weight of A. sarothamni females during February and March (Fig. 4) reflects maturation of the ovaries, not increased feeding, because the weight of males decreased slightly during the same period. The average male weights on September 19, February 8, and March 7, respectively, were: 0.735 mg., 0.719 mg., and 0.698 mg. Also, the size of the gut in females decreases, if anything, because when the ovaries mature they come to occupy most of the abdomen. Some females had mature ovaries as early as the first part of March and by early April practically all had fully developed ovaries. The continued weight increase after this time may be due to the death of small specimens.

A considerable proportion of males overwinter but most of them die early in the spring. The sex ratio of males to females in early February was 0.62 : 1, but it decreased to 0.25 : 1 by late March and then to 0.17 : 1 by April 21. Mating takes place in the autumn and most, if not all, of the overwintered females are fertilised. However, there is copulation again in the spring and probably also on warm days in the winter because adults mate freely when brought into the laboratory during the winter.

Spring copulation is unnecessary in the majority of cases for females to produce their full compliment of eggs. In an extreme case, a female laid 177 fertile eggs in the spring without pairing since autumn, and 10 others laid an average of 65 eggs without remating after they were collected in late February. However, two females that oviposited and then ceased for two and five weeks,respectively, started to oviposit again after another mating. Thus, males that survive the winter may be important in replenishing the sperm supply in the spring.

The spring oviposition period extended from late March to early May, by which time all overwintered adults had died. Incubation is slow at the temperatures experienced in March and April. The first eggs were found on March 22, but it was a full month later before first-instar larvae were collected. An incubation period of four weeks seems likely from the data in Table 29, where slightly over three weeks was found to be the incubation period at a temperature higher than that in the field. Eggs that were laid in the constant temperature cabinet ($74^{o}$F.) between March 30 and April 6 were incubated on a window-sill. Some of the eggs were held at $74^{o}$F. for 0 to 24 hours and others for 24 to 48 hours before being placed outside. Mean temperature on the window-sill was $5^{o}$F. higher than in a Stevenson screen. A. sarothamni eggs require a shorter incubation period than either A. nemorum (Table 3) or A. confusus (Table 22) eggs. Under the conditions described above, the mean incubation period for eggs held at $74^{o}$F for 0 to 24 hours and then placed on the window-sill, for the three species, respectively, was: 19.1, 21.3, and 28.3 days.

TABLE 29. Incubation period of Anthocoris sarothamni D. & S. eggs laid in a constant temperature cabinet, then subjected to normal diurnal temperature fluctuations. Mean temperature, 53°F. March 31 to May 1, 1960.

| Number of eggs | Incubation at 74°F. (hours) | Total incubation (days) Range | Mean |
|---|---|---|---|
| 15 | 0 - 24 | 15 - 24 | 19.1 |
| 14 | 24 - 48 | 10 - 18 | 15.3 |
| 40 | Continuous | 4 - 5 | 4.7 |

Spring and summer generations.

The population of A. sarothamni in the sample plot in the spring of 1959 was too small to obtain details of the life-cycle. During the summer there was an increase in population, and in 1960 there were sufficient numbers to obtain the data given in Fig. 14. A. sarothamni breeds only on Sarothamnus. No criteria were found for distinguishing the first- and second-instar larvae of A. sarothamni and A. nemoralis so it was necessary to rear the larvae from the samples until they could be identified. As the young larvae are delicate, many were injured while collecting, or were killed by older specimens. These were assigned to a species on the basis of size. A. nemoralis is larger than A. sarothamni but the size range overlaps. It is probable that some of the former were counted as A. sarothamni. The difficulty in distinguishing the two species only lasts for two to three weeks in May. A. nemoralis breeds very sparingly on Sarothamnus during the summer, so the problem does not occur at that time.

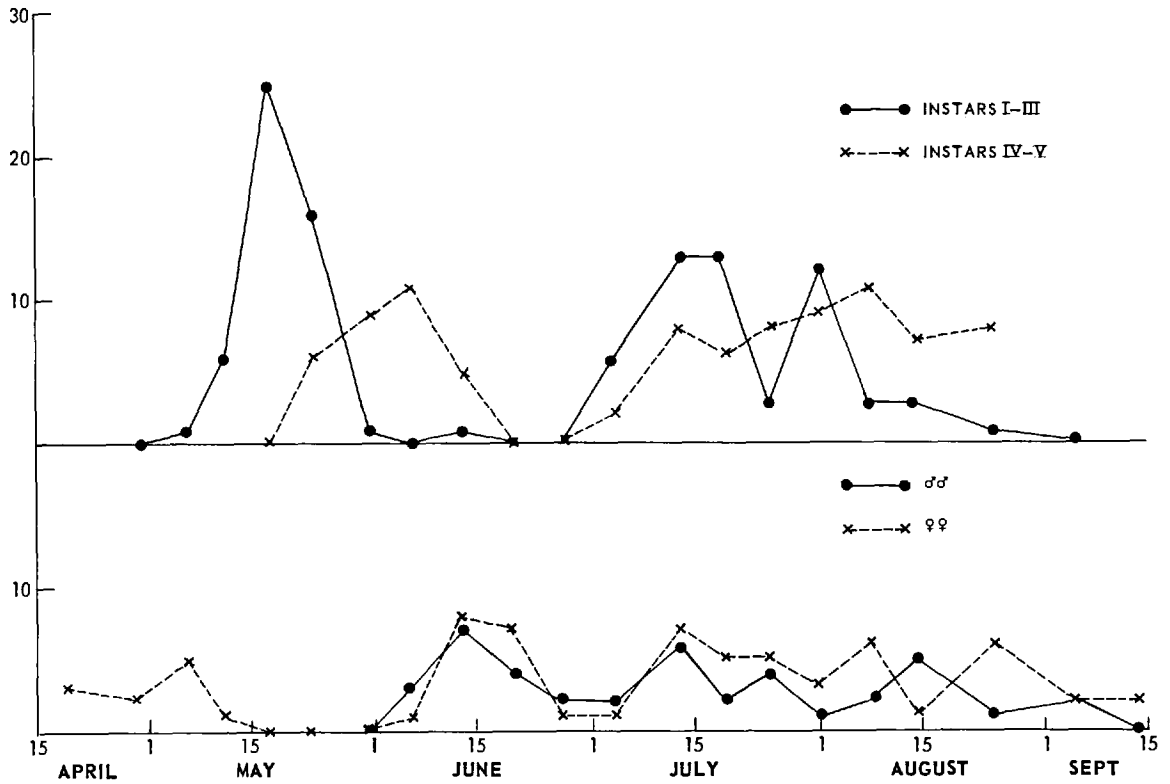



Fig. 14. Number of *Anthocoris sarothamni* D. & S., larvae and adults, in weekly collections from *Sarothamnus*, April to September, 1960.

A. sarothamni was not the dominant breeding population on Sarothamnus during this study. In the spring of 1959 it was overshadowed by both A. nemoralis and A. nemorum; in the summer of both years by A. nemorum; and in the spring of 1960 by A. nemoralis. Sands, 1951, stated that it lives in company with equal numbers of A. nemoralis and fewer A. nemorum, while Dempster, 1960, found that A. nemorum outnumbered A. sarothamni on Sarothamnus in 1957 and 1958.

There is considerable variation in the start of larval emergence. Larvae were first found at Silwood Park in 1960 on April 21, but in the sample plot the first larva was collected on May 6. Peak emergence occurs in mid-May and adults appear in early June. Thus the period of larval development almost coincides with that of A. nemoralis.

The second generation commences in early July and larvae are present until late August (Fig. 14). The generations appear to be clearly demarkated because very few larvae were collected in the last two weeks of June in either 1959 or 1960.

The life-cycle of A. sarothamni is associated with the occurrence of the two psyllids, Psylla spartiophilus and Arytaina genistae. The aphid Acyrthosiphon spartii, is also preyed upon to some extent (Sands, 1951 and Smith, 1957), but the present investigation indicates that the psyllids are the major prey. The period of abundance of the broom aphid, from late May to early July, does not coincide with the life-cycle of A. sarothamni. On the other hand, the spring generation of A. sarothamni is in phase with the time of larval occurrence of the two psyllids. P. spartiophilus larvae are abundant from late March until the end of May,

and the adults remain on Sarothamnus until the latter part of June. A. genistae, which overwinters as adults, oviposits from early spring until late April, and first-generation larvae are present until July. Usually there is a second, overlapping generation so there are some larvae present throughout the summer.

There are two distinct colour forms of A. sarothamni larvae. Sands, 1957, described the fifth-instar larva as "dark olive-brown to greenish-black (with) the first two abdominal tergites .....slightly paler". This is the usual colour of the spring-generation larvae, but during the summer many specimens were distinctly paler. These specimens were bi-coloured with yellow, or yellow-grey areas on the head, prothorax, wing-pads, and the first two abdominal tergites, and the remainder of the dorsum and appendages were dark brown or black. The colour patterns of the two forms are illustrated in Fig. 15.

The light-coloured form seems to be associated with high temperatures. Most of the specimens reared in the laboratory at 74°F. were of this form, and it was only found in the field during the hottest part of the summer. In Scotland, where the summers are cooler than in Southern England, Dr. A.R.Hill has not observed this form (personal communication). Baraud, 1955, states that temperature, humidity, illumination and the diet can influence the colour of insects. Knight, 1924, found that, with Perillus bioculatus (Fab.), pale forms owe their colour to high temperatures while darker forms are produced during periods of low temperature.

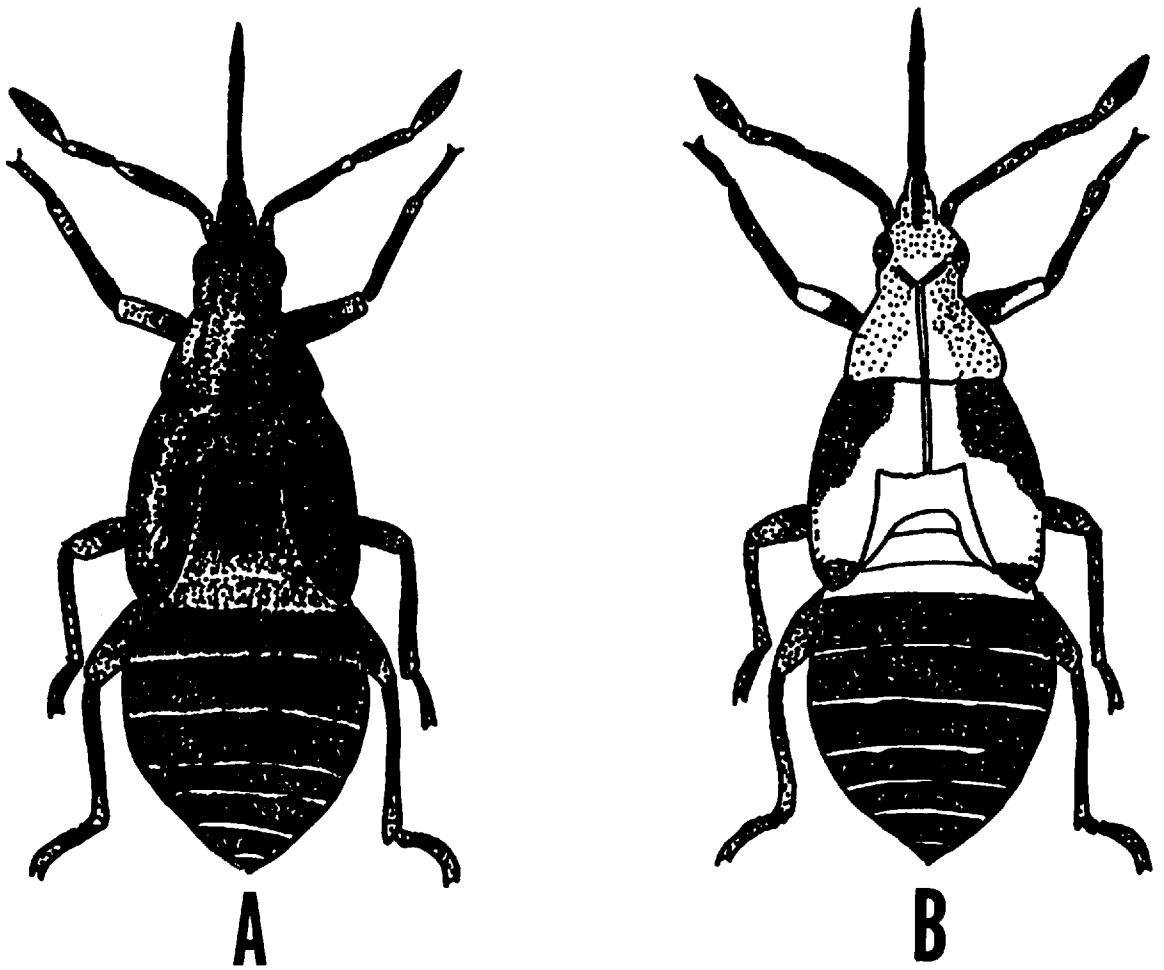



Fig. 15. Variation in colour pattern of *Anthocoris sarothamni* D. & S. fifth instar larvae: A. Normal, dark form (after Sands, 1957); B. Variant obtained in laboratory rearing and from the field in July and August.

Pre-hibernation period.

Hitherto it has been accepted that A. sarothamni is confined to Sarothamnus. However, during the present study, a number of adults were collected from other trees, Urtica, and grasses (Table 1). There was a distinct dispersal commencing at the end of the first generation in early June, 1960. Adults were common on trees and shrubs adjacent to a plantation of Sarothamnus (not the sample plot) at Silwood Park from June until September. The largest numbers were collected on Ulmus bushes, where 267 specimens were collected in 11 weekly samples. No specimens were collected from these bushes in 1959. Forty-two adults were collected from an adjacent Acer in 1960, but only nine in 1959. Five adults were collected during June and July 1960 from a suction trap located about 100 yards from the plantation; only two adults were collected in 1959.

The plantation was not available for sampling in the present study, but it is known that an exceptionally large breeding population was present in the spring of 1960. The reason for the dispersal of A. sarothamni from this location at the end of the spring generation becomes apparent from the records kindly provided by Prof. O. W. Richards, Dr. N. Waloff and Dr. J.P.Dempster, on psyllid abundance in 1959 and 1960. Table 30 compares the mean number of P. spartiophilus and A. genistae larvae for 1959 and 1960. There was a moderate number of psyllids in the early summer of 1959 and a second generation of A. genistae in July and August. In 1960, the numbers of P. spartiophilus were exceptionally high and there was also a moderate first generation of A. genistae. However, the summer

generation of A. genistae virtually failed, resulting in a dispersal of A. sarothamni from the Sarothamnus. It thus seems probable that the size of the summer generation of A. genistae is a factor regulating the numbers of A. sarothamni.

TABLE 30. Mean numbers of psyllid larvae per 100 grams of Sarothamnus in the plantation at Silwood Park. May to August, 1959 and 1960. (Unpublished data, Richards, Waloff and Dempster).

| | 1959 | 1960 |
|---|---|---|
| May | 42.1 | 783.6 |
| June | 32.1 | 10.6 |
| July | 11.2 | 0.1 |
| August | 6.5 | 0.2 |

Table 31 compares the condition of ovaries of females collected on Sarothamnus, Urtica and Ulmus, after the completion of the first generation. Some of the specimens collected on Sarothamnus were probably too teneral for ovarial development to have commenced, but three of the 14 had fully-developed fat bodies and immature ovaries, indicating reproductive diapause. Practically all specimens from Ulmus were in reproductive diapause; this suggests that they were on Ulmus for pre-hibernation feeding on jassids. The females from Urtica appear somewhat intermediate, and some may have returned to Sarothamnus to produce a second generation.

TABLE 31. Condition of ovaries in Anthocoris sarothamni D. & S. females collected on Sarothamnus, Urtica and Ulmus. June 20 to July 18, 1960.

| | Number dissected | No ovarial development | Mature, or developing ovaries |
|---|---|---|---|
| Sarothamnus | 14 | 8 | 6 |
| Urtica | 10 | 6 | 4 |
| Ulmus | 40 | 37 | 3 |

Overwintering.

There was an exceptionally large population of A. sarothamni in the Sarothamnus plantation at Silwood Park in 1959. This afforded an opportunity to obtain records of the overwintering habits of a species that is usually rather scarce. This species occurs on Sarothamnus throughout the year, hence the duration of hibernation cannot be reckoned as the time between the autumnal decline and their return to the host plant in the spring.

The major hibernation site of A. sarothamni is in the curled pods that remain on the bushes throughout the winter. This was proved by a comparison between collections, in mid-February, from bushes with numerous pods and bushes with few pods. In addition, litter samples from beneath the bushes were examined for A. sarothamni (Table 32). Some of the bugs were collected on the beating sheet but the majority were obtained when the samples were brought into the laboratory and the higher temperatures induced activity.

TABLE 32. Numbers of hibernating Anthocoris sarothamni D. & S. adults collected from the Sarothamnus plantation, February, 1960.

| | Males | Females |
|---|---|---|
| Ten bushes with numerous pods | 14 | 13 |
| Ten bushes with few pods | 3 | 3 |
| Litter samples from beneath bushes | 1 | 0 |

There is some circumstantial evidence that a portion of the population overwinters away from the host plant. Butler, 1923, gives a record of A. sarothamni being collected from a dead fir hedge in

winter. The records of dispersal in 1960 have been given in a previous section; in addition, several adults were collected from other trees in September and October, 1959. It is probable that at least some of these specimens would overwinter before returning to Sarothamnus. The population level in autumn, winter and spring also suggests that there is a migration of females to Sarothamnus from other sources in early spring. The following numbers of females were collected in samples from 20 bushes: autumn, 29; winter, 29; and spring (March 21), 50, (March 31), 42.

The condition of the gut showed that feeding takes place during the winter. The possible prey include A. genistae adults, psyllids, mirid and aphid eggs, plus smaller numbers of other insects hibernating in the pods. The colour of the gut was a deep orange, which is typical of feeding on psyllids. A. genistae adults are suspected to be the major prey during the winter.

## 5. Anthocoris gallarum-ulmi (DeG.).

A. gallarum-ulmi is known only to breed in the curled leaf-galls produced by Eriosoma ulmi on Ulmus. Southwood and Leston, 1959, state that it is found infrequently in aphid galls on Fraxinus, Prunus, Ribes and Crataegus, but presumably these records are for adults. A. gallarum-ulmi was not common at Silwood Park in 1959; overwintered adults were present in the spring, but the host aphid population was insignificant and no larvae of A. gallarum-ulmi were collected. E. ulmi was relatively abundant in 1960 and supported sufficient numbers of A. gallarum-ulmi to make a field study possible.

### Spring emergence and overwintered adults.

Cobben, 1958, stated that, in Holland, the adults of this species emerge in early April, and my results are in close agreement; it was first collected on April 13 in 1959, and on April 12 in 1960. This species does not aggregate on Ulmus immediately after spring emergence, probably because E. ulmi does not become numerous until early May. During this investigation A. gallarum-ulmi was collected in April from Salix, Acer, Quercus and Sarothamnus in addition to Ulmus.

Both Cobben, 1958, and Southwood and Leston, 1959, report that mating occurs in the spring. In view of the habits of other Anthocoris, it is probable that most of the females are mated the previous autumn. The total numbers of overwintered specimens collected in April and May in the two years of this study were three males and 17 females. This disproportionate sex ratio strongly suggests pre-hibernation mating.

At the time of emergence there is at least slight ovarial development in A. gallarum-ulmi females (Fig. 3). Some females have mature ovaries by the end of April. By this time A. gallarum-ulmi has aggregated on Ulmus and the galls of E. ulmi are becoming evident. Larvae occur about the end of May; Southwood and Leston, 1959, reported larvae in the last week of May, and in 1960 they were first collected on May 25. The overwintered females die off about the middle of June. No overlap of generations was noted in 1960.

Summer generation.

In 1960, a sample of curled Ulmus leaves was taken at weekly intervals from late May until July and examined for A. gallarum-ulmi and aphids. This method was superior to the weekly samples obtained by beating because it gave a uniform collection unit, and also because beating fails to dislodge many of the larvae and adults from within the curled leaves. A total of 150 galls contained 139 anthocorids, while six 10-minute beating samples during the same period produced only 11 specimens.

Larval development of this species is rapid (Fig. 16A). The earliest summer-generation adults were found on June 20, or only three to four weeks from when the first larvae occurred. Cobben, 1958, found new adults in June, but Southwood and Leston, 1959, report a slightly later date (early July) for the summer-generation adults. They also found larvae as late as the first week of August, but in 1960 the latest larvae occurred in early July.

The numbers of A. gallarum-ulmi per gall are graphed in Fig. 16B. Over half of the galls contained no anthocorids at the time of sampling although in many cases the galls had been abandoned after the food supply was exhausted. This was indicated by the presence of exuviae in some galls. The maximum number of larvae found in a gall was nine. Aggregation results from two factors: (a) eggs are often laid in groups of three to six in the mid-rib or petiole, and (b) when the number of galls containing aphids decreases, then the number of Anthocoris per gall tends to increase. The percentage of galls containing E. ulmi dropped rapidly during June (Fig. 16C) as a result of predation combined with dispersal by alate aphids. Many A. gallarum-ulmi larvae were collected in galls that contained no aphids. It is suspected that these were obtaining a maintenance diet by feeding on honeydew, but would eventually leave the gall in search of aphids. Reuter, 1884, and Cobben, 1958, reported that A. gallarum-ulmi feeds on aphid secretions and this was verified in the present study. However, the larvae also require some animal protein for growth (see p.137).

Pre-hibernation period.

Cobben, 1958, and Southwood and Leston, 1959, could find no proof of a second generation of this species. It is concluded from the present work that A. gallarum-ulmi is entirely univoltine. No trace of a second generation was found in the field. All females dissected after June had immature ovaries and females reared in the laboratory did not oviposit although mating took place (p.170).

After the adults mature in June or July they disperse from Ulmus and can be collected sporadically from many species of plants (Table 1). There is no further reproduction of E. ulmi on Ulmus so during the summer the adults of A. gallarum-ulmi must build up their fat reserves by feeding on other prey.

No data were obtained on the period when this species enters hibernation.

Overwintering.

Only six specimens of A. gallarum-ulmi, five males and one female, were collected in hibernation. All of these were collected under bark scales on Acer. Cobben, 1958, only found this species hibernating under bark scales on Platanus in Holland although several other trees with suitable bark were searched.

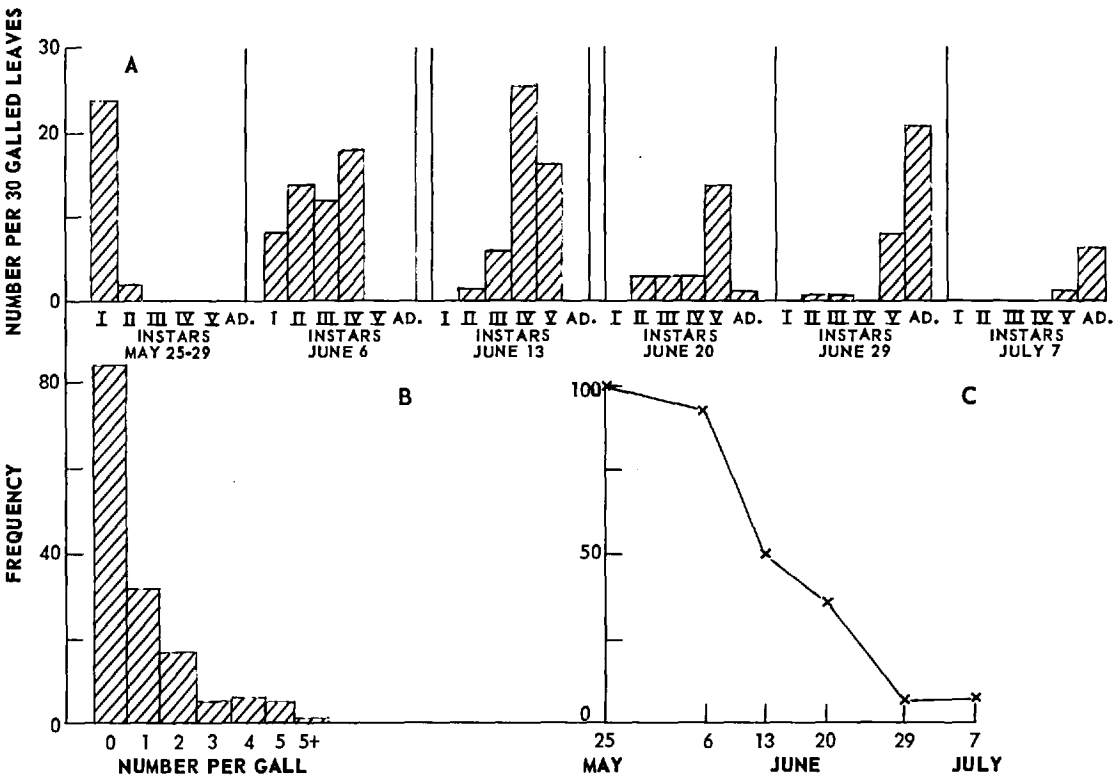



Fig.16. A. Number of *Anthocoris gallarum-ulmi* (DeG.), larvae and summer generation adults, collected in samples of galled *Ulmus* leaves, May to July, 1960.

B. Frequency distribution of *A. gallarum-ulmi* per gall.

C. Percentage of galls containing live *Eriosoma ulmi* (L.), May to July, 1960.

## 6. Anthocoris minki Dohrn

This species was first recorded in England in 1954, when LeQuesne described it as A. confusus chinai. Subsequently, he recognised it as being the European species, A. minki (LeQuesne, 1958). Nothing is known of the biology, except that it is restricted to Fraxinus, although there are a few records of adults being collected from Acer and Ulmus (LeQuesne, 1954; Southwood and Leston, 1959). A single male of this species was collected at Silwood Park in the autumn of 1958. No specimens were collected in the spring of 1959, but in July a large Fraxinus was found that harboured a fair population of A. minki so this species was studied from July, 1959 to September, 1960.

Spring emergence and overwintered generation.

Overwintered adults were first collected on Fraxinus on April 7, 1960. The ovaries of these females were completely undeveloped (Fig. 3). A. confusus is the only other species that has undeveloped ovaries at spring emergence. Twenty-six overwintered adults were collected from April to June; all of these were females.

A. minki first occurred on Fraxinus when the male flowers were dehiscing. Insect prey is extremely scarce at this time: only mirid eggs and first-instar larvae, and a few psocids were collected. No psyllid eggs were seen, but Lal, 1934, states that they are concealed in the buds, and it is possible that A. minki could feed on these.

Psyllid eggs began to hatch at bud burst in the last week of April, providing a plentiful supply of preferred prey for A. minki. Two of three

females dissected at this time had mature ovaries, while the third was undeveloped. The first eggs were found on May 16, but in view of the previous statement, oviposition probably started in early May. Eggs hatched in late May, which suggests an incubation period of three to four weeks. There was a short interval between the time when the last overwintered adults were collected on June 13, before the new generation adults occurred.

Summer generation.

The life-cycle of A. minki, as studied in 1960, is graphed in Fig. 17. The first larvae were collected on May 31, but as two specimens were already third instar, hatching apparently started about the middle of May. Peak abundance of larvae occurred one month later, and the first summer-generation adult was collected on June 20. The adult population reached a maximum during the second week of July when practically all the larvae had matured.

Fig. 17 indicates that there was only a single generation of A. minki in 1960. Twenty females dissected between June 27 and July 12 all had immature ovaries. However, four larvae were collected during August and September in 1959, and again in 1960 some larvae were collected in August from Fraxinus outside the sample area. Thus it is possible that under exceptional circumstances a partial second generation is produced.

The life-cycle of A. minki is closely correlated with the occurrence of the larvae of Psyllopsis fraxinicola, the predominant insect on Fraxinus in this area. P. fraxini (L.) also occurred on the same trees but in much

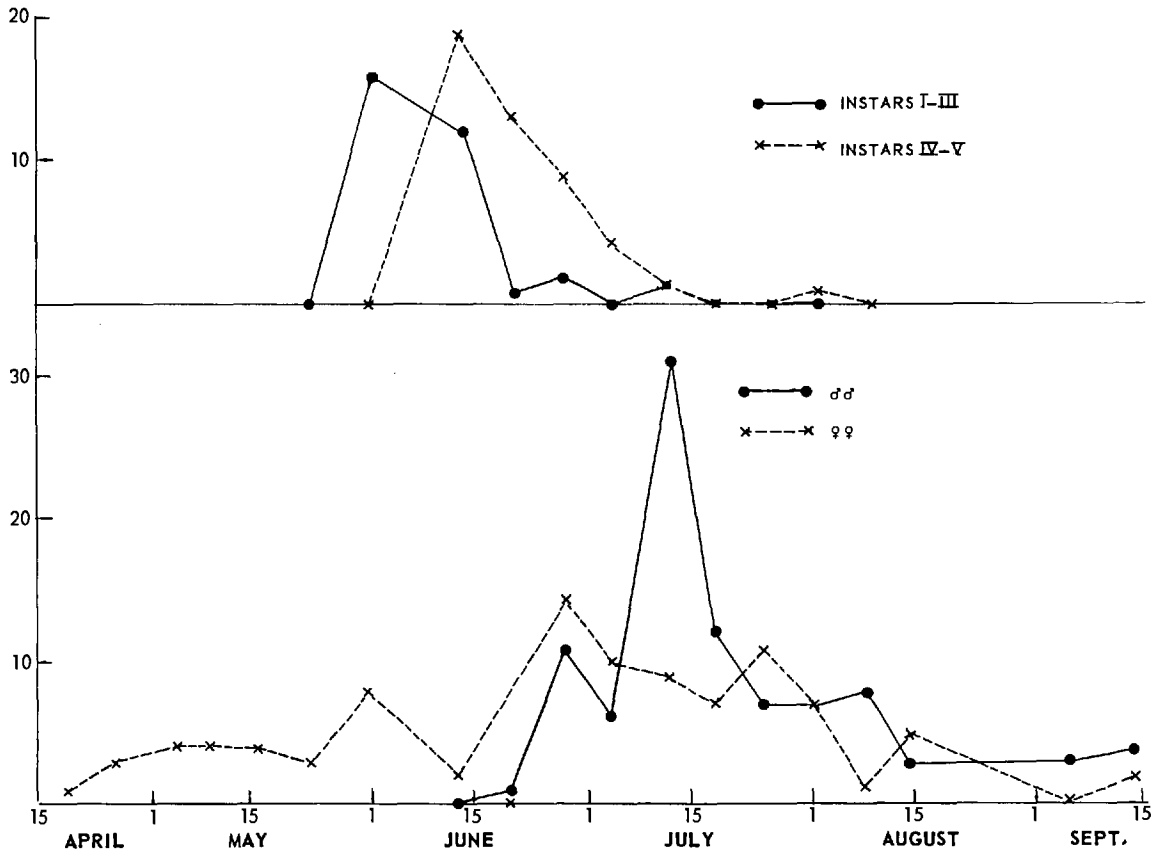



Fig. 17. Number of *Anthocoris minki* Dohrn, larvae and adults, in weekly collections from *Fraxinus*, April to September, 1960.

smaller numbers. A. minki eggs are laid about two weeks after the psyllid eggs start to hatch. The larvae of A. minki emerge while the psyllids are still early-instar larvae. Both the prey and the predator complete larval development by mid-July. If there is a second generation of A. minki, they would have to feed chiefly on adult psyllids.

Lal, 1934, stated that in Scotland P. fraxinicola causes damage to Fraxinus. It produces characteristic, copper-coloured galls formed by the involution of the margins of the leaves. This type of damage was present, but uncommon, at Silwood Park. Most of the early-instar psyllid larvae occurred in clusters along the mid-rib, enveloped in a cottony secretion. The older larvae were less gregarious. A. minki larvae were present in most of the curled leaves that were examined. Lal, 1934, reported earwigs, capsids, thrips and spiders as occurring in the psyllid galls, but he does not mention any Anthocoris.

Pre-hibernation period.

As indicated in Table 1, A. minki was only collected from Fraxinus at Silwood Park. This does not necessarily mean that it is less dispersive than other Anthocoris because very few collections were made from trees adjacent to Fraxinus. However, A. minki was collected from its host plant throughout the summer and autumn, so unlike A. gallarum-ulmi, it does not entirely leave its host plant after the breeding season. A.minki was present on Fraxinus when sampling ceased in October, 1959, but the numbers had decreased markedly since early September, so most of the population was in hibernation by October. The sex ratio during late summer and autumn was 1.71 : 1 in 1959, and 1.41 : 1 in 1960.

Overwintering.

Only one specimen of A. minki was collected during the winter of 1959-60; a male obtained from litter beneath Fraxinus on February 19. Several other samples from the same location were searched without success. No specimens were found under Fraxinus bark, or on neighbouring trees. In view of the relative scarcity of the host tree, and consequently a low absolute population of A. minki, it is not surprising that only one specimen was found in hibernation.

## Summary of life-histories of *Anthocoris* spp.

The life-histories of the six species of *Anthocoris*, based on studies in 1959 and 1960, are compared diagramatically in Figs. 18, and 19. A short account of the life-history of each species is given below.

*A. nemorum*.

This ubiquitous predator has two generations per year in Southern England, although it is reported to have three in Southern France (Bonnemaison and Missonier, 1956), and only one in Scotland (Hill, 1957). The adults that overwinter are chiefly female; they emerge from hibernation in mid- to late March and aggregate especially on *Salix*. The population gradually disperses to other plants as these leaf out and become inhabited with suitable prey. Oviposition commences in mid-April, larvae occur about one month later, and the first adults occur in the latter half of June. There is an overlap of generations in late June and early July. Second-generation larvae are present from July to October. The extreme length of the generations is due to an extended oviposition period and variability in larval duration. *A. nemorum* hibernates in a variety of sites, such as under bark scales, in litter, in plant stems and similar protected niches.

*A. nemoralis*.

This species is usually considered to occur on a wide range of trees. However, the present study indicates that it breeds primarily on trees infested with psyllids. *A. nemoralis* leaves hibernation at the same

time as does A. nemorum and it also aggregates on Salix before the main dispersal to other trees. The larvae develop faster than A. nemorum larvae; spring-generation adults occur at the end of May or early June, and most of the population has matured by the third week of June. The primary spring host plants are practically abandoned during post-teneral flights in June when the adults disperse to trees heavily infested with aphids. A small second generation is produced. Tilia was the only tree sampled in the present study that harboured a significant number of second generation larvae. Most of the adults of this species apparently enter overwintering sites in July and August but a few are still present on trees in October.

A. confusus.

A. confusus is semi-restricted in its breeding sites; over 90 per cent of the larvae were collected from Fagus, Tilia, Quercus and Acer. All of these trees are infested with callaphidid aphids. A. confusus emerges from overwintering slightly later than A. nemorum or A. nemoralis and it does not start to oviposit until early May, or almost one month later than the other two species. Larvae are present from the end of May until mid-August. These larvae are predominantly all of one generation but a few of the earliest adults that mature in June oviposit so there is a trace of a second generation. Most adults enter hibernation in late August or September but a few can be collected on trees in early October. A favoured hibernation site is under bark scales on Acer.

A. sarothamni.

This species hibernates in the dehisced pods that remain on Sarothamnus bushes and probably also beneath the bark-scales of other trees. The adults are active and feed during warm days in the winter and ovarial development is well advanced at the time of spring emergence. Oviposition commences in late March and larvae first occur about four or five weeks later. The period of larval development coincides with that of A. nemoralis; peak emergence occurs in mid-May and adults appear in early June. A second generation of larvae occurs during July and August. The size of this generation is apparently determined by the proportion of first generation females that reproduce instead of entering reproductive diapause. Psyllids on Sarothamnus comprise the chief prey of A. sarothamni; if the numbers of prey are low when the spring-generation adults mature then the size of the second generation of A. sarothamni is correspondingly reduced.

A. gallarum-ulmi.

This species breeds in the curled leaf galls formed by Eriosoma ulmi on Ulmus. It emerges from hibernation (apparently chiefly under bark scales of Acer) in mid-April. Oviposition occurs during May when the galls are forming. Larvae were only present from late May until early July in 1960. There is a single generation of A. gallarum-ulmi per annum. The adults disperse from Ulmus during June and July and can be collected sporadically from other trees until August.

A. minki.

A. minki leaves hibernation sites and returns to its host plant, Fraxinus, in early April. The primary prey, Psyllopsis fraxinicola, emerge from overwintered eggs in late April and A. minki starts to oviposit shortly thereafter. Larvae of the first generation are present from mid-May until mid-July. There may be a small second generation of this species from July until September but this is improbable because the only prey available would be adult psyllids. A. minki adults are present on Fraxinus throughout the autumn but the numbers gradually decrease during September and October.

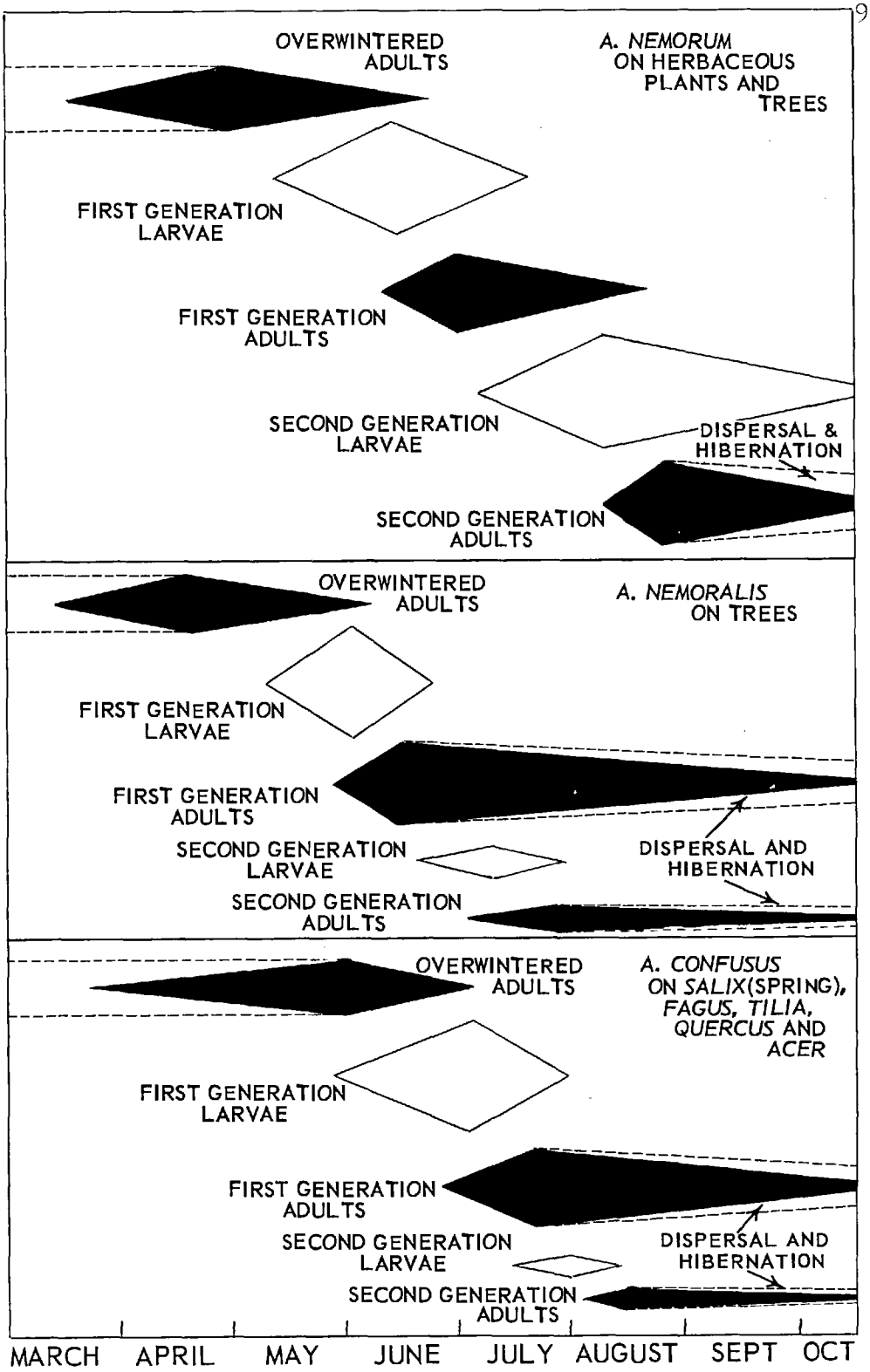



Fig. 18. Seasonal life-histories of Anthocoris nemorum (L.), A. nemoralis (Fab.), and A. confusus Reut. Based on studies at Silwood Park, Berkshire, 1958 to 1960.

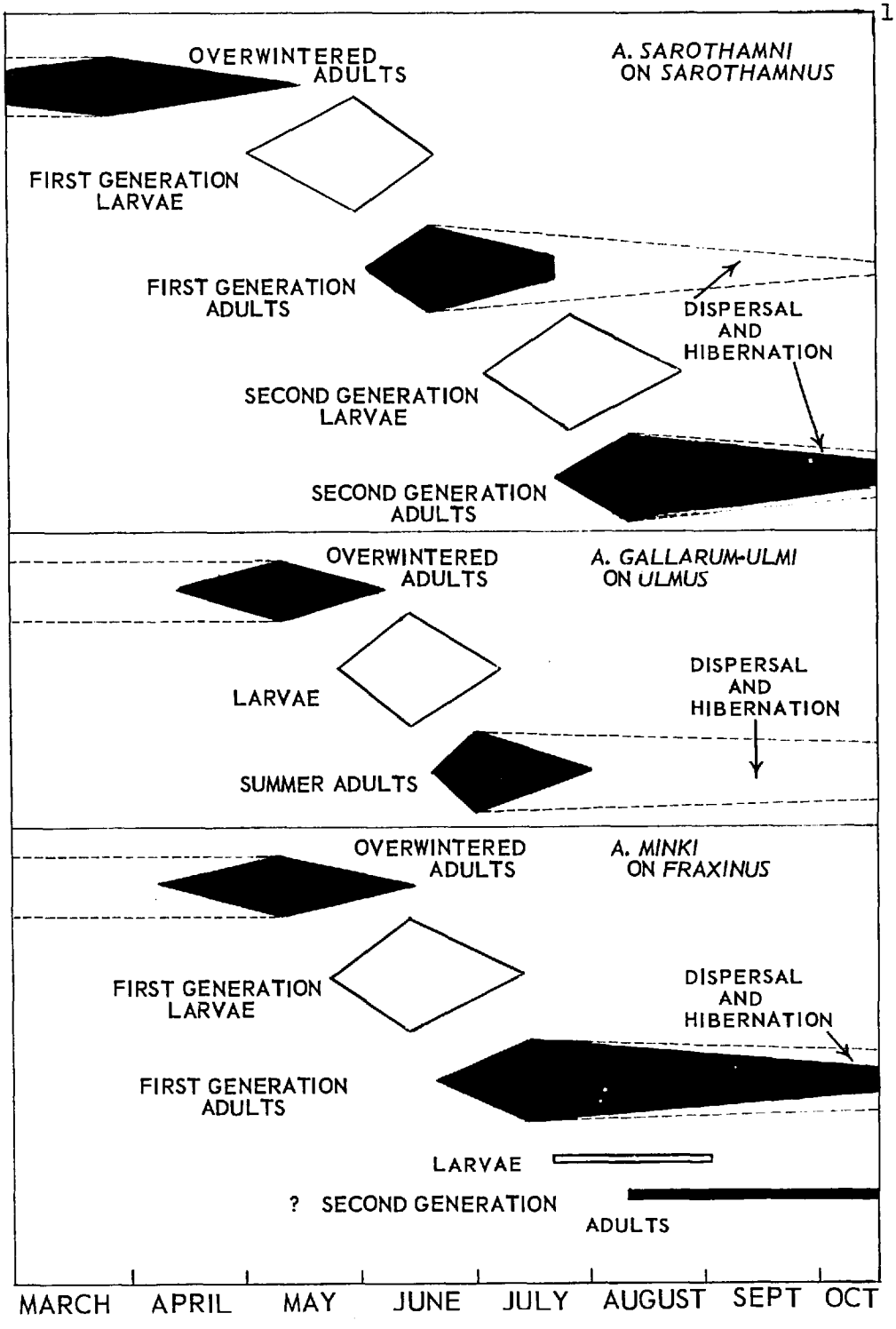



Fig. 19. Seasonal life-histories of Anthocoris sarothamni D. & S., A. gallarum-ulmi (DeG.), and A. minki Dohrn. Based on studies at Silwood Park, Berkshire, 1958 to 1960.

## RESULTS: PART II. LABORATORY STUDIES OF *ANTHOCORIS* SPP.

### 1. Breaking Reproductive Diapause.

Most *Anthocoris* have a facultative reproductive diapause, according to the definition of Lees, 1955, because they have more than one generation per year, but the number and size of the generations is dependent on extrinsic factors. Research workers who have studied *A. nemorum* in Britain have experienced difficulty in rearing continuous generations because autumn-collected specimens cannot be induced to oviposit. However, specimens collected in late winter will oviposit normally in the laboratory after one to two weeks pre-oviposition period (Mr. C. Muir, Dr. E. Collyer, and Dr. A.R.Hill, personal communication). *A. antevolens* was found to have a reproductive diapause in North America; it would, however, oviposit when collected from the field in late January (Anderson, unpublished).

A study of reproductive diapause is beyond the scope of this thesis; indeed, it is not particularly relevant to the major theme of the study. However, it was desirable to rear anthocorids during the winter so that larval feeding tests could be conducted when field studies were not in progress; attempts were made to induce oviposition in early winter. Some success was achieved along these lines, and, although the precise stimuli have not been elucidated, the data are presented as a contribution towards solving the problem.

A. nemorum.

Attempts to induce oviposition with this species were made in September and October 1958. Ten females fed on Aphis fabae all died without ovipositing. Two females collected on October 27 were fed on Rhopalosiphum insertum (Walker); one laid 12 eggs after a pre-oviposition period of 39 days. A further attempt was made to obtain eggs in late December, using specimens collected from hibernation. Sixty per cent of the specimens oviposited after pre-oviposition periods of seven to 12 days in the constant temperature cabinet (74°F., and continuous illumination). This experiment indicated that the dormant period could be broken after exposure to normal winter temperatures for about three months.

A further experiment was set up in September, 1959 in an attempt to break diapause. Twenty females collected on September 17 were weighed, placed with males in individual tubes embedded in saturated plaster of Paris, and starved for 25 days in the constant temperature cabinet. At the end of this period, half of the females had died; the other 10 were re-weighed and placed in rearing cages with Aulacorthum circumflexum as food. The females that survived starvation were heavier than those that died; the mean weight of the former was 1.546 mg. as compared to 1.463 mg. for the latter. Weight loss during starvation averaged 14.0 per cent, which is slightly less than the 16-17 per cent weight loss determined for over-wintering period (Table 9).

The oviposition and longevity of the above specimens are compared in Table 33 with a control series of four females collected on October 17 and fed from that date. Reproductive diapause was broken in 70 per cent

of the specimens, although one of these did not oviposit. Mean egg production of 41 eggs per female is considerably lower than normal, but this may in part be due to the rather drastic combination of high temperature and starvation. Two of the four control specimens oviposited 30 and 10 eggs after pre-oviposition periods of 12 and 27 days, respectively. It should be emphasised that these specimens were collected one month later than the starved series, and hence may have had an additional month of a dormant period in the field.

The above experiment has conclusively demonstrated that reproductive diapause in A. nemorum can be broken in early autumn at 74°F. by starvation for three to four weeks, followed by feeding on a suitable host insect. No period of low temperature is required. The lack of an adequate control experiment precludes definite conclusions on the necessity of the starvation period. If it is required, further experiments on the optimum length of the period would be a fruitful line of research.

A. confusus and A. nemoralis.

An attempt was made to obtain eggs from about 40 specimens in the autumn of 1958. Unfortunately, the feeding habits of these species were unknown at the time and the aphid used, A. fabae, has since been shown to be completely unsuitable as food. Insufficient numbers were available in the autumn of 1959 for further experiments on breaking of diapause. Eggs were obtained from 9 specimens that survived two treatments: (a) six specimens fed on A. fabae for one to three months and then transferred to a suitable prey, and (b) three females that survived in a starvation

TABLE 33. Oviposition of Anthocoris nemorum (L.) females collected on September 17, 1959. Starved for 25 days, then fed Aulacorthum circumflexum (Buckt.) Continuous light and 74°F. range 72-76 F.

| Specimen | Preoviposition (Days) | Total eggs | Days lived after feeding commenced | Remarks |
|---|---|---|---|---|
| 1 | 5 | 78 | 25 | |
| 2 | 8 | 48 | 20 | |
| 3 | 9 | 50 | 23 | |
| 4 | 9 | 13 | 13 | |
| 5 | 10 | 40 | 20 | |
| 6 | 11 | 17 | 21 | |
| 7 | - | 0 | 13 | 4 mature eggs in ovaries. |
| 8 | - | 0 | 7 | No ovarial development |
| 9 | - | 0 | 26 | " " " |
| 10 | - | 0 | 39 | " " " |
| Controls: collected on Oct. 17 and fed from that date. | | | | |
| 1 | 12 | 30 | 22 | |
| 2 | 27 | 10 | 36 | |
| 3 | - | 0 | 10 | No ovarial development. |
| 4 | - | 0 | 21 | " " " |

experiment and were fed on a suitable prey after three to six weeks.

These bugs oviposited in four to eight days after feeding on suitable prey. A. confusus can be reared through continuous generations during the spring and early summer with pre-oviposition periods of about one week (p.171).

These results are similar to those obtained for A. nemorum, and show that diapause can be broken without a period of low temperature. However, it is also possible that the percentage of specimens that

oviposited would also have done so if they had been fed on a suitable prey from the start of the trials.

A. sarothamni.

Limited success was achieved in breaking reproductive diapause of A. sarothamni in October, 1959. Three of five females developed eggs within 20 to 30 days after field collection when kept at 74°F. The maximum egg production was only nine, but the females were fed on A. circumflexum. If a more suitable prey had been available, egg production would possibly have been more normal.

## 2. Larval Rearing Studies.

The majority of the laboratory studies were concerned with rearing of larvae under various conditions of amount and type of food. A. nemorum was chiefly used for the basic studies because it is the most common species. It proved to be an unfortunate choice in some respects as it is not typical of the genus and it is not the easiest species to rear. Once the initial difficulties (obtaining oviposition and determining suitable prey) were overcome, then all six Anthocoris species could be reared with varying degrees of success.

### Mortality.

Some species are more easily reared than others under laboratory conditions. The percentage survival based on several experiments with each species, is given in Table 34. The data excludes experiments where mortality was obviously higher than the usual for the species or where a rational explanation of the cause of death was evident.

TABLE 34. Percentage survival of Anthocoris larvae in laboratory rearings when fed on suitable prey, 1959 and 1960.

| Species | Number of larvae | Survival (%) |
|---|---|---|
| A. nemoralis | 76 | 92.11 |
| A. confusus | 80 | 70.00 |
| A. gallarum-ulmi | 77 | 68.83 |
| A. minki | 74 | 59.46 |
| A. sarothamni | 73 | 54.79 |
| A. nemorum | 229 | 54.15 |

It is of interest to compare these mortality figures with the data from other studies. Fewkes, 1958, only succeeded in rearing 6 to 10 per cent of his nabids from first-instar larvae to adults. Johnson, 1937, gives a range of 34 to 69 per cent survival for Cimex lectularius (L.) when reared on different hosts and allowed one blood meal per instar. Hill, 1957, does not quote the mortality for his rearings of A. nemorum; however, his histograms of duration of instars show that he had about 100 larvae complete the first instar but only about 30 that completed the fifth instar. It is possible, of course, that he may not have attempted to rear all the larvae through to adults.

There is a differential mortality between species when reared on different substrates. A. sarothamni could not be reared on filter paper, while A. nemoralis survived equally well on either if fed on a suitable prey. Table 35 compares the survival of these two species fed on three different prey when reared on a substrate of leaves and moist filter paper. A. sarothamni was also reared on Arytaina genistae on filter paper with a sprig of Sarothamnus in the cage. The presence of this plant material contributed to survival, but it was inadequate for normal rearing. It seems probable that mortality of A. sarothamni on filter paper is due to the condition of the substrate, probably excess moisture, and not to a requirement for plant food.

When A. nemoralis was fed on the very unsuitable Aphis fabae, then mortality was extremely high. The fact that a few specimens survived on the leaf substrate suggests that with unfavourable prey this species also profits from a plant substrate.

The type of substrate did not affect the duration of larval life or the weight of the resultant adults. There was no difference in length of larval life or adult weight for A. nemoralis larvae reared on leaves as compared to filter paper, and the few A. sarothamni that survived on filter paper were well within the size range of those reared on leaves.

TABLE 35. Survival of Anthocoris sarothamni D. & S. and A. nemoralis (Fab.) larvae when reared on leaf and filter paper substrates.

| | Filter paper | | Leaf | | Filter paper plus Sarothamnus sprig. | |
|---|---|---|---|---|---|---|
| Host | No. of specimens | Survival (%) | No.of specimens | Survival (%) | No.of specimens | Survival (%) |
| A. sarothamni | | | | | | |
| Arytaina genistae | 11 | 9.09 | 20 | 65.00 | 21 | 33.33 |
| Acyrthosiphum pisum | 11 | 9.09 | 14 | 71.43 | | |
| Aulacorthum circumflexum | 9 | 0 | 27 | 22.22 | | |
| A. nemoralis | | | | | | |
| Acyrthosiphon spartii | 15 | 93.33 | 14 | 100 | | |
| Aulacorthum circumflexum | 17 | 94.12 | 16 | 81.25 | | |
| Aphis fabae | 23 | 0 | 17 | 27.78 | | |

There seemed to be less mortality of A. nemorum reared on leaves than on filter paper. However, when an experiment was set up to determine this, then no difference in mortality was found. Of 13 larvae reared on Aulacorthum circumflexum on each substrate, five died on leaves and three on filter paper. The mean weights, in milligrams, of adults were: filter paper, ♂♂ 1.16, ♀♀ 1.54; leaf, ♂♂ 1.17, ♀♀ 1.55. Thus it is concluded that the differential mortality for A. nemorum in other experiments was either due to unsuitable hosts or to variation in the

vigour of the larvae, and not to rearing conditions. There was no difference in mortality of A. confusus on leaves and filter paper. All experiments with A. gallarum-ulmi and A. minki were conducted using leaves as a substrate.

## Duration of instars of Anthocoris.

The duration of larval life of Anthocoris spp. varies according to the species. Table 36 gives the mean larval duration of each species when reared at a constant temperature on the most suitable prey found in this investigation. Males develop slightly faster than females. This was consistent for all six species but in no case was the difference significant ($P < 0.05$). Thus the durations for both sexes are pooled in all the results. The species fall into three groups as regards their development time under optimal conditions: A. sarothamni and A. nemoralis are the quickest; A. gallarum-ulmi, A. confusus and A. minki are intermediate; and A. nemorum is the slowest.

TABLE 36. Mean duration of larval period of Anthocoris spp. reared at 74°F., range 72-76°F, on their most suitable prey. Bracketed means not significantly different ($P < 0.05$).

| Species | No. of specimens | Larval duration (days) Mean | Range |
|---|---|---|---|
| A. sarothamni | 8 | 14.88 | 14-16 |
| A. nemoralis | 13 | 14.92 | 11-18 |
| A. gallarum-ulmi | 12 | 17.08 | 15-19 |
| A. confusus | 22 | 17.36 | 17-19 |
| A. minki | 11 | 17.91 | 17-20 |
| A. nemorum | 22 | 23.73 | 18-31 |

Analysis of Variance.

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Species | 5 | 928.00 | 185.600 | 37.20 |
| Residual | 82 | 409.08 | 4.988 | |
| Total | 87 | 1337.08 | | |

$P < 0.05$ when $V.R > 2.79$.
L.S.D. required between means (Tukey test):
@ N = 10 = 1.996.

It is apparent from the foregoing results why A. nemorum is considered to have been an unfortunate choice for rearing experiments. It combines the undesirable features of high mortality in culture, and the slowest rate of development. Each experiment with A. nemorum required more attention because of daily feeding and records. More serious than this, however, was that much of the data had to be discarded because results are only based on specimens that reached maturity. It was felt that this was the safest policy in that the causes of mortality were not always completely understood.

The rate of larval development is governed by temperature and by the quality and quantity of food. Data on duration of instars is of little value for comparative studies unless temperature records and prey species are given. It is possible to compare the larval duration of different species if the length of each instar is expressed as a proportion of the total duration. These ratios are relatively constant for each species regardless of rearing conditions. An exception to this would be the case where a standard quantity of food was offered daily; the amount could be sufficient for the earlier stages but sub-minimal for the larger larvae and hence it would retard their rate of development.

Table 37 compares the duration of instars of each species of Anthocoris expressed as a percentage of the total larval period. No two species give identical results but the general pattern is the same except for A. nemorum. The fourth and fifth instars are longer in comparison with the first and second instars for this species. The results for A. nemorum are in very close agreement with the intervals

calculated from Hill's, 1957, data. The pattern for the other species is: third= second < fourth < first < fifth. The fifth instar lasts for about one-third of the total larval period for all species.

TABLE 37. Mean duration of larval instars of Anthocoris spp. calculated as percentages of the total duration.

| Species | Number of specimens | Instar I | II | III | IV | V |
|---|---|---|---|---|---|---|
| A. sarothamni | 10 | 20 | 13 | 14 | 17 | 36 |
| A. nemoralis | 8 | 19 | 17 | 15 | 17 | 32 |
| A. gallarum-ulmi | 15 | 19 | 13 | 13 | 16 | 39 |
| A. confusus | 11 | 18 | 16 | 17 | 17 | 32 |
| A. minki | 20 | 19 | 15 | 14 | 18 | 34 |
| A. nemorum | 25 | 14 | 11 | 15 | 21 | 39 |
| A. nemorum | (Hill, 1957) | 14 | 12 | 15 | 20 | 39 |

Growth rate.

Daily weighings were made for a series of Anthocoris to determine the pattern of growth throughout the larval period. These experiments were conducted with A. nemorum fed on Aphis fabae and A. confusus and A. nemoralis fed on Rhopalosiphon insertum. The larvae were anaesthetized with carbon dioxide and weighed on a five milligram torsion balance. Mean daily weights are graphed against time in Fig. 20. All weights are based on specimens that reached maturity. The pattern of weight increase for all three species is very similar, except that A. nemorum takes significantly longer to develop. More than two-thirds of the total weight is added in the last two instars. The difference in weight between males and females first becomes evident in the third instar, as noted by Fewkes, 1958, in nabids. A. nemoralis females became heavier

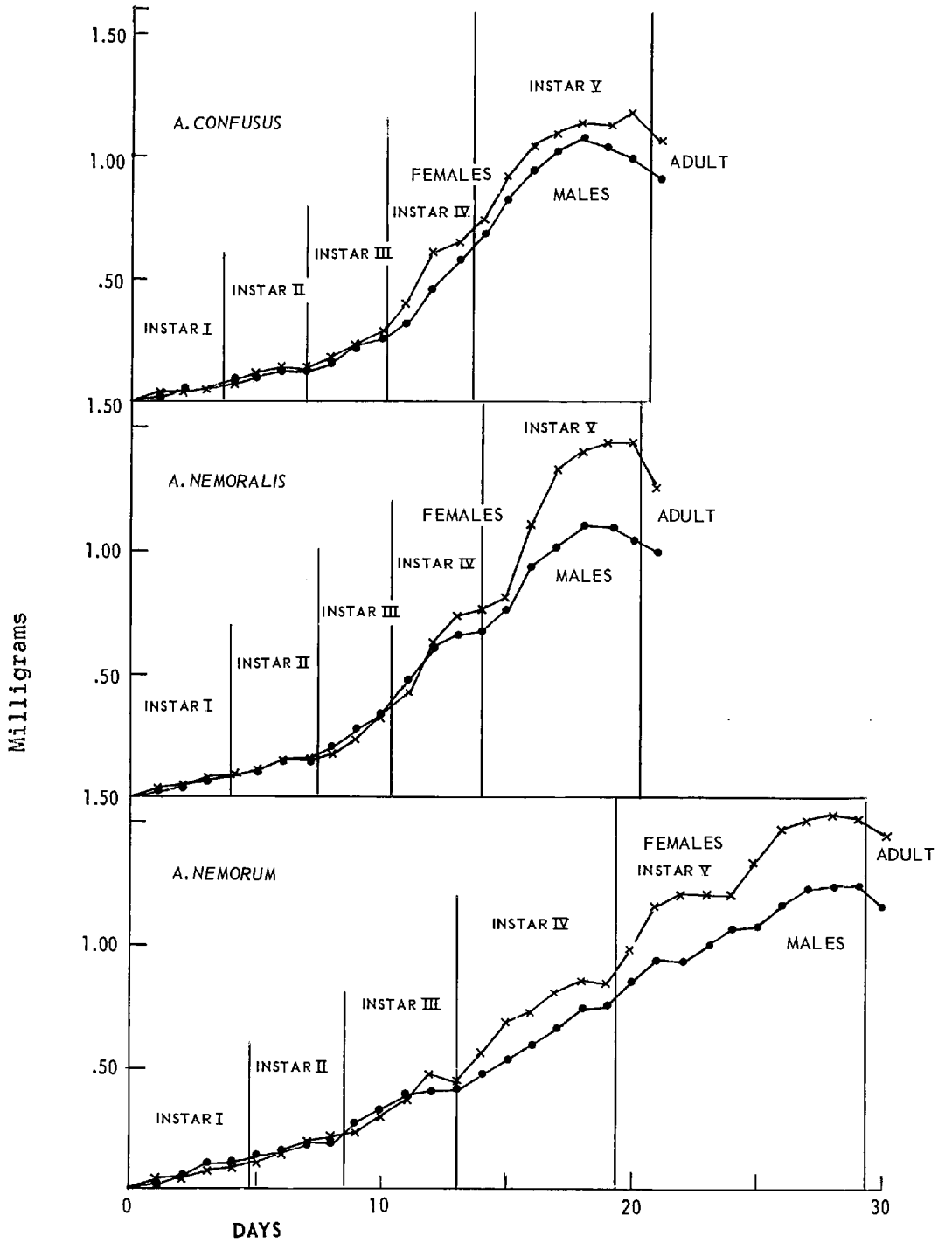



Fig. 20. Mean daily weights of *Anthocoris nemorum* (L.), *A. nemoralis* (Fab.), and *A. confusus* Reut. larvae reared at 74° F. (range 72-76° F.). *A. nemorum* fed on *Aphis fabae* (Scop.); *A. nemoralis* and *A. confusus* fed on *Rhopalosiphum insertum* (Walker).

in the fourth instar but this result is based on only two females.

The first meal in each instar is taken shortly after the exoskeleton has hardened. In many cases the first weighing in an instar was made after a meal had been consumed. Hence, mean initial weights of all instars are higher than they should be. This has the effect of smoothing out the daily growth curve, which in actual fact is a more erratic process. Adults do not normally feed for the first day so the initial weight of this stage is accurately represented in the graphs. The growth rate in these experiments is slower than the true average because the anaesthetic delayed maturation and decreased the weight. However, it appears to have a relatively uniform effect throughout the instars and between species so comparisonsmay be made.

Fewkes, 1958, illustrated the feeding pattern of nabid larvae. In the most simple case, where only a single meal is taken during an instar, he determined four phases: (a) a slight weight decrease during the pre-feeding period; (b) a rapid weight increase due to feeding; (c) a rapid reversal which gradually tails off as conversion to body tissue proceeds; (d) a sharp but relatively small drop during moulting. There is the same general trend with Anthocoris growth but more than one meal is consumed in each instar so the hypothetical situation is never reached. The feeding and growth pattern may be illustrated by the fifth instar. The first meal is taken within a few hours of moulting and results in a large and rapid weight increase. Thereafter feeding takes place intermittently. Weight increase in the first portion of the instar is continuous but erratic because between meals there is some loss due

to tissue conversion and elimination of faeces. Feeding and weight increase proceed at a slower rate during the mid-portion of the instar. In the final part, feeding virtually ceases and weight begins to decrease two or three days before moulting. The same pattern occurs in the other instars but it is somewhat telescoped by the shorter duration and may not be evident when records are only taken at daily intervals. Weight of food consumed per instar is considered in detail in a further section (p.147).

Fig. 21A illustrates the growth rate of A. nemorum males and females based on the initial weight of each instar. The pooled growth rates of males and females of A. nemorum, A. nemoralis and A. confusus are given in Fig. 21B. The curves are all sigmoid, which is characteristic of the usual growth curves. According to Richards, 1949, a straight line relationship between weight and time is obtained when weight is transformed to a linear dimension by using a one-third power transformation. The regression lines for cube root of initial instar weight on time are given in Figs.22 and 23. Fig. 22B illustrates the linear relationship between growth and time for A. nemorum larvae, calculated from head width measurements given by Southwood and Scudder, 1956.

The regression lines for weight increase are calculated on the initial weights of instars I to V and a very good fit is obtained for all three species. Growth during the final instar proceeds at a decreased rate so the initial adult weights do not fall on the calculated regression lines. If, however, the maximum fifth instar weight is plotted, then a

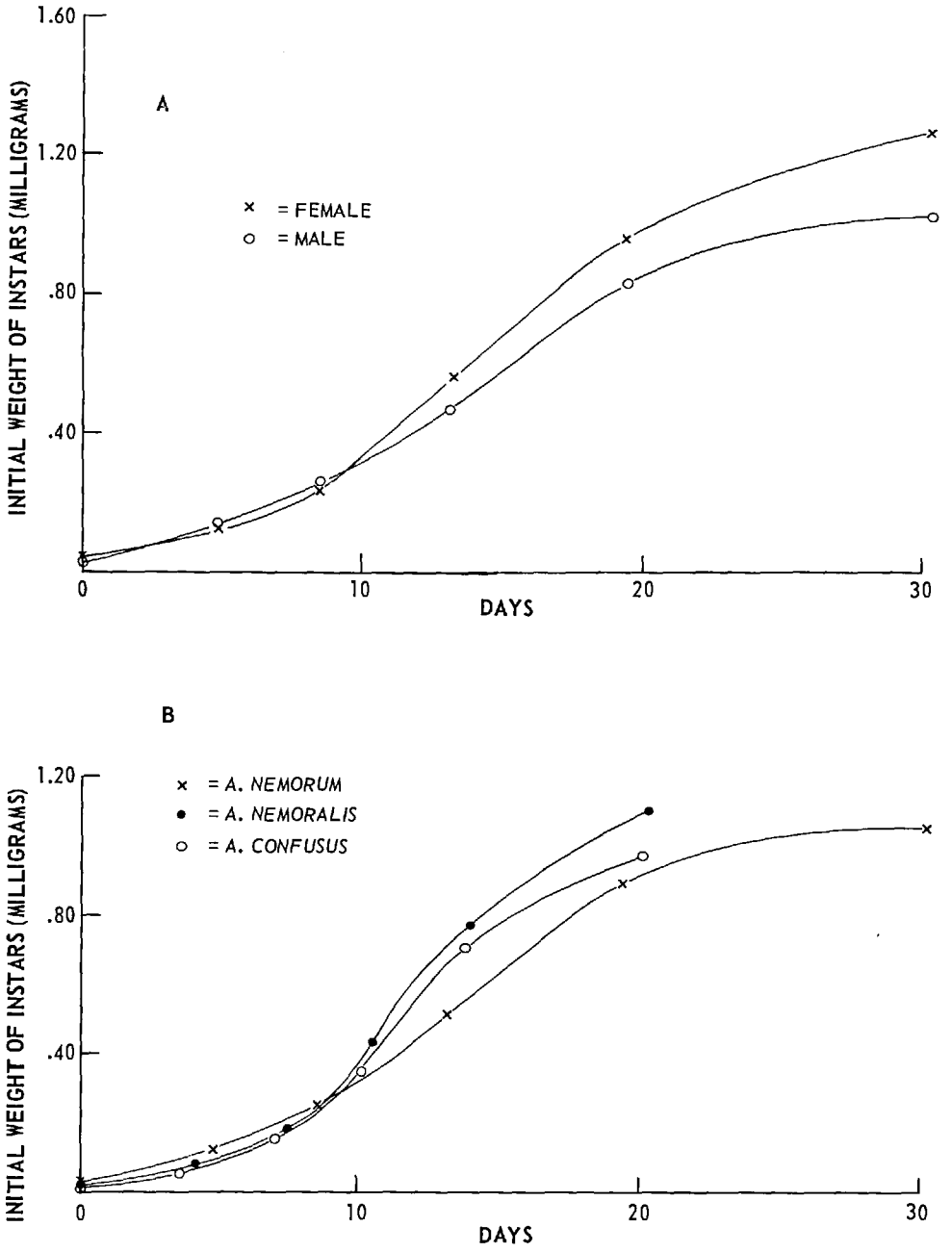



Fig. 21. A. Graph of mean initial weights of instars against time for *Anthocoris nemorum* (L.) males and females. Fed on *Aphis fabae* (Scop.) at 74° F, (range, 72-76° F.).
B. Graph of mean initial weights of instars against time for *A. nemorum*, *A. nemoralis* (Fab.), and *A. confusus* Reut., males and females combined. *A. nemorum* fed on *Aphis fabae*; *A. nemoralis* and *A. confusus* fed on *Rhopalosiphon insertum* (Walker). All rearing at 74° F. (range, 72-76° F.).

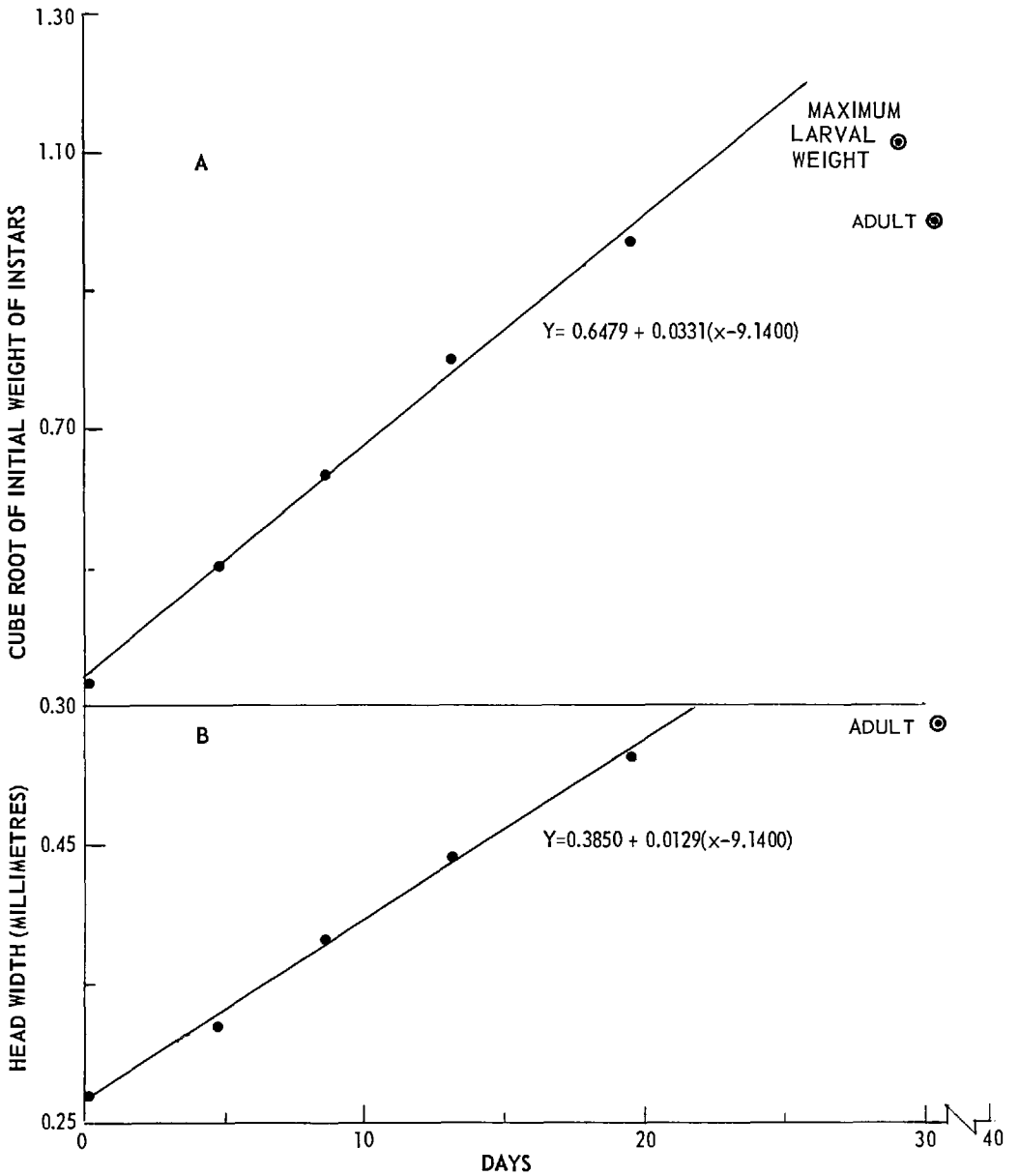



Fig. 22 A. Regression of cube root of weight on time for *Anthocoris nemorum* (L.) larvae. Reared on *Aphis fabae* (Scop.) at 74° F. (range, 72-76° F.)

B. Regression of head width on time for *A. nemorum* larvae. (Measurements from Southwood and Scudder, 1956).

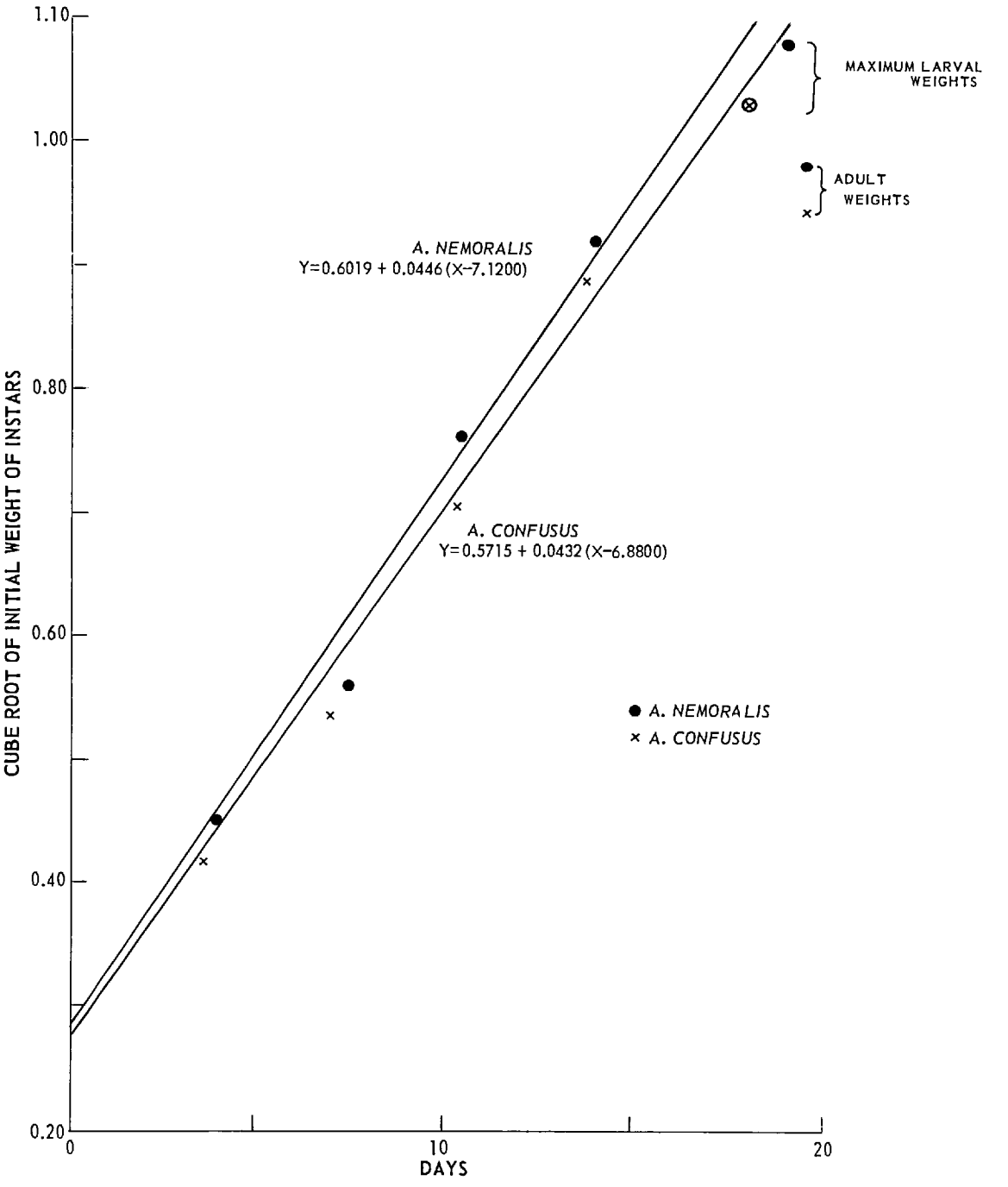



Fig. 23. Regression of cube root of weight on time for *Anthocoris nemoralis* (Fab.) and *A. confusus* Reut. larvae. Fed on *Rhopalosiphum insertum* (Walker) at 74° F. (range, 72-76° F.).

good fit is obtained for A. nemoralis and A. confusus but this correction is insufficient for A. nemorum. Similarly, the adult head width, Fig. 22B, does not fall on the calculated regression line for larval growth because there is very little size increase between the last instar and adult.

The explanation for decreased growth rate during the final instar is probably that there is a shift from size increase to the development of adult characters such as the sex organs; it also coincides, of course, with a change in the hormone balance.

## 3. Basic Feeding Studies.

In view of the scanty, and sometimes contradictory nature of reports in the literature it was necessary to obtain some information on the searching behaviour and method of attack by Anthocoris. In particular it was desirable to find out how they overcame their prey; whether they exhibited a preference for different sizes or species of prey, and the amount, if any, of plant feeding.

### Searching and attack.

When starved Anthocoris were observed on a leaf in rearing cages they moved around actively probing with the rostrum. They often inserted the stylets into the leaf as soon as they were released in the cage. If a bug encountered a drop of water it would stop and drink for some time. Prey were not attacked immediately even in the small ($\frac{3}{4}$-inch diameter) rearing cages; instead it appeared they were only encountered by chance and often the anthocorid would step on an aphid without attacking it. Most of the searching is done with the rostrum; once this makes contact with a prey then an attack usually follows. If the prey is small in relation to the size of the predator then there is very little struggle and feeding commences immediately. Feeding may be continuous or intermittent. The prey is often pierced in several locations and the predator may return to the corpse to continue feeding at some later time.

A small anthocorid that encounters a large aphid will usually move away rapidly if the aphid kicks or moves. The larvae may probe at the legs of the aphid or even climb up on to its dorsum. The reaction of

the aphid is, to some extent at least, dependent on the size of the predator attacking it. An aphid resists or struggles more violently when pierced by a late-instar larva or an adult than when pierced by a small larva.

Dixon, 1958, has described the defensive reaction employed by some aphids that spread siphuncular wax on their attackers. Aphis fabae was the only aphid used in the present study that utilized this method of protection. Invariably as a reaction to attack, droplets of the oily fluid appeared at the tips of the siphunculi. This could only be spread on to the anthocorid if the point of attack was on the posterior part of the body. If the predator was waxed it usually retreated and attempted to remove the wax with the forelegs. Only a small proportion of specimens were waxed, but the death of some larvae was attributed to large encrustations of wax on the head and rostrum. Waxing is probably less effective against sucking insects than mandibulate predators because there is less chance of the wax touching a vulnerable area. The stylets cannot be waxed because they are inserted in the aphid, the rostrum is slender thus presenting a small surface, and the aphid cannot usually reach the predator's head when impaled on the rostrum.

Laboratory experiments conclusively demonstrated that Anthocoris inject a paralytic substance into their prey. A. nemorum females were allowed to attack specimens of Acyrthosiphum pisum and Aphis fabae for a period ranging between three and eight seconds. Of 30 A. pisum and 17 A. fabae, ranging in age from second instar to adult, and in weight from 0.10 to 3.00 mg., only two survived until the following day.

On the other hand, three A. fabae that were pierced in the abdomen with a fine pin all survived for 24 hours even though droplets of body fluid exuded from the puncture. Heinze, 1955, reported that A. pisum can be pierced with a pipette slightly thinner than its tibia and the wound will heal and the aphid can feed and reproduce normally.

Mostof the aphids in these tests were pierced in the abdomen, but three that were attacked in a leg were also paralyzed. It is not possible from these limited data to demonstrate a precise relationship between speed of paralysis, the duration of attack, and the size of the aphid. In general aphids weighing less than 0.5 mg. were immobilized within five minutes by an insertion of up to five seconds, while larger aphids retained some mobility for 10 to 60 minutes.

The following observations on the progress of paralysis were made on an A. pisum larvae weighing 1.76 mg. that was attacked near the base of a coxa for seven seconds: 10 minutes, walking; 20 minutes, walking on four legs; 40 minutes, immobile, with tetanic kicking motions; 60 minutes, immobile, with antennae twitching; 120 minutes, dead.

Influence of prey size on preference.

Smith, 1957, stated that A. nemorum and A. sarothamni showed a preference for small Acyrthosiphum spartii when given a choice of large and small specimens. Similar results were obtained during the present study with various Anthocoris and several aphid species. The result is especially obvious when young Anthocoris are caged with larvipositing females of a preferred species; under these conditions it sometimes

happens that only the newly-born aphids are killed and the adults continue to reproduce, thus affording a constant food supply. In one instance a third instar A. confusus was reared to maturity on the progeny of two Aulacorthum circumflexum females and both adults were still alive at the end of the time. If Anthocoris are offered a generous supply of a mixed population of an unsuitable aphid, all will be killed although few, if any, are sucked. This phenomena is important in relation to prey preference and is more fully discussed in relation to the choice-chamber experiments in the following section. Dosse, 1956, noted that the phytoseiid mite, Typhlodromus tiliae Oudemans also killed large numbers of unsuitable prey without being able to utilize the nutrient for growth.

An experiment was set up to determine the relative preference of A. nemorum larvae for small and large A. pisum. Six specimens were reared to maturity in individual cages and a daily count was made of the numbers of aphids killed. Each instar was offered two large A. pisum ($1.19 \pm 0.05$ mg.) and an increasing number of small aphids for each instar. The daily number of small aphids (mean weight of 10 = 1.50 mg.; range = 1.11 - 1.93 mg.) for each instar was: I,5; II,10; III,10; IV,15; and V,20. The results are given in Table 38.

This table clearly indicates that there is a differential kill of small and large aphids. It is important to note that there was no great increase in the percentage of large aphids killed by the fourth and fifth-instar larvae. Assuming strictly random searching, the predators would encounter large and small aphids in the same ratio as they are in the

TABLE 38. Total numbers of large and small Acyrthosiphum pisum (Harr.) killed per instar by six Anthocoris nemorum (L.) larvae. Temperature 74°F., range 72-76°F.

| Instar | Ratio of large to small aphids present. | Large aphids. (1.19 ± 0.05 mg.) | | | Small aphids. (Wt. of 10 = 1.50 mg., range 1.11 - 1.93 mg.) | | |
|---|---|---|---|---|---|---|---|
| | | Offered | Killed | Per cent killed. | Offered | Killed | Per cent killed |
| I | 2:5 | 48 | 13 | 27.08 | 120 | 64 | 53.33 |
| II | 2:10 | 36 | 9 | 25.00 | 180 | 120 | 66.67 |
| III | 2:10 | 50 | 13 | 26.00 | 250. | 176 | 70.40 |
| IV | 2:15 | 74 | 23 | 31.08 | 555 | 447 | 80.54 |
| V | 2:20 | 142 | 26 | 18.31 | 1420 | 811 | 57.11 |
| Total | | 350 | 84 | 24.00 | 2525 | 1618 | 64.08 |

cages; for example, in the fifth instar there would be 10 small aphids contacted for each large aphid encountered. This is neglecting the differential in size which would increase the contacts with large aphids. One could postulate that the difference obtained between percentage kill of large and small aphids was due to an inability to catch or to kill large aphids. If this were the case, then the percentage of large aphids should increase as the predator becomes larger (late-instar A. nemorum are only slightly smaller than the large aphids.) However, as indicated in the table, there is no marked increase in the percentage of large aphids killed by late instar larvae, in fact there is a decrease in the percentage killed by the fifth-instar larvae. Thus it is safe to say that under the conditions of the rearing cages there was a preference for small aphids over larger ones.

In spite of the above statements concerning the preference of Anthocoris for small prey, it soon became apparent that they were able to kill extremely large prey in the confined conditions of the cages. First-instar larvae were often reared on fourth-instar A. pisum that weighed more than 20 times the initial weight of the Anthocoris. Many of the young larvae killed the aphids by crawling up their legs on to their backs and then paralysing them. Under field conditions a large aphid that was aware of an impending attack by a small Anthocoris would probably escape by walking away.

Choice-chamber experiments.

It was hoped that a simple test could be worked out whereby the predominant potential prey in the field could be ranked in order of preference for each species of Anthocoris. Preliminary experiments indicated that different aphids had different food values, using growth rate and survival as indices of food value. It was therefore decided to run a controlled experiment to determine whether the same information could be obtained using the technically simpler method of choice-chamber tests. Third-instar larvae of A. nemorum were set up in individual rearing cages and given a choice of equal-sized aphids of two species, as follows: three specimens were given five Aphis fabae and five Acyrthosiphon pisum; three specimens were given five A. fabae and five Aulacorthum circumflexum; and three were given five A. pisum and five A. circumflexum. The dead aphids were counted daily and both the living and dead ones were replaced. The experiment was continued until the larvae moulted to the fifth instar. The total kill of each aphid species is given in Table 39.

TABLE 39. Total kill of aphids by Anthocoris nemorum (L.) larvae when given a choice of five specimens weighing 0.40 - 0.50 mg. each of both species per day. Three larvae reared individually in each series.

| Aphis fabae | Acyrthosiphon pisum | Aulacorthum circumflexum |
|---|---|---|
| 125 | 92 | - |
| 82 | - | 27 |
| - | 92 | 43 |

Using the Chi-squared test, with Yates' correction for continuity (Fisher and Yates, 1953), a significant preferential kill is indicated in the following order: A. fabae > A. pisum ($P < 0.05$) > A. circumflexum ($P < 0.01$). This order of kill is exactly the reverse of the anticipated result, based on the comparative growth rates of A. nemorum on these three aphids. However, as A. nemorum has an extremely wide host range under natural conditions, it was still possible that this result indicated a true host preference. The experiment was then repeated using A. confusus larvae; this species can be reared on A. circumflexum and A. pisum but not on A. fabae. It will reproduce normally when fed on A. circumflexum, but only very poorly on A. pisum (p.172). Four A. confusus were reared from newly-moulted third-instar larvae to adults on each of the three combinations of aphids. (Table 40).

TABLE 40. Total kill of aphids by Anthocoris confusus Reut. larvae when given a choice of five specimens, weighing 0.40 - 0.50 mg. each of both species per day. Four larvae reared individually in each series.

| Aphis fabae | Acyrthosiphon pisum | Aulacorthum circumflexum |
|---|---|---|
| 205 | 200 | - |
| 195 | - | 85 |
| - | 195 | 82 |

The ranking of preferential kill by A. confusus is: A.fabae= A. pisum> A. circumflexum ($P<0.01$). The results for A. confusus were even more anomalous than for A. nemorum because the former was showing a significant preference for a species on which it could not survive. The experiments were carried out using a substrate of filter paper instead of a leaf to ensure that the aphids were not feeding. It was thought possible that this may have resulted in the A. circumflexum aggregating on the ceiling of the chamber which could explain its increased survival. However, when the experiment was repeated using a leaf in the cage, there was no difference in the results.

The order of killing preference in the two experiments does not indicate a feeding preference because most of the A. fabae were not sucked, while the A. circumflexum and A. pisum were at least partially consumed. Fewkes, 1958, found that under laboratory conditions nabids killed more prey than they consume, hence number killed was not a useful criterion of food consumption. This is also the case with Anthocoris but it was not feasible to weight the aphids killed in these tests because slightly sucked aphids take up water from the substrate. Hence weighings are virtually meaningless when an excess of food is supplied.

The above experiments indicated that choice-chamber experiments were not a valid method for determining prey preference of Anthocoris. The actual meaning of the results, that is, the preferential kill, must have some other explanation. Some possible explanations, that were not investigated, include: (a) colour differences in the prey may

elicit differential attack responses; (b) unpalatable aphids may have tended to aggregate; if one was attacked and rejected, then another near by would be attacked; (c) differential susceptibility to paralysis could cause greater mortality of some species; and (d) some aphids may have been more active and thus less vulnerable to attack.

Dunn, 1960, has suggested that Anthocoris in aphid galls kill their prey by the fumigant action of a compound produced by the scent glands. This mechanism could explain the observations that large numbers of unsuitable prey in the rearing cages were often killed but not consumed. I have no data that precludes the possibility of Anthocoris killing by a fumigant action but this does not seem to be the entire explanation of the results. In some instances where 20 to 30 A. fabae were killed by a single anthocorid it was noticed that droplets of body fluid were exuding from stylet punctures on each aphid, indicating that all had been attacked, but it does not show when they were attacked. Also, when an A. confusus larva was reared on a leaf floating on water in a petrie dish, it killed 40 A. fabae in a day; a fumigant in this instance would have been dissipated because it was not in a confined space.

An equally feasible postulate for the excessive kill of unsuitable prey is that the taste of an unpalatable aphid aggravates, or excites the predator, resulting in increased searching and killing activity. This does not imply that Anthocoris develop a "lust" for killing, as suggested by Dunn, 1949, for cecidomyid larvae, but merely an increased search for an acceptable prey.

Water intake and plant feeding.

Peska, 1931, stated that A. nemorum would suck water droplets from the surface of a leaf and suggested that when they sucked on leaves they were probably seeking moisture. He also believed that when they were seen feeding on Salix catkins, that they were not primarily after plant juices but that they were actually feeding on insect larvae within the catkin. Hill, 1958, demonstrated that oviposition can take place in the absence of plant material and that larvae can be reared to maturity entirely on animal food. Although it is apparent that plant feeding is not entirely necessary there is no data avilable to indicate whether Anthocoris can derive nourishment from plants.

In order to show a relationship between plant feeding and water intake, it was first necessary to obtain some information on the water requirements of Anthocoris. These bugs are prone to biting humans in hot weather which suggests that they are utilizing perspiration to retain their water balance. As has been mentioned previously (p. 13), Anthocoris adults are subject to quite rapid desiccation and can only live for two to three days in the laboratory without access to moisture. Table 41 indicates the water loss of A. nemorum and A. confusus males, and their ability to take up free water from moist filter paper. The specimens were starved for two days, but had access to moisture, prior to the experiment so the gut would be largely evacuated, and the weight loss would be due to desiccation. After the original weighing they were placed in individual, dry 2 x $\frac{1}{2}$-inch tubes and kept in the laboratory

for 24 hours at 62° to 70°F. and 65 to 70% R.H. They were then weighed, given access to moisture, and reweighed one hour later. The A. confusus were desiccated for a further 48 hours and then given moist filter paper again. The weight increases were due to actual water intake, and not to moisture adhering to the body because the weight of dead specimens did not increase. As indicated in the table, A. confusus males actually increased their weight by intake of water, while A. nemorum almost regained their initial weight. Thus, water loss may be an important factor and feeding on leaves would be one method of compensating for this.

TABLE 41. Mean weight changes of starved Anthocoris confusus Reut. and A. nemorum (L.) males when kept in dry tubes and then given access to moisture. Laboratory conditions: 62° to 70°F., and 65 to 70% R.H.

| | A. confusus | A. nemorum |
|---|---|---|
| Mean original weight | 0.774 ± 0.127 mg. | 1.156 ± 0.102 mg. |
| Weight at 24 hours | 0.669 ± 0.117 | 0.966 ± 0.096 |
| Decrease (% of original weight) | 9.69 | 16.38 |
| Weight after 1 hour with moisture | 0.775 ± 0.107 | 1.127 ± 0.152 |
| Increase (% of minimum) | 10.87 | 13.33 |
| Weight at 72 hours | 0.659 ± 0.104 | All dead |
| Weight after 1 hour with moisture | 0.798 ± 0.103 | |
| Increase (% of minimum) | 21.09 | |

Four experiments were conducted to assess the food value of plant material for Anthocoris: (a) length of life of unfed first- and third-instar A. nemorum larvae on bean leaves as compared with filter paper; (b) longevity of A. confusus females in reproductive diapause; (c) longevity and egg production of A. nemorum females on filter paper,

bean leaves and Salix catkins as compared with animal protein; and (d) longevity and oviposition of gravid A. nemorum females on Salix leaves as compared with filter paper. The experiment with A. confusus females was discussed previously (p. 71), and it is sufficient here to state that there was no difference in length of life on leaves or filter paper either in the autumn or in the spring. The results of the other three experiments are given in Tables 42 to 44.

First- and third-instar A. nemorum larvae both lived slightly longer on bean leaves than on filter paper, but the difference is not significant ($P < 0.05$) (Table 42). It is concluded that the larvae derive little or no nourishment from the leaves. It is possible that the leaf surface provided a somewhat more suitable rearing substrate; this is discussed with reference to larval rearing on p.107. Peska, 1931, stated that newly emerged larvae rarely lived for more than 24 hours without food. This must refer to a lack of water, because the larvae can survive for up to four days without food when they have access to moisture. Predacious Heteroptera that are partially phytophagous have been studied by Barber, 1936, (Orius insidiosus (Say)) and by Franz and Szmidt, 1960 (Perillus bioculatus); in both cases it was the young larvae that were plant feeders. By analogy, it would be expected that if any stage of Anthocoris was partially phytophagous, then it would be the young larvae.

The potential plant foods available to adult Anthocoris include both pollen and leaves. In a preliminary experiment, four A. nemorum hibernating females that were offered daffodil pollen had no ovarial development after one week, while two females fed on insect and mite eggs oviposited in seven and eight days.

TABLE 42. Length of life of newly-moulted Anthocoris nemorum (L.) larvae on bean leaves and moist filter paper with no animal food available. 74°F., range, 72-76°F. Number of specimens indicated by ( ).

| | Mean days lived | | |
|---|---|---|---|
| | Bean leaf | Filter paper | |
| First Instar | (25) 2.96 ± 0.74 | (25) 2.60 ± 0.54 | Not significant ($P < 0.05$) |
| Third Instar | (16) 4.19 ± 1.38 | (19) 4.00 ± 1.14 | " " " |

Diets of leaves, Salix catkins, and catkins plus aphids, are compared with natural prey and with no food in Table 43. A. nemorum females were collected under bark in February and early March and kept at 34°F. until the experiment was set up on March 16. The natural prey were eggs and larvae on Malus twigs, consisting of a mixture of aphids, psyllids and mites. The Salix catkins were replaced at two to three-day intervals and fumigated with methyl bromide to kill animal prey. This treatment killed most insects but an occasional lepidopteran larva survived within the catkin. Two females fed on catkins that laid 80 per cent of the eggs in this treatment were each observed feeding on one larva.

It is apparent from this experiment that plant food, even from the protein-rich anthers, is inadequate for egg production. The few eggs laid by females fed on leaves or catkins were mostly small and deformed. The slight amount of oviposition was probably largely due to the utilization of stored food reserves because ovarial development took place even in two specimens that received only water. The weight increase at seven days is another indication of the lack of available nutrients in the plant diet. Females on leaves lost weight during this period. The apparent

TABLE 43. Length of life and oviposition of Anthocoris nemorum (L.) females when fed on animal and plant diets at 74°F., range 72-76°F. March, 1959. Bracketed means are not significant ($P < 0.05$).

| Food | No. of specimens | Mean Wt. increase @ 7 days (mg.) | Mean days lived | Oviposition (%) | Mean eggs produced |
|---|---|---|---|---|---|
| Eggs and larvae on Malus twigs | 13 | 0.90 | 22.8 | 100 | 57.9 |
| Aphis fabae | 14 | 0.45 | 17.7* | 64 | 35.9 |
| A. fabae + ♂♂ Salix catkin | 11 | 0.39 | 15.8 | 64 | 30.1 |
| Bean leaf | 10 | -0.26 | 13.9 | 40 | 1.0 |
| ♂♂ Salix catkin | 9 | 0.15 | 11.7 | 56 | 2.3** |
| Water | 10 | -0.11 | 9.5 | 0 | 0 |

* 2 females dissected @ 14 days not included.
** 2 females that laid 80% of the eggs observed feeding on larvae.

Analysis of Variance.

1. Length of life (all treatments).

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Foods | 5 | 1273.6245 | 254.7249 | 9.88 |
| Residual | 59 | 1521.3955 | 25.7864 | |
| Total | 64 | 2795.0200 | | |

$P < 0.05$ when $V.R > 2.78$
L.S.D. required between means (Tukey test) @ N= 10 = 4.54 days.

2. Oviposition. (Eggs and larvae, A. fabae and A. fabae plus catkins.)

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Foods | 2 | 23755.389 | 11877.6950 | 16.79 |
| Residual | 35 | 24757.981 | 707.3708 | |
| Total | 37 | 48513.370 | | |

$P < 0.05$ when $V.R. > 4.18$
L.S.D. required between means @ N= 12 = 20.90

weight increase of specimens on Salix catkins was largely due to encrustations of pollen and not to food intake. There was no significant difference in egg production between specimens fed on A. fabae and those receiving A. fabae plus Salix catkins; oviposition in both of these treatments was significantly lower than in the series fed eggs and larvae on Malus twigs.

The only significant differences in length of life are: (a) females fed on eggs and larvae on Malus twigs lived longer than any other series; (b) those fed on A. fabae lived longer than on catkins or water; and (c) those fed on A. fabae plus Salix catkins lived longer than on water. Pollen from the Salix catkins stuck to the adults in the high humidity of the rearing cages. An excess of pollen probably hastened the death of some specimens. However, as there were no significant differences between the series fed on A. fabae and on A. fabae plus catkins in longevity or egg production, it is considered that even under optimum conditions the results of the experiment would not have been greatly altered.

The number of insects on Salix decreases when the flowering period is completed but the oviposition period of A. nemorum extends for over a month after the flowering. Thus, it was thought that plant food might be utilized in egg production at that time. Twenty-two gravid females collected on April 16, 1959 were paired according to weight and the host plant from which they were collected. One of each pair was placed on a Salix leaf and the other on moist filter paper. The only animal food available was the eggs that were not inserted. Fifty per cent were loose on the filter paper and 40 per cent on the leaves. The results, in Table 44, analysed by a paired t-test show no difference in longevity or egg production for the two series.

TABLE 44. Length of life and egg production of 11 pairs of gravid Anthocoris nemorum (L.) females when fed on Salix leaves as compared to water, at 61°F., range 48-71°F. April-May, 1959.

| | Mean days lived | Mean eggs produced |
|---|---|---|
| Salix leaves | 12.5 | 17.2 |
| Moist filter paper | 11.5 | 18.5 |
| | Not significant ($P < 0.05$) | Not significant ($P < 0.05$). |

Maintenance diets.

In the previous experiment it was established that A. nemorum females did not benefit from feeding on daffodil pollen or on Salix catkins. The results of the latter were somewhat doubtful because in the high humidity of the cages the bugs tended to become very coated with pollen, which could have contributed to early death. It was pointed out, however, that this was not an extreme mortality factor because the females fed on A. fabae plus catkins lived almost as long as those fed on A. fabae. The catkins were removed from the tree for fumigation a day before they were used. This did not affect the pollen, but it decreased the flow of nectar. It was therefore decided to determine whether dilute sugar solution could be utilized as food.

Twenty A. nemoralis females collected on Salix on March 21, 1960 were used in the experiment to determine the value of sugar solution as food. They were paired according to weight and set up in individual tubes; one was fed on sugar solution on filter paper and the other only received water. The results in Table 45 indicate a significant increase in length of life for the group fed on sugar solution. There was no difference in egg production between the two groups; five females fed on sugar laid

30 eggs while four in the control group also laid 30 eggs. The fact that there were some eggs produced does not necessarily indicate that the ovaries could mature in the absence of animal protein. There is some ovarial development in this species at the time of spring emergence (Fig. 3) and the females had probably fed to some extent before they were collected. Thus, while sugar solution is useful as a maintenance diet it is not adequate for normal egg production. A. nemoralis and other Anthocoris that aggregate on Salix in the spring probably suck nectar from catkins when prey is scarce.

TABLE 45. Length of life of 10 pairs of Anthocoris nemoralis (Fab.) females when fed on sugar solution as compared with water, March to April, 1960. Temperature: mean, 65°F., range 50-80°F.

| | Mean days lived | Increase (%) |
|---|---|---|
| Sugar solution | 13.3 | 33.3 (significant $P < 0.05$) |
| Water | 9.9 | |

Another type of maintenance diet for Anthocoris is the honeydew secreted by psyllids and aphids. The only species previously reported to feed on this substance is A. gallarum-ulmi (Reuter, 1884: Cobben, 1958); it was suggested by these authors that honeydew is the primary food for A. gallarum-ulmi. Five species of Anthocoris larvae were given honeydew in the absence of animal prey and in all but one test it greatly increased the survival time as compared with starvation (Table 46). Only five specimens were used in each test because it was difficult and time-consuming to present the honeydew to the bugs in a satisfactory manner. An adequate supply had to be obtained from the field and then droplets of the fluid had to be transferred to leaves in the rearing cages. The surface film

was often ruptured during transfer and the droplet was lost. Thus it was desirable to use honeydew that was enclosed in a relatively tough membrane. Psyllid secretion was more satisfactory in this respect than that of most aphids, but honeydew of Eriosoma ulmi was also quite good. The duration of the supply of each type of honeydew in the field was limited so the series could not be repeated.

TABLE 46. Feeding tests of Anthocoris larvae on honeydew at 74°F., (range, 72-76°F.). Five larvae in each test, except the starved controls, where numbers are indicated in ( ).

| Species and Instar | Source of honeydew | Days lived Mean | Days lived Range | Number that completed an instar |
|---|---|---|---|---|
| A. minki | | | | |
| First | Psylla mali | 30.0 | 13-60 | 2 |
| First | Psyllopsis fraxinicola | 22.8 | 9-31 | 3 |
| A. confusus | | | | |
| First | Eriosoma ulmi | 16.0 | 9-27 | 0 |
| First | P. mali | 9.4 | 4-17 | 0 |
| First | Control (9) | 3.8 | 3- 5 | 0 |
| A. nemorum | | | | |
| First | E. ulmi | 10.0 | 6-13 | 0 |
| First | Control (50) | 2.8 | 2- 4 | 0 |
| Third | P. mali | 14.8 | 9-26 | 1 |
| Third | Control (35) | 4.1 | 3- 8 | 0 |
| A. gallarum-ulmi | | | | |
| First | P. mali | 10.6 | 7-15 | 0 |
| First | Control (5) | 2.8 | 2- 4 | 0 |
| Second | E. ulmi | 5.0 | 3-10 | 1 |
| A. sarothamni | | | | |
| First | P. mali | 8.2 | 5-11 | 0 |

The results of the feeding tests are summarized in Table 46 and where possible they are compared with a control series of starved specimens. It is clearly evident that honeydew can be utilized as a maintenance diet but that it is unsuitable for growth. Only seven of 45 bugs completed an instar and they required more than twice the normal time. Five A. minki larvae averaged 17 days before moulting to the second instar. On a normal insect diet this species develops to adult in 18 days. A. minki appears to be far superior to the other species in its ability to survive on this diet. It is somewhat surprising that the second-instar A. gallarum-ulmi larvae only lived five days on E. ulmi honeydew while first-instar larvae lived 10 days on Psylla mali honeydew. Zoebelein, 1956a & b, stated that different honeydews have different food values; one would expect that A. gallarum-ulmi would survive best on the product of its natural host. This result may be due to an actual difference in nutritive value of the two types of honeydew or it could mean that first-instar larvae can survive longer than second-instar larvae. The latter would have survival value for a species because the newly-emerged larvae could feed on honeydew until they were strong enough to attack living prey.

In view of the small number of Anthocoris used and the extreme range of survival times it is unwise to attempt to draw more detailed conclusions from the data. However, the initial studies appear promising. Tests on the food values of different types of honeydew and its role as a complimentary food to animal prey would be an interesting and profitable study. Zoebelein, 1956a, recorded 246 insect species

feeding on honeydew on various conifers plus, Fagus, Quercus, Ulmus, Tilia, Acer and Crataegus but none of these was Heteroptera.

Influence of food on colour of larvae.

Sands, 1958, found that the colour of Anthocoris larvae varied according to the host plant from which they were collected. In particular, he stated that A. nemorum and A. nemoralis collected on Sarothamnus were extremely dark in ground colour. The results of the present investigation bear this out; in general the darkest forms of these two species occur on Sarothamnus and the lightest forms occur on Salix. Similarly, A. confusus larvae on Fagus are usually lighter in colour than those collected from other plants.

An attempt was made to determine the causative agent of this colour variation by recording the colour of larvae reared on three species of aphids in the present and absence of leaves. A. nemoralis was chosen as the test species because it has a characteristic colour pattern and also the lighter form has been considered as a separate variety, superbus Westhoff (Butler, 1923, Massee, 1954). The progeny of a single female were reared under the following conditions: on Aphis fabae with and without bean leaves; on Acyrthosiphon spartii, with and without Sarothamnus leaves; and Aulacorthum circumflexum with and without bean leaves. Colour photographs were taken of the fifth-instar larvae. The transparencies were then projected and a subjective estimate was made by two observers of the intensity of colour of: head; prothorax; meso- and metathorax; ground colour of abdomen; and the degree of light colour on the lateral angles of the tergites. Each area was given a scale of five

so an entirely dark specimen would receive a score of 25, or a total of 50 for the two observers. The actual range within the experiment was 12.5 to 49.5.

The results are given in Table 47 and examples of the range of variation within each treatment are illustrated in Fig. 24. It is obvious from these photographs that there is an extreme of variation even though the larvae were all progeny of the same female. The resulting adults also ranged from light to dark specimens so the value of distinguishing the variety superbus is extremely doubtful.

TABLE 47. Total mean colour values for Anthocoris nemoralis (Fab.) fifth-instar larvae fed on three species of aphids on two substrates. Colour values based on a scale of 0 (light) to 10 (dark) for each of the following: head; prothorax; meso- and metathorax; abdomen (ground colour); and lateral angles of the tergites.

| | Aphis fabae | | Acyrthosiphon spartii | | Aulacorthum circumflexum |
|---|---|---|---|---|---|
| | Bean leaf | Filter paper | Bean Leaf | Filter paper | Bean Leaf |
| No. of specimens | 7 | 13 | 14 | 11 | 12 |
| Colour value | 42.64 | 35.65 | 32.11 | 25.96 | 28.54 |

Pooled means and number of individuals for each aphid (excluding substrate):

| | | |
|---|---|---|
| A. fabae | (7) | 42.64 |
| A. spartii | (27) | 33.81 |
| A. circumflexum | (23) | 27.30 |

All are significantly different with L. S. D. = 6.01.

Analysis of Variance

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Aphids | 2 | 1384.737 | 692.369 | 10.25 |
| Residual | 54 | 3659.803 | 67.774 | |
| Total | 56 | 5044.540 | | |

$P < 0.05$ when V.R. $>$ 3.93

L.S.D. @ N = 15 = 6.01 (Tukey test).

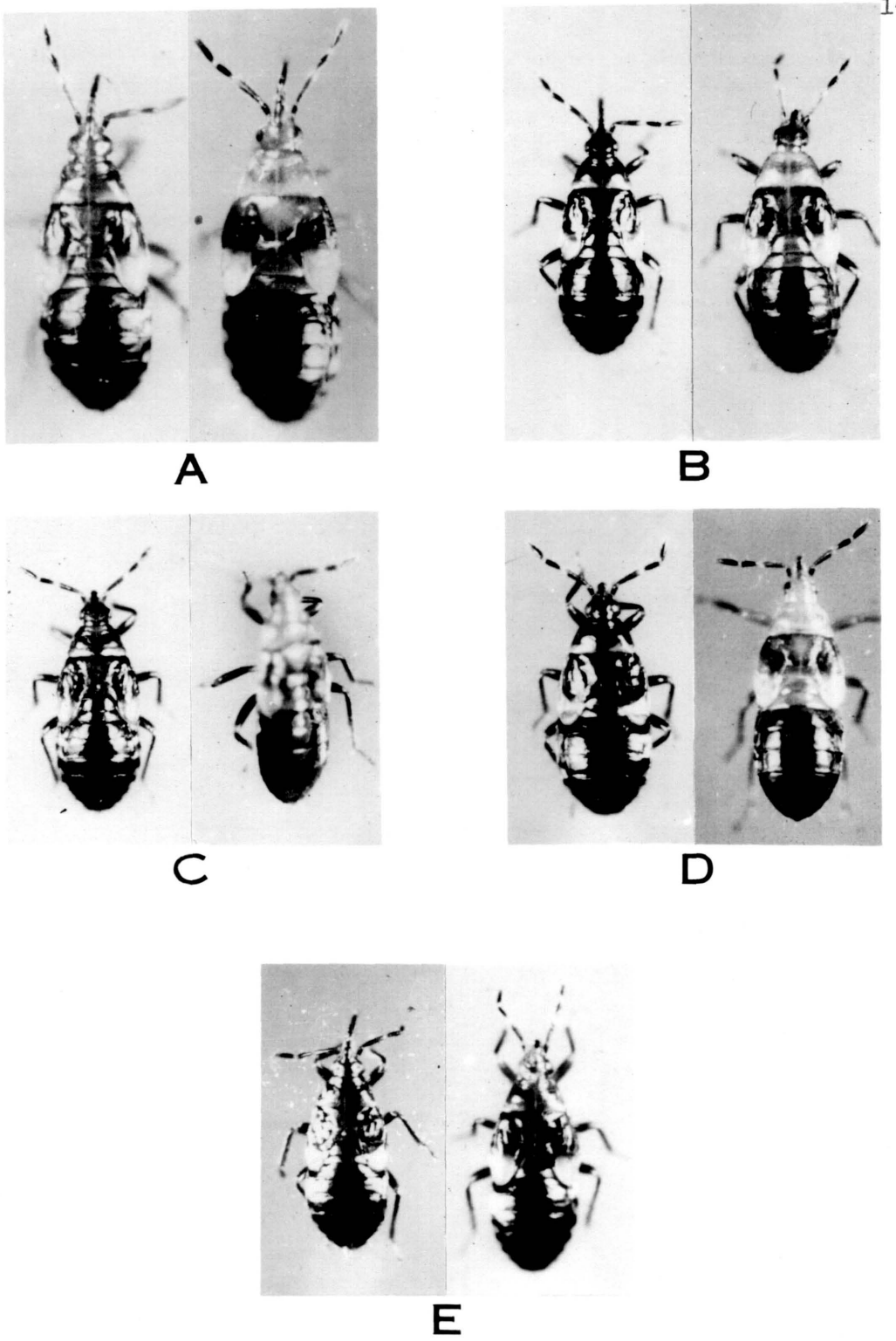



Fig. 24. Range of colour variation in sibling *Anthocoris nemoralis* (Fab.) larvae reared on different aphids: A. on *Aulacorthum circumflexum* (Buck.) on bean leaf; B. on *A. circumflexum* on filter paper; C. on *Acyrthosiphon spartii* Koch on bean leaf; D. on *A. spartii* on filter paper; E. *Aphis fabae* (Scop.) on bean leaf.

There are only five treatments considered in Table 47 because no larvae matured in the A. fabae on filter paper series. No difference was obtained in testing between leaf and filter paper (excluding A. fabae). When the three aphids are considered, however, feeding on A. fabae produced significantly darker specimens than either of the other two aphids and A. spartii produced darker specimens than A. circumflexum.

It is thus established that the prey insect can influence the colour of the predator. If this result is used to explain field observations it could mean that the darker colouration of Anthocoris on Sarothamnus is the result of the prey on that plant. The major prey insects on Sarothamnus are the psyllids, Psylla spartiophilus and Arytaina genistae, and the aphid, A. spartii; none of these stands out as the type of food that one would expect to result in very dark colouration. I suspect that the experiment failed to detect the influence of the plant, which could act either directly through the Anthocoris sucking the plant, or indirectly through the host insect. If this is the case, then two possible reasons for not detecting the plant influence are: (a) excised leaves as used in these tests may not impart the same effect as growing plants; (b) the experiment was conducted in July and August by which time Sarothamnus has completed its growth period; the amount of alkaloids in the leaves is considerably lower at that time than it is during April and May (Smith, 1957). A. nemoralis occurs very sparingly on Sarothamnus at this time of year so it was not possible to check whether they are lighter coloured in the summer than in the spring.

## Food Consumption.

All previous studies of feeding by Anthocoris have been based on the numbers of prey consumed (Peska, 1931; Collyer, 1953; Hill, 1957 and Smith, 1957. Results obtained by this method are open to doubt because they are based on the number of prey killed, and as was shown in a previous section, this is not a direct indication of the amount of food consumed. Fewkes, 1958, found that when nabids were reared under laboratory conditions the denser the artificial prey population the higher the kill, although the actual weight consumed may not be greater. He concluded that "the number of prey killed in an instar is meaningless if the number of standard prey available is not stated". These remarks apply equally well to feeding by Anthocoris.

### Minimal food requirements.

The initial question to be resolved before the weight of food consumed could be calculated was a determination of the minimal requirements. Larval aphids were used in all detailed feeding experiments because production of progeny by adults would complicate the results. It was necessary to prevent weight increase of the prey due to feeding so the experiments were conduced using filter paper as a substrate.

Preliminary experiments were carried out with A. confusus and A. gallarum-ulmi to determine whether they could reach maturity on one aphid per day (Table 48). These experiments indicated that Anthocoris can develop on surprisingly little food. The resultant adults took an abnormally long time to develop and their weights were very low. The weights for

A. confusus reared to maturity on one aphid per day are just within the limits for field-collected specimens but the experimental A. gallarum-ulmi were smaller than any field-collected specimens.

TABLE 48. Weight and duration of larval life of Anthocoris confusus Reut. and A. gallarum-ulmi (DeG.) reared to maturity on one aphid per day as compared with specimens reared on an excess of the same aphid.

| Host | Number reared | Number matured ♂♂ | Number matured ♀♀ | Mean days to maturity | Mean weight (mg.) ♂♂ | Mean weight (mg.) ♀♀ |
|---|---|---|---|---|---|---|
| A. confusus | | | | | | |
| Brevicoryne brassicae (2nd - 3rd instar) | 5 | - | 3 | 32 | - | 0.623 |
| Control (excess aphids) | 4 | 1 | 2 | 22 | 0.730 | 0.845 |
| Rhopalosiphum insertum (4th instar) | 5 | 3 | 2 | 25 | 0.683 | 0.800 |
| Control (excess aphids) | 10 | 3 | 5 | 20 | 0.910 | 1.060 |
| A. gallarum-ulmi | | | | | | |
| Aphis fabae (3rd - 4th instar) | 4 | - | 3 | 36 | - | 1.230 |
| Control (excess aphids) | 3 | 2 | 1 | 26 | 1.680 | 2.080 |

More detailed studies of food consumption were conducted with A. nemorum larvae. The initial study was a comparison of daily consumption by series offered one, five and ten Aphis fabae larvae per day. Twenty A. nemorum larvae were set up in each series. The aphids used were third and fourth-instar larvae, with a mean weight of 0.294 mg., and a range of 0.16 to 0.50 mg. It was not feasible to weight the required 320 live aphids plus a potential 320 dead ones each day. Instead, it was decided to use mean live weight and to weigh the dead aphids.

Weighing of aphids in the five and ten aphid per day series was eventually abandoned because the figures obtained for food consumption were

meaningless; in many instances there was a "negative consumption" because the dead aphids had increased in weight by taking up water from the substrate. Daily weighing of dead aphids was continued throughout the experiment for the series fed one aphid per day. Comparisons of aphids killed, mortality, larval development, and adults weights are given in Tables 49 and 50. The rate of development in this experiment was slow because it was conducted at laboratory temperature. Male weights are adjusted by a factor of 1.29 to compensate for weight differential between sexes (p.165).

Adults reared on one A. fabae per day took significantly longer to mature and were smaller than those reared on five or ten aphids per day. Differences between the latter two series were not significant for either weight or time. Larval mortality was also greater in the series fed one A. fabae per day. Thus, one late-instar A. fabae larva per day is below the minimal requirements for normal growth of A. nemorum. The mean weight of females, 1.41 mg., is however, well within the weight range of field-collected specimens.

The rate of development of larvae fed one aphid per day is compared with the pooled rate for the other two series in Table 51. Significantly slower development on one per day occurred in the third instar and became progressively delayed in the following instars. The trend is apparent even in the second instar although it is not statistically significant ($P < 0.05$). Thus, sub-optimal conditions commenced in the second instar and became more acute as development proceeded. There was a sufficient amount of food available for the younger larvae because they did not consume as large a proportion of the available food as did the older larvae. The results indicate that the quality of the food, as well as the quantity, is lacking.

TABLE 49. Mean numbers of Aphis fabae (Scop.) killed per instar by Anthocoris nemorum (L.) larvae at three levels of available prey. Weight of aphids: mean, 0.294 mg., range, 0.16-0.50 mg. Laboratory temperature: mean, 65°F., range, 48-79°F. April to June, 1959.

| Instar | Number of prey: One per day | five per day | Ten per day |
|---|---|---|---|
| I | 6.0 | 14.6 | 24.9 |
| II | 4.3 | 13.2 | 17.9 |
| III | 5.6 | 15.0 | 24.1 |
| IV | 11.7 | 37.0 | 50.1 |
| V | 17.1 | 61.6 | 93.7 |
| Total | 44.7 | 141.4 | 210.7 |

TABLE 50. Duration of larval life, weight of adults, and mortality of Anthocoris nemorum (L.) reared on three levsl of Aphis fabae (Scop.) at 65°F., (range, 48-79°F.), April to June, 1959. Bracketed means not significant ($P < 0.05$).

| Number of prey | Larval life (days) | Adult weight* (mg.) | Number of Adults | Mortality (%) |
|---|---|---|---|---|
| One per day | 50.00 | 1.418 | 9 | 55 |
| Five per day | 40.92 ) | 1.612 ) | 13 | 35 |
| Ten per day | 39.25 ) | 1.563 ) | 12 | 40 |

* Weight of males adjusted by 1.29 to be comparable with female weights.

Analysis of Variance.

1 Larval life.

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Foods | 2 | 663.446 | 331.723 | 18.93 |
| Residual | 31 | 543.174 | 17.522 | |
| Total | 33 | 1206.620 | | |

$P < 0.05$ when V.R. $> 4.18$

L.S.D. required between means (Tukey test)
@ N = 11, = 3.64; @ N = 12.5 = 3.42.

Adult weight.

| Items | D.F | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Foods | 2 | 0.2081 | 0.1041 | 10.73 |
| Residual | 31 | 0.2996 | 0.0097 | |
| Total | 33 | 0.5077 | | |

$P < 0.05$ when V.R. $> 4.18$

L.S.D. required between means
@ N = 11, = 0.088; @ N = 12.5, = 0.081.

TABLE 51. Progression of larval instars of Anthocoris nemorum (L.) fed one fourth-instar Aphis fabae (Scop.) per day as compared with pooled results for series fed on five and ten A. fabae per day, laboratory temperature, 65°F., range 48-79°F. April to June, 1959. * indicates significant differences between means. $P < 0.05$).

| Instar | Duration of instars (accumulated days) | | |
|---|---|---|---|
| | One aphid per day | 5-10 aphids per day | Difference |
| I | 7.50 | 7.36 | 0.14 |
| II | 12.00 | 10.92 | 1.08 |
| III | 18.44 | 15.76 | 2.68* |
| IV | 31.33 | 25.20 | 6.13* |
| V | 50.01 | 40.12 | 9.89* |

Wigglesworth, 1950, suggests that the wasteful method of feeding by aphids is probably due to the need for some substance that can only be obtained by sucking excessive quantities of plant juice. By analogy, it is probable that growth in A. nemorum larvae was retarded because the required quantity of some essential growth factor could not be obtained from one A. fabae per day.

Other factors that need to be considered in working with minimal food requirements are the area of search and the timing of meals. The small size of the rearing cages practically eliminates the possibility of searching time having an adverse effect on growth. However, the timing of meals could be important. Not all of the aphids were killed because of reduced feeding in the pre-moulting periods; the mean kill was 44.8 aphids in 50 days. Consumption from each aphid was also reduced prior to each moult. The bugs could probably have made more efficient use of their ration of prey if more had been available during the peak periods of metabolic activity after each moult.

The minimal requirements for normal growth of A. nemorum larvae, in terms of the number of fourth-instar A. fabae larvae required, are somewhere between one and five larvae per day. It is probable that two or three aphids per day would provide a sufficient diet for these bugs.

Food consumption measured by weight.

An indication of the amount of food required by A. nemorum larvae was obtained from the previous feeding experiment with Aphis fabae. The results showed that the amount necessary for normal growth could not be obtained from a single fourth-instar A. fabae per day.

A larger species of aphid was used for the next experiment, as it was preferable to continue feeding experiments with a single aphid a day instead of increasing the number. One fourth-instar Acyrthosiphon pisum larva per day was sufficient for normal growth of A. nemorum larvae; specimens reared on this diet matured in 30 days and weighed 1.58 mg; a control series fed an excess of A. pisum matured in 29 days and weighed 1.55 mg.

The aphids selected for the experiment were in the weight range of 1.00 to 1.50 mg. The feeding experiments were carried out on a filter paper substrate so allowance was made for weight-loss due to starvation of the aphid. This was calculated as one-half the weight loss in 24 hours on the assumption that the average meal was taken at 12 hours. The factor for A. pisum was 0.04 mg. per aphid, and for A. fabae in the previous experiment, 0.007 mg. The food consumed by A. nemorum larvae was calculated as : original weight of prey minus dead weight at 24 hours, minus the starvation factor.

Food consumption was also estimated in an experiment where larvae were fed Rhopalosiphum insertum eggs and the number of eggs sucked per day was counted. The weight consumed per egg was estimated from weights of samples of eggs and weights of the partially sucked remains. These weights were obtained from samples of eggs fed on by third- to fifth-instar larvae. An excess of food was available in this experiment; the number of eggs offered per day in each instar was: I,five; II and III,10; IV,15 and V,20. The results of this experiment suggest that the amount of food consumed by first-instar larvae was under-estimated. It is probable that as they only had five eggs available, this instar consumed more per egg than the older larvae.

Of the three experiments on weight of food consumed, only the one with A. pisum gives a determination based on daily weighings of the prey. The tests with A. fabae and with R. insertum eggs are estimates of weight, based on sample weighings.

The difference in weight of food consumed by developing males and females reared on A. pisum is indicated in Table 52. Females consumed significantly more than males ($P < 0.05$). The difference is first evident in the third instar, which is in accord with Fig. 20, where the weight of males and females also begins to deviate in the third instar. The difference in consumption in the fifth instar is not statistically significant. This may be a real effect, but it may also be due to too small a sample. The difference in food consumption between the sexes is in direct proportion to the differences in adult weights. The mean weight of males and females were 1.240 and 1.556 mg. respectively (= 1 : 1.26); the ratio of food consumed was 1 : 1.32.

TABLE 52. Mean weight of food consumed per instar by developing male and female Anthocoris nemorum (L.) reared on one Acyrthosiphon pisum (Harr.) per day, at 74°F., (range, 72-76°F.). * indicates significant difference between means ($P < 0.05$).

| Instar | Mean weight of food consumed (mg.) | | |
|---|---|---|---|
| | Females | Males | Difference |
| I | 0.514 | 0.452 | 0.062 |
| II | 0.729 | 0.765 | - 0.036 |
| III | 1.037 | 0.558 | 0.479* |
| IV | 2.459 | 1.373 | 1.086* |
| V | 4.303 | 3.677 | 0.626 |
| Total | 9.042 | 6.825 | 2.227* |

TABLE 53. Mean weight of food consumed by Anthocoris nemorum (L.) when reared on three different diets: Acyrthosiphon pisum (Harr.) and Aphis fabae (Scop.), one fourth-instar larva per day; Rhopalosiphum insertum (Walker) eggs, excess.

| Instar | Mean weight consumed (mg.) | | |
|---|---|---|---|
| | A. pisum | A. fabae | R. insertum eggs. |
| I | 0.483 | 0.558 | 0.160 |
| II | 0.749 | 0.747 | 0.323 |
| III | 0.798 | 1.114 | 0.581 |
| IV | 1.916 | 2.668 | 1.012 |
| V | 3.990 | 4.070 | 2.152 |
| Total | 7.934 | 9.150 | 4.228 |

The weight of food consumed by each instar of A. nemorum larvae reared on A. pisum is compared in Table 53 with estimates of consumption by larvae reared on one A. fabae per day, and on R. insertum eggs. The series reared on A. fabae required 15 per cent more food than those reared on A. pisum. This is a small amount considering the extremely different conditions of the two experiments. Not only was the A. fabae experiment

conducted at a lower temperature, but also the diet was lacking in both quantity and quality. These results suggest that on a given type of prey (i.e. an aphid) the amount of food required for development is quite constant. Fewkes, 1958, found that the weight of food required for development of Stalia major (Costa) was relatively constant and that the amount was not affected by temperature differences of about $10^{o}C$..

There is a marked difference in the weight of food consumed between the larvae reared on A. pisum larvae and those reared on R. insertum eggs. The latter required 47 per cent less food than the former under similar rearing conditions. This is evidence of the difference in concentration of nutrients in the two diets and indicates that dry weights of the food consumed would be a more suitable method of comparison. The results cannot be interpreted to mean that there is a difference in the food value of the two diets because the time to maturity and the adult weights were almost identical for the two series. The amount of food eaten by first-instar larvae fed on R. insertum eggs was apparently underestimated, as was mentioned previously. This discrepancy would not have much effect on the total because the percentage consumed by first-instar larvae is only a small fraction of the total.

An overall comparison of food consumption in the three experiments is best illustrated by the graph of cumulative food consumption in Fig. 25. All three curves are sigmoids, with the difference in slopes indicating the differential rate of consumption. The divergence is most evident in the later instars when the greatest amount of food is required. The concentrated diet of R. insertum eggs gives more of a linear relationship

between food consumption and rate of development than the aphid diets. The sigmoid curves of food consumption on aphid diets are very similar to the growth curves in Fig. 21. This, of course, is merely an indication of the close relationship between food consumption and weight increase, or growth.

The linear relationship between larval weight and weight of food consumed on the two aphid diets is illustrated by the regression lines in Fig. 26. The larval weights are the initial instar weights for A. nemorum in the growth-rate experiment (Fig. 21A) adjusted by a constant factor derived from the ratio of adult weights in that experiment and the adult weights in the food consumption experiments:

Mean weight of adults (from Fig. 21A) = 1.155 mg.
Mean weight of adults reared on A. pisum = 1.398
Correction factor = $\frac{1.398}{1.155}$ = 1.2104.

The corresponding factor for A. fabae was 1.0416. This correction assumes that the weight difference observed between adults of the two series had been uniform throughout the larval duration.

Weight of food consumed during the fifth instar does not fall on the regression line calculated for the first four instars because the amount required in the final instar is in excess of the amount required for growth in the other instars. Apparently the processes of maturation that occur during the fifth instar utilize more food than does size increase. Franz and Szmidt, 1960, state that the fifth instar larvae of the predatory pentatomid Perillus bioculatis consume 69 per cent of the total larval food consumption.

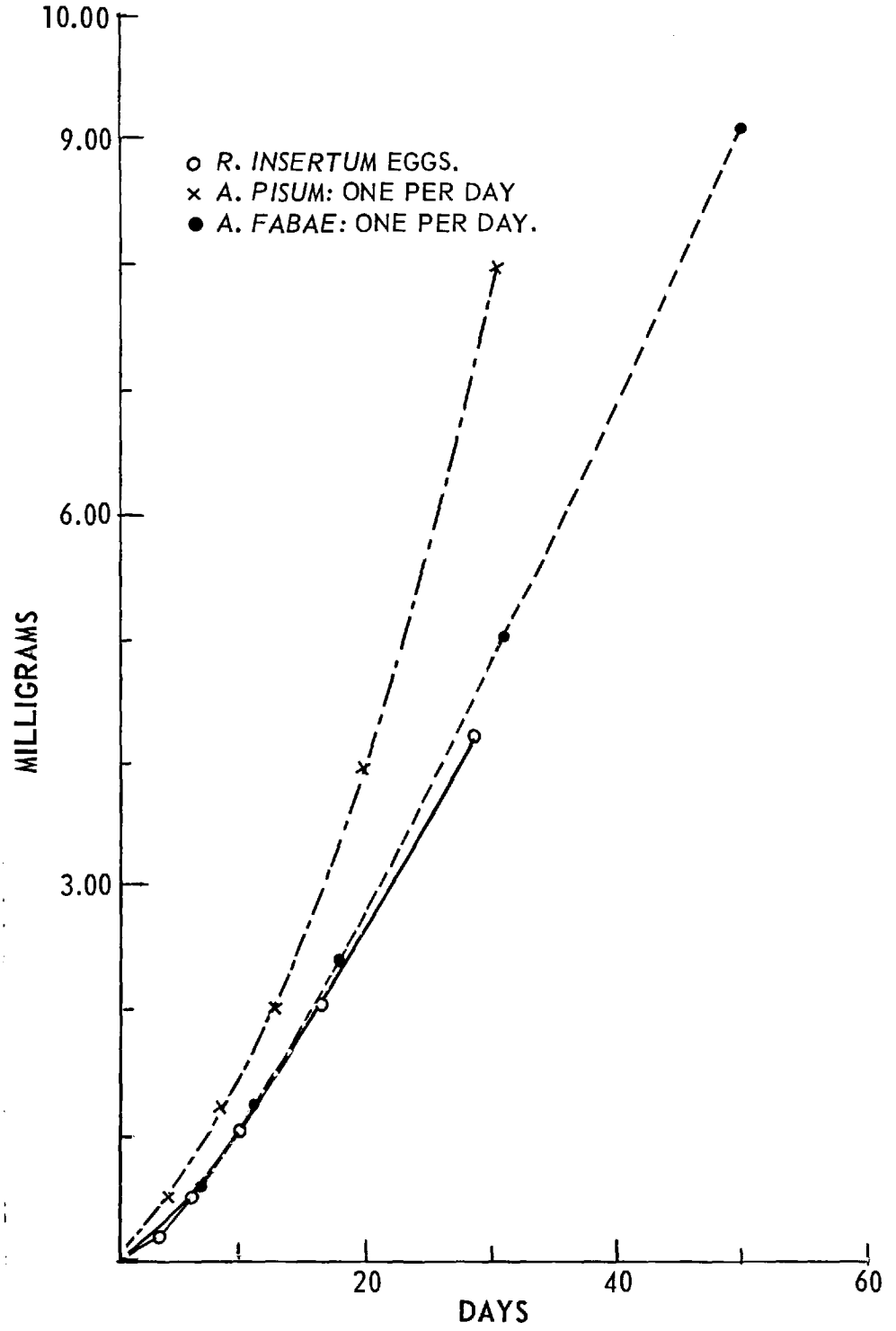



Fig.25. Cumulative food consumption of *Anthocoris nemorum* (L.) larvae fed on three different diets. Rearing temperatures: on *Rhopalosiphum insertum* (Walker) eggs and *Acyrthosiphon pisum* (Harr.) larvae, 74° F. (range, 72-76° F.); on *Aphis fabae* (Scop.) larvae, 65° F.(range, 48-79° F.).

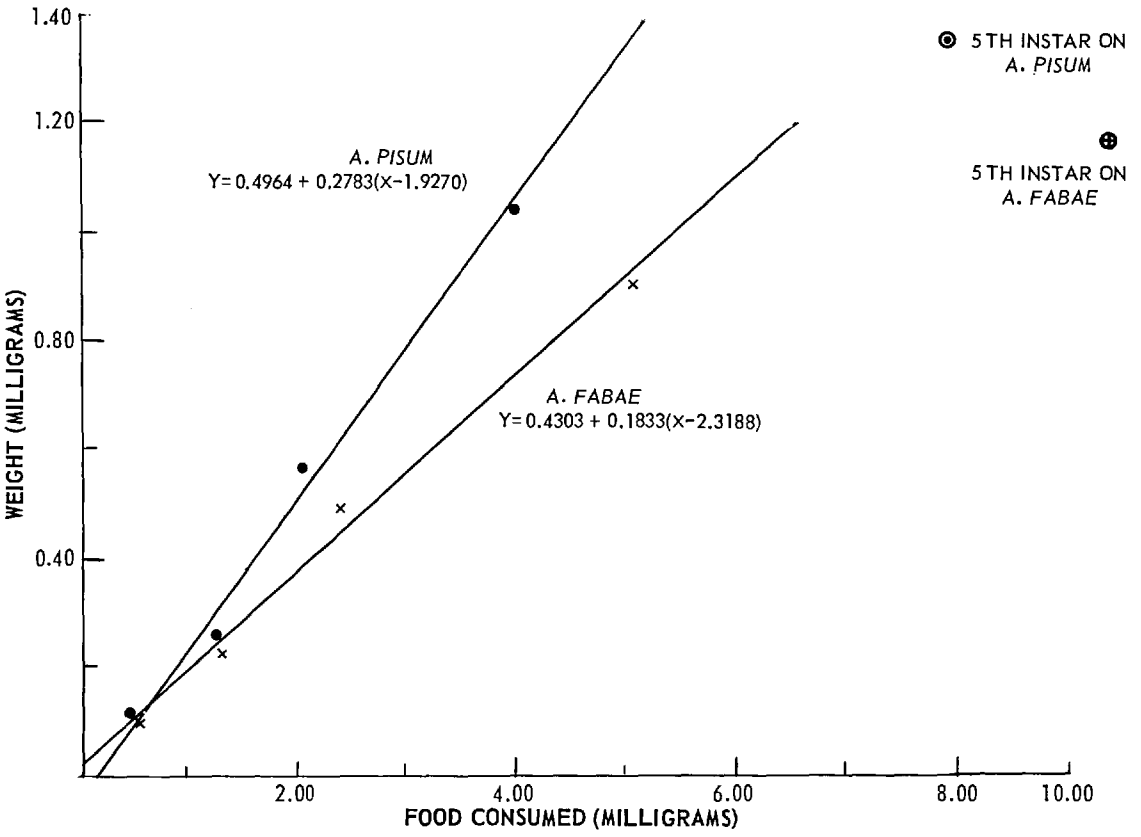



Fig. 26. Regression of weight on food consumption for *Anthocoris nemorum* (L.) larvae. Fed one fourth-instar *Acyrthosiphon pisum* (Harr.) larva per day at 74° F. (range, 72-76° F.) and one fourth-instar *Aphis fabae* (Scop.) larva per day at 65° F. (range, 48-79° F.).

The slope of the regression lines is a method of comparing the efficiency of utilization of the food consumed. The example in Fig. 26 shows that the growth rate on one A. pisum per day was superior to the rate on one A. fabae per day. The value of this particular example is not great except that it shows the retarded growth rate caused by subminimal quantity and quality of the A. fabae diet.

Gross efficiency of food utilization.

Recent work on the efficiency of food conversion by nabids (Fewkes, 1960) and Cimex lectularius (Johnson, 1960b) has indicated that insect prey and blood can be converted to body tissue with a high degree of efficiency. Gross efficiency, as defined by Johnson, is:

$$\% \text{ efficiency} = \frac{100 \text{ (difference in mean weights of successive unfed instars)}}{\text{mean weight of meal(s).}}$$

This does not measure such factors as weight of faeces and exuvia or water and carbon dioxide loss.

No experiments were conducted in the present study specifically to determine the efficiency of food conversion by Anthocoris but the experiments on larval growth and larval food consumption can be combined to obtain an estimate of efficiency for each instar of A. nemorum. The gross efficiency of A. nemorum larvae reared on A. fabae, A. pisum and R. insertum eggs is given in Table 54. The weight increase per instar is based on the mean initial instar weight of larvae (Fig. 21A) adjusted for differences in adult weight. Food consumption per instar is obtained from Table 53.

The gross efficiency of Rhodnius prolixus Stal fed on rabbit blood calculated from the data of Buxton, 1930, is given in Table 55. These data

TABLE 54. Gross efficiency of food conversion by *Anthocoris nemorum* (L.) larvae reared on three different diets.

| Host | Instar of *A. nemorum* | Food consumption (mg.) | Weight increase per instar (mg.) | Efficiency (%) |
|---|---|---|---|---|
| *Acyrthosiphon pisum*, one fourth-instar larva per day | I | 0.483 | 0.109 | 22.6 |
| | II | 0.747 | 0.151 | 20.3 |
| | III | 0.798 | 0.315 | 39.4 |
| | IV | 1.916 | 0.481 | 25.1 |
| | V | 3.990 | 0.297 | 7.4 |
| | Total (and weighted mean efficiency) | 7.934 | 1.353 | 17.0 |
| *Aphis fabae*, one fourth-instar larva per day | I | 0.558 | 0.094 | 16.8 |
| | II | 0.740 | 0.130 | 17.6 |
| | III | 1.114 | 0.271 | 24.3 |
| | IV | 2.668 | 0.414 | 15.5 |
| | V | 4.070 | 0.255 | 6.3 |
| | Total (and weighted mean efficiency) | 9.150 | 1.164 | 12.7 |
| *Rhopalosiphum insertum* eggs, excess | I | 0.160 | 0.105 | 65.4 |
| | II | 0.323 | 0.146 | 45.0 |
| | III | 0.581 | 0.302 | 52.0 |
| | IV | 1.012 | 0.462 | 45.7 |
| | V | 2.152 | 0.285 | 13.2 |
| | Total (and weighted mean) | 4.228 | 1.300 | 30.7 |

TABLE 55. Gross efficiency of food conversion by *Rhodnius prolixus* Stal. fed on rabbit blood. (Calculated from Buxton, 1930).

| Instar | Food consumption (mg.) | Weight increase per instar (mg.) | Efficiency (%) |
|---|---|---|---|
| I | 5.77 | 1.78 | 30.8 |
| II | 15.25 | 4.15 | 27.2 |
| III | 43.50 | 10.50 | 24.1 |
| IV | 113.25 | 30.15 | 26.6 |
| V | 279.10 | 51.95 | 18.6 |
| Total (and weighted mean) | 456.87 | 98.53 | 21.6 |

enable a comparison of efficiency to be made with another family of Heteroptera.

The weighted efficiencies of A. nemorum are much lower than the 50 per cent determined for Stalia major by Fewkes, 1960, and (except for R. insertum eggs) also much lower than the 28 to 33 per cent for C. lectularius given by Johnson, 1960b. However, the overall efficiency of R. prolixus is only 22 per cent, which is in the same range as the 17 per cent efficiency of A. nemorum fed on A. pisum.

Johnson, 1960b, found that the efficiency of C. lectularius fed on the blood of different hosts varied positively with the proportion of dry matter in the blood. Differences in water content of the food probably account for the large difference between the present results and the results of other studies. A. nemorum was fed on aphids and aphid eggs, while Fewkes, 1960, used larvae of Carpophilus dimidiatus (Fab.), a beetle that lives in stored grain. Buxton, 1932, gives the water content of phytophagous insects as 82 to 90 per cent, and that of stored products' insects as only 50 to 60 per cent. The difference in water content can also explain the difference in efficiency when A. nemorum was fed on aphids and aphid eggs; the water content of eggs would be lower than that of aphids, hence gross efficiency would be higher on the former. However, the low efficiency of R. prolixus compared with C. lectularius does show that there are basic differences between species in their efficiency of food conversion.

There is a consistent trend in efficiency between instars of A. nemorum. The figure for first instar larvae fed on R. insertum eggs

is obviously too high due to an underestimation of food consumption (p.148). If this figure is discounted, then the trend is: maximum efficiency in the third instar; intermediate efficiency in the first, second and fourth instars (less than five per cent variation); and minimum efficiency in the fifth instar. Both of the blood-feeding insects, C. lectularius and R. prolixus, have a maximum efficiency in the first instar, an intermediate minimum in the third instar, and a minimum in the fifth instar (Johnson, 1960b; Buxton, 1930). On the other hand, Fewkes, 1960, found that the minimum efficiency for S. major is in the first and second instars and then there is a progressive increase up to the fifth instar. Fewkes' result for the final instar is, however, only based on one specimen. The lack of agreement in the different studies as to which instars are the most efficient at food conversion indicates that this factor varies even between families of Heteroptera. The very low efficiency of fifth-instar A. nemorum is in part explained by the fact that the initial weight in each instar contains some specimens that had consumed some food, while adult weights were all on unfed specimens. Thus, weight increase in the fifth instar is underestimated.

Weight of food consumed by adults.

An experiment was set up to compare oviposition and longevity of overwintered A. nemorum females fed one Acyrthosiphon pisum larva per day (weighing 1.00 to 1.50 mg.) and a series fed an excess of A. pisum. The females were taken from hibernation on January 20, 1960, and kept on a filter paper substrate at 74°F.

The results in Table 56 show that one A. pisum larva per day is an adequate amount of food for normal oviposition. Mean oviposition on both diets compares remarkably well with an average of 68.9 eggs obtained by Hill, 1957, for A. nemorum fed on A. pisum at laboratory temperature. Hill's specimens lived longer, 35.4 days as compared with 27.1 days, but his temperature was lower than that of the present experiment.

TABLE 56. Oviposition and length of life of Anthocoris nemorum (L.) overwintered females fed on two levels of Acyrthosiphon pisum (Harr.), at 74°F. (range, 72-76°F.). January - March, 1960.

| Amount of food per day | Number of females | Mean pre-oviposition (days) | Number of eggs Mean | Number of eggs Range | Days lived Mean | Days lived Range |
|---|---|---|---|---|---|---|
| One fourth-instar A. pisum larva | 10 | 8.4 | 70.9 | 21-127 | 27.2 | 11-49 |
| Excess A. pisum | 8 | 8.6 | 72.5 | 10-114 | 27.1 | 22-33 |

The specimens fed on one aphid per day were weighed daily and the weight of food was determined in the same manner as described for larvae in the previous sections. Total food consumption ranged from 4.88 mg. to 21.24 mg., with a mean of 15.51 mg.; on a daily basis the mean was 0.628 mg., and the range, 0.400 to 1.007 mg. There was no apparent relationship between daily consumption and days lived, or between total weight of food and total oviposition.

The pattern of feeding by A. nemorum females is illustrated in Fig. 27. Consumption per day is based on the number of females living at a given time. For example, the point for day 35 is the mean consumption for three females. The rate of feeding was high when the females were

first brought out of hibernation and remained so during the pre-oviposition period. When oviposition commenced, the rate decreased and then feeding continued at a steady, low, level for the remainder of the lifetime. Some specimens stopped feeding a few days before death but others continued to feed up to the day they died.

The average daily consumption during the oviposition period fluctuated greatly. If the data are graphed as the mean for bi-weekly intervals then a relatively smooth line is obtained. These results suggest that the feeding is cyclic with peaks between two and four days. This cycle did not appear to be correlated with an oviposition cycle. Hill, 1957, also found no oviposition rhythm.

Weight increase of females is compared with weight of food consumed in Fig. 28. The weight is given as the mean percentage increase above the initial weight of the surviving females; this method compensates for the variation in initial weights. Fig. 28 shows that food consumption is not closely associated with weight increase except that both are high in the preoviposition period. Food consumption decreases when oviposition begins, while body weight levels off, and then begins to increase slightly after about one week.

The graphs of adult weights during the spring emergence period (Fig. 4) also show that mean weights continue to increase throughout most of the oviposition period. This could mean that in the field the light females die earlier than heavy females, thus giving an apparent mean weight increase as the period progresses. This explanation cannot be used to

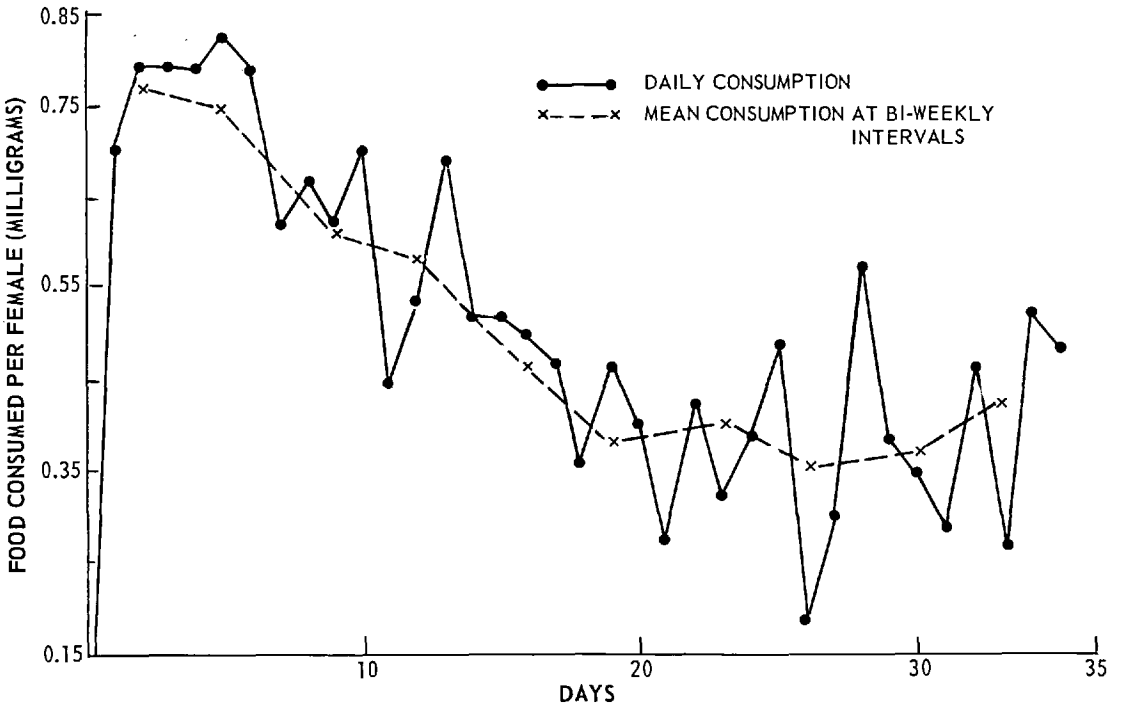



Fig. 27. Mean daily food consumption of 10 *Anthocoris nemorum* (L.) females. Hibernating females were placed at 74° F. (range, 72-76° F.) on Jan. 20, and each fed one fourth-instar *Acyrthosiphon pisum* (Harr.) larva per day. The broken line is the same data graphed as mean food consumption at bi-weekly intervals.

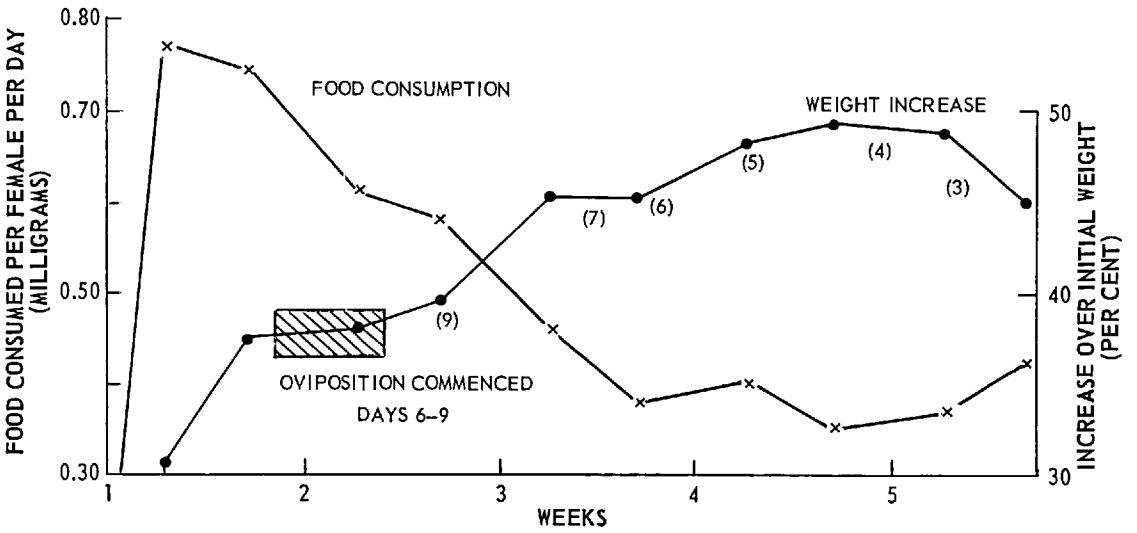



Fig. 28. Mean weight increase of 10 *Anthocoris nemorum* (L.) females, compared with mean daily food consumption, graphed at bi-weekly intervals. Hibernating females were placed at 74° F. (range, 72-76° F.) on Jan. 20, and each fed one fourth-instar *Acyrthosiphon pisum* (Harr.) larva per day. Number of females surviving indicated in ( ).

interpret the results in Fig. 28 because the data were corrected by using the percentage weight increase of the surviving females. The mean weight of females within 24 hours of death showed a 45.6 per cent increase over the initial weight so it is apparent that they continued to increase in weight throughout most of their lifetime.

It is understandable that the greatest food consumption would occur when the ovaries are maturing. To maintain a constant weight once the ovaries are fully mature and oviposition has started, it is only necessary to replace the daily weight of eggs produced plus the weight loss due to metabolism. The explanation as to why body weight increases while food consumption decreases is apparently either that the metabolic rate decreases or else the conversion of food becomes more efficient.

Food consumption of A. nemorum throughout its lifetime.

It is possible to obtain a rough estimate of the total amount of food required by A. nemorum from the results of the two previous sections. The mean consumption per female for a nine day pre-oviposition period was 6.98 mg.. Total weight consumed during the 30-day larval life was 9.04 mg. for females and 6.83 mg. for males, or an average of 7.93 mg. for both sexes. The amount of food required from adult stage to adult is therefore 14.91 mg.

The weight of food consumed by an average overwintered female living 27 days was 15.51 mg. If we assume that these females lived an equivalent time before hibernating and were feeding at the same rate (which is probably a very generous estimate), then adult food consumption would be about 31 mg. By adding to this 9 mg. required for female larval development, a total

lifetime consumption of 40 mg. is obtained.

The number of aphids required, based on the above calculations, would be 15 fourth-instar Acyrthosiphon pisum larvae for a complete generation, or a lifetime consumption of only 40 aphids of this size (assuming that no food was wasted by the prey being only partially consumed). These requirements are remarkably low compared with Peska's, 1931, figure of 500 to 600 aphids sucked in a lifetime, or even Hill's, 1957, figure of 58.6 aphids consumed during the larval stages. However, as the size of the prey and the mean meal weight are unknown factors it is not possible to compare the different results.

## 5. Food Value of Different Prey for *Anthocoris* spp.

One of the primary objects of this study is to determine the types of prey that are suitable for each species of *Anthocoris*. It was shown previously (p.124) that choice-chamber experiments gave misleading results in this respect. The life-history studies (Part I) have to a large extent verified the hypothesis that *Anthocoris* distribution is associated with the distribution of prey species. In order to verify the field results, experiments were set up to determine the suitability of various prey for larval development. Accordingly, a study was made of the rate of development and size of adults of all six species of *Anthocoris* reared on several host insects. Attempts were also made to obtain oviposition from females reared on different prey. Some supplementary tests were conducted on the relative value of different prey for oviposition and longevity of females.

Larvae of the six *Anthocoris* species were fed on the aphids, *Aphis fabae*, *Acyrthosiphon pisum* and *Aulacorthum circumflexum*, and the apple psyllid, *Psylla mali*. In addition, most species were reared on one prey species from their field habitat.

All rearing was done in a constant temperature cabinet, so comparisons can be made between species and between prey. The criteria used for estimating the food value of prey were: (a) duration of larval life; (b) weight of the resulting unfed adults: and (c) mortality. The adult weight and maturation time can be expressed as a rate of growth; this has the advantage that the two estimates can then be expressed as a single figure.

$$\text{Growth Rate} = \frac{\text{Weight of unfed adult}}{\text{days to maturity}}$$

The growth rate of males is lower than that of females because the latter are heavier although maturation time for both sexes is approximately equal. The sex ratio was unequal in many of the feeding tests; this was overcome by adjusting the weight of males to the equivalent female weight. The adjustment factor, which varies according to species from 1.19 to 1.29, was calculated from the weight ratio of newly emerged field-collected males and females. The Growth Rate Index used in the following tables is the adjusted growth rate multiplied by 100 to obtain a number greater than one.

Mortality is an obvious criterion of food value, but it can also be misleading. Differences of one extra death in small-scale tests gives a large difference in percentage mortality. The causes of death in these tests were often not apparent. Most deaths occurred near or during a moult; but in other cases apparently healthy larvae died in mid-instar. Samples of fungi on dead bugs were determined by Dr. M. Madelin, Imperial College, but no entomophagous species were found. It is possible, however, that other fungi growing on the insects may have contributed to mortality. Some deaths may have been caused by unnoticed injury during transfer to new rearing cages. Young larvae were occasionally trapped in condensation or in aphid secretion. Accidental death in this manner could not be distinguished from mortality due to the experiment so all these deaths are included in the mortality figure. All larvae that died within the first 24 hours were discounted because the deaths were probably due to injury or drowning; larvae can live without food for a few days, so death in the first day would not be caused by lack of food.

The percentage mortality in the feeding tests cannot be considered

an exact indication of food value. Mortality is only a useful criterion where differences are very large. The average mortality of each species is given in a previous section (p. 106).

A. nemorum.

The results for A. nemorum reared on six species of prey are compared in Table 57. A. nemorum feeds on all of these insects under natural conditions. Aulacorthum circumflexum is the most suitable prey, giving a significantly larger growth rate index than all others except Psylla mali. At the other end of the range there is no significant difference between the indices for Rhopalosiphum insertum eggs, the red spider, Panonychus ulmi, or Aphis fabae. Mortality was much lower, however, for the series fed on R. insertum eggs. Acyrthosiphon pisum has an intermediate food value; only A. circumflexum has a higher growth rate index and only A. fabae has a lower one. It is especially interesting that A. nemorum does not grow well on A. fabae or P. ulmi as it is considered to be an important predator of these two economic pests.

The results of the larval development studies of A. nemorum are of the type expected for a non-specific and widespread predator. Although there are differences in growth rates on different prey, there are no clear-cut preferences. Also there is considerable variation within each treatment as one would expect from such a plastic species as A. nemorum.

Virtually no success was obtained in inducing reared A. nemorum females to oviposit; only six of 50 females laid eggs. Two females reared on A. circumflexum oviposited in 10 and 14 days, while the range for four females reared on A. fabae that oviposited (at 65°F) was 16 to 49 days.

TABLE 57. Growth rate and mortality of Anthocoris nemorum (L.) larvae reared on different prey at 74°F., range, 72-76°F. Bracketed means not significant, $P < 0.05$.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Mean |
|---|---|---|---|---|---|---|---|
| Aulacorthum circumflexum | 44 | 22 | 50.00 | 23.73 | 1.536 | 4.17 - 8.74 | 6.56 |
| Psylla mali | 15 | 9 | 40.00 | 27.78 | 1.626 | 4.35 - 6.96 | 5.89 |
| Acyrthosiphon pisum | 56 | 22 | 60.71 | 30.41 | 1.549 | 2.77 - 7.15 | 5.21 |
| Rhopalosiphum insertum eggs | 22 | 19 | 13.64 | 30.68 | 1.423 | 1.84 - 6.44 | 4.83 |
| Panonychus ulmi | 16 | 11 | 38.46 | 29.73 | 1.282 | 3.67 - 4.90 | 4.33 |
| Aphis fabae | 34 | 14 | 58.82 | 32.00 | 1.306 | 2.85 - 5.55 | 4.17 |

* Male weights adjusted by 1.29 to be equivalent to female weights.

Analysis of Variance

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 5 | 60.2280 | 12.0456 | 11.15 |
| Residual | 91 | 98.2797 | 1.0800 | |
| Total | 96 | 158.5077 | | |

$P < 0.05$ when $V.R. > 2.78$

L.S.D. required between means (Tukey test) :

@ N = 10, = 1.31; @ N = 14, = 1.15; @ N = 18, = 0.98.

Eggs were also obtained from five females reared on A. pisum that were placed together in a Watkins and Doncaster cage. It was not possible to determine how many of these females oviposited.

Reasons for lack of oviposition apply to most Anthocoris spp. in these studies. Many of the adults died within one to two weeks that is, in less time than ovarial maturation is completed. The date of fertilization could not be determined. This would have an important bearing on the length of the pre-oviposition period because ovarial development does not take place in virgin females. The females that died and those that did not oviposit within a few weeks were dissected. The size of the pouch sperm/was used as an indication of whether fertilization had occurred. It was not possible to distinguish sperm in dead females or in those dissected in the normal manner because the method entailed setting them in melted wax which killed the sperm. Several of the females in these trials were not mated, even some which had been observed in apparent copulation. The males used in these tests were field-collected, if possible, but in some cases it was necessary to use reared specimens. Further studies are required to determine whether impotent males were responsible for the failure of egg production.

A. gallarum-ulmi.

This species has the most restricted breeding niche of any of the species studied but it could be successfully reared on all five test insects (Table 58). There is no significant difference between any of the growth rate indices, analysed by analysis of variance; also a "t"-test revealed no different in growth rate between the natural host, Eriosoma ulmi,

and the poorest prey, Acyrthosiphon pisum. Although the natural prey of A. gallarum-ulmi is an aphid, the largest specimens were those reared on Psylla mali.

TABLE 58. Growth rate and mortality of Anthocoris gallarum-ulmi (DeG.) larvae reared on different prey at 74°F., range, 72-76°F. Bracketed means not significant, P. < 0.05.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Mean |
|---|---|---|---|---|---|---|---|
| Eriosoma ulmi | 15 | 12 | 20.00 | 17.08 | 2.180 | 9.74 - 17.29 | 12.89 |
| Psylla mali | 21 | 13 | 38.10 | 18.46 | 2.330 | 9.75 - 15.33 | 12.78 |
| Aulacorthum circumflexum | 13 | 9 | 28.57 | 17.44 | 2.168 | 10.89 - 14.21 | 12.46 |
| Aphis fabae | 16 | 11 | 31.25 | 16.18 | 1.955 | 8.16 - 18.88 | 12.16 |
| Acyrthosiphon pisum | 12 | 8 | 33.33 | 19.13 | 2.012 | 8.33 - 13.76 | 10.62 |

* Male weights adjusted by 1.19 to be equivalent to female weights.

Analysis of Variance

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 4 | 30.19 | 7.5475 | 1.97 |
| Residual | 48 | 183.45 | 3.8218 | |
| Total | 52 | 213.64 | | |

P < 0.05 when V.R. > 3.13.

Larval mortality was relatively low on all diets. The fact that it was lowest when A. gallarum-ulmi was fed on E. ulmi (20 per cent vs. 29-38 per cent) is probably an indication of the nutrient value of the natural prey.

A. gallarum-ulmi has the largest growth rate index of all six

Anthocoris spp. because it develops rapidly and it is the largest species.

No oviposition was obtained from reared A. gallarum-ulmi females. Five were reared and fed on E. ulmi and four each on Aphis fabae and P. mali. Some specimens were kept for six weeks before being dissected, when they were found to have immature ovaries and enlarged fat bodies. This species has only one generation per year in the field so it is understandable that it would enter reproductive diapause even under laboratory conditions.

A. confusus.

Larval rearing of A. confusus is summarised in Table 59. This species breeds chiefly on trees infested with aphids of the family Callaphididae, so none of the test insects was natural prey. Under laboratory conditions A. confusus was successfully reared on some aphids of the family Aphididae and also on the apple psyllid, Psylla mali. There was no significant difference in growth rate indices for larvae reared on Acyrthosiphon pisum, Aulacorthum circumflexum or P. mali. Mortality was highest in the specimens reared on A. pisum which may be indicative of the unsuitability of this prey. Although growth rate was retarded for the series fed on Rhopalosiphum insertum this is tentatively ascribed entirely to the detrimental effects of daily anaesthetization (p.113).

Results for rearing on Aphis fabae were entirely negative. A. fabae larvae were killed in large numbers, up to 15 to 20 per day, but growth was very slow. In this particular experiment all A. confusus fed on A. fabae died before the fourth instar.

TABLE 59. Growth rate and mortality of Anthocoris confusus Reut. larvae reared on different prey at 74°F., range, 72-76°F. Bracketed means not significant, P. < 0.05.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Mean |
|---|---|---|---|---|---|---|---|
| Acyrthosiphon pisum | 20 | 10 | 50.00 | 17.20 | 1.218 | 6.47 - 7.56 | 7.08 |
| Aulacorthum circumflexum | 29 | 22 | 24.14 | 17.36 | 1.212 | 5.47 - 8.35 | 6.99 |
| Psylla mali | 15 | 10 | 33.33 | 18.20 | 1.211 | 4.70 - 7.71 | 6.69 |
| Rhopalosiphum** insertum | 12 | 10 | 16.67 | 20.40 | 1.067 | 3.92 - 6.50 | 5.29 |
| Aphis fabae | 21 | 0 | 100. | - | - | - | - |

* Male weights adjusted by 1.19 to be equivalent to female weights.

** Specimens anaesthetized and weighed daily.

Analysis of Variance.

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 3 | 22.7847 | 7.5949 | 14.30 |
| Residual | 48 | 25.5032 | 0.5313 | |
| Total | 51 | 48.2879 | | |

$P < 0.05$ when $V.R. > 3.46$

L.S.D. required between means (Tukey test)

@ N = 10, = 0.93; @ N = 16, = 0.74.

A. confusus was the only species that was successfully reared through continuous generations in the laboratory. Preliminary experiments in 1958 had shown that continuous rearing of this species was possible because oviposition was even obtained from stunted females reared to maturity on one Brevicoryne brassicae (L.) and one R. insertum per day. The females that

oviposited were fed on the bamboo aphid, Takecallis arundicolens (Clarke); this aphid was a very suitable food for A. confusus, giving a larval growth rate index of 7.13 for three specimens. Unfortunately it was not available in sufficient numbers for further tests.

Four generations of A. confusus were reared on A. circumflexum between January and early June, 1960. Adults of the fourth generation were of a normal weight and eggs were obtained, so rearing could have been continued.

The difference between suitable prey for larval growth and for reproduction in this species is well illustrated by comparing the pre-oviposition period of laboratory-reared females fed on A. circumflexum, A.pisum and P. mali. Twelve females fed on A. circumflexum had a mean pre-oviposition period of 7.5 days. On A. pisum, two females oviposited at 17 and 18 days while a further two had partially developed ovaries when dissected at 25 days. Four females fed on P. mali did not oviposit within three weeks; they were then fed a natural prey, Eucallipterous tiliae for 10 days and dissected. All had fully developed fat bodies and undeveloped ovaries. Apparently the initial feeding on psyllids had initiated reproductive diapause.

The above results show that the range of prey on which larvae can develop is not as restricted as the suitable prey for immature adults. On the other hand, overwintered adults will even oviposit if fed on A. fabae. Five females fed on A. fabae laid an average of 10.5 eggs, as compared with 119.5 eggs for eight females fed on A. circumflexum and R. insertum. The overwintered females utilize the stored food reserves for egg production, thus even feeding on an unsuitable prey such as A. fabae is sufficient for slight egg production.

A. nemoralis.

In contrast to the previous three species, the larvae of A. nemoralis exhibit striking differences in growth rate on various prey (Table 60). The ranking of suitability of the four insects tested was: Psylla mali > Aulacorthum circumflexum = Acyrthosiphon spartii > Aphis fabae. The fact that the psyllid was more suitable than aphids corroborates the field results that showed that A. nemoralis bred chiefly on trees infested with psyllids. The difference in the growth rate indices between P. mali and A. circumflexum is due to size difference of the predator, because the mean larval duration was equal. The growth rate index for A. spartii is probably equally applicable to A. pisum because the two species are very closely related, if not in fact, the same species (Lambers, 1947).

Aphis fabae is unsuitable as prey for A. nemoralis. In the series considered in Table 60, reared on bean leaves, only five of 18 matured; none matured of 23 reared on a filter paper substrate. The mortality per instar, combining the two experiments was: first, 14; second, 4; third, 9; fourth, 3; fifth, 4; and 2 died while moulting to adult. Most of the specimens died while moulting. Half of the appendages failed to darken on two specimens that moulted to the fourth instar; the cuticle hardened so the legs were functional, but both specimens died shortly after. A few larvae also died due to waxing by A. fabae.

No attempt was made to compare oviposition of A. nemoralis reared on different prey. However, one female reared from third instar to adult on Arytaina genistae and fed as an adult on A. circumflexum oviposited 225 eggs in a 39-day period; this was the largest number of eggs obtained from any species during this study.

TABLE 60. Growth rate and mortality of Anthocoris nemoralis (Fab.) larvae reared on different prey at 74°F., range, 72-76°F. Bracketed means not significant, $P < 0.05$.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Growth Rate Index Mean |
|---|---|---|---|---|---|---|---|
| Psylla mali | 14 | 13 | 7.14 | 14.92 | 1.612 | 7.22 - 13.75 | 11.00 |
| Aulacorthum circumflexum | 33 | 29 | 12.12 | 14.90 | 1.237 | 5.00 - 11.31 | 8.38 ) |
| Acyrthosiphon spartii | 29 | 28 | 3.45 | 16.07 | 1.117 | 4.58 - 10.38 | 7.45 ) |
| Aphis fabae | 18 | 5 | 72.43 | 23.80 | 0.752 | 2.44 - 4.33 | 3.20 |

* Male weights adjusted by 1.21 to be equivalent to female weights.

Analysis of Variance.

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 3 | 243.0835 | 81.0278 | 39.07 |
| Residual | 71 | 147.2477 | 2.0739 | |
| Total | 74 | 390.3312 | | |

$P < 0.05$ when V.R. $> 3.34$

L.S.D. required between means (Tukey test)

@ N = 21, = 1.26; @ N = 28.5, = 1.08.

An experiment was set up to compare psyllids and aphids as prey for A. nemoralis adults. Fifth-instar, second-generation larvae reared in a sleeve cage on A. spartii on Sarothamnus were collected in July, 1960. They were reared to maturity on A. pisum; 13 were fed as adults on A. pisum and 11 were fed on P. mali. Two males were placed with each female. Eight females fed on A. pisum died within five days, while four fed on P. mali died within 10 days. Of the remaining specimens, four fed on A. pisum oviposited in 10 to 14 days and three fed on P. mali oviposited

in 9 to 15 days. The remaining six females were dissected after 16 days; five were apparently in reproductive diapause, while the sixth (fed on P. mali) contained developing eggs. Thus, based on the numbers ovipositing and the length of the pre-oviposition period there was no apparent difference between aphids and psyllids as prey. However, the 50 per cent mortality in the first few days of adult life may have masked potential differences. This extreme mortality may have resulted from the rearing conditions on Sarothamnus. A. nemoralis does not normally breed on this plant during the summer and the reduced vitality of the adults could have been the result.

A. sarothamni.

The results of A. sarothamni larval rearing in Table 61 show a clear-cut difference in the suitability of psyllids as compared with aphids. There is no significant difference in the growth rate indices of Arytaina genistae larvae or adults or between A. genistae and Psylla mali but both psyllids are more suitable than the aphids. The apple psyllid, P. mali, gives an intermediate result between larvae and adults of the natural host, A. genistae. It is interesting to note that the food value of psyllid larvae and adults is almost equal; no doubt under natural conditions the larvae would be the more common prey.

Acyrthosiphon pisum is a more suitable prey than Aulacorthum circumflexum for A. sarothamni. This is shown by the significant difference in growth rate and the differential mortality. The fact that A. sarothamni can develop reasonably well on A. pisum may indicate that it feeds to some

TABLE 61. Growth rate and mortality of Anthocoris sarothamni D. & S. larvae reared on different prey at 74°F., range, 72-76°F. Bracketed means not significant, $P < 0.05$.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Growth Rate Index Mean |
|---|---|---|---|---|---|---|---|
| Arytaina genistae larvae | 12 | 8 | 33.33 | 14.88 | 1.182 | 7.26 - 8.33 | 7.95 ) |
| Psylla mali | 16 | 8 | 50.00 | 16.38 | 1.172 | 6.59 - 8.17 | 7.18 ) |
| A. genistae adults | 30 | 13 | 56.67 | 16.54 | 1.100 | 4.03 - 8.71 | 6.82 ) |
| Acyrthosiphon pisum | 15 | 11 | 26.67 | 18.36 | 1.017 | 3.81 - 7.41 | 5.60 |
| Aulacorthum circumflexum | 27 | 6 | 77.78 | 21.00 | 0.855 | 3.10 - 5.21 | 4.10 |
| Aphis fabae | 12 | 0 | 100 | - | - | - | - |

* Male weights adjusted by 1.21 to be equivalent to female weights.

Analysis of Variance

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 4 | 65.1068 | 16.2767 | 17.07 |
| Residual | 41 | 39.0843 | 0.9533 | |
| Total | 45 | 104.1911 | | |

$P < 0.05$ when $V.R. > 3.12$

L.S.D. required for significance between means (Tukey test)

@ N = 8, = 1.40; @ N = 10.5, = 1.22; @ N = 12, = 1.04.

extent on Acyrthosiphon spartii on Sarothamnus. Indeed, Smith, 1957, claimed that this species showed a marked "preference" for A. spartii when given a choice of aphids from Sarothamnus and from other plants. It was shown in a previous section, however, that preferences determined in this manner are unreliable (p.126).

No larvae fed on A. fabae completed the first instar. The number of days lived ranged between two and seven, discounting the specimens that died within one day. Some of the larvae were conspicuously waxed by A. fabae which would contribute to mortality.

The food value of aphids and psyllids for overwintered A. sarothamni females is compared in Table 62. The females were collected from overwintering sites in early March and paired according to weight; one of each pair was fed on Arytaina genistae adults and the other received A. pisum. Those fed on the latter received an excess of food, while those on A. genistae were given one or two psyllids per day. The results show that fecundity and longevity were greater for the series fed on psyllids. Unfortunately the small size of the samples and extreme variation preclude statistical significance. Comparison of mean weights at three and seven days shows that the females utilized A. genistae for ovarial development more quickly than A. pisum; by seven days most of the females fed on the latter also had mature, or almost mature, ovaries, so the mean weights of the two series were equal.

Mean egg production for the females is higher than that of A. nemorum. It is concluded that A. sarothamni can reproduce normally when fed on one or two adult A. genistae per day. Adult psyllids are probably the chief prey of this species during late winter but once the psyllid eggs begin to hatch in mid- to late March, larvae would be the chief prey.

Most of the females that were obtained from the larval rearing experiments were placed with males and kept for oviposition studies. The results were inconclusive; six of 25 females oviposited but dissections

TABLE 62. Comparison of Arytaina genistae Latr. and Acyrthosiphon pisum (Harr.) as diets for overwintered Anthocoris sarothamni D. & S. females. Six females fed on each diet. Rearing temperature, 74°F., range, 72-76°F.

| | Mean initial weight (mg.) | Mean wt. @ 3 days | Mean wt. @ 7 days | Mean pre-oviposition | No. of eggs Mean | No. of eggs S.E. | Days lived Mean | Days lived S.E. |
|---|---|---|---|---|---|---|---|---|
| A. genistae | 0.913 | 1.147 | 1.212 | 4.8 | 98.7 | 53.7 | 35.0 | 31.9 |
| A. pisum | 0.943 | 1.023 | 1.205 | 6.5 | 58.2 | 29.4 | 27.5 | 13.5 |

indicated that several of the others had not been fertilized. Only one of six fed on A. genistae adults oviposited (at five days) but two were not fertilized and another died after two days. Two specimens reared on A. pisum oviposited at seven and nine days, and three fed on A. circumflexum oviposited at six, 14 and 17 days. However, five females reared on A. genistae larvae, but fed as adults on aphids, all entered reproductive diapause.

A. minki.

The growth rate indices for A. minki in Table 63 show a superiority of psyllids over aphids as prey. There is a significant difference between psyllids and aphids, while mortality is relatively uniform throughout the experiment. Acyrthosiphon pisum and Aulacorthum circumflexum are of equal food value for A. minki, but once again Aphis fabae is completely unsuitable. Several larvae offered this prey all died within two or three days.

The females reared on the four prey were mated and kept for oviposition tests. Three, of five, fed on the natural prey, Psyllopsis fraxinicola larvae, oviposited in 9-22 days, one died at three days, and the fifth was not mated. Of 14 females fed on the other prey, three that were

TABLE 63. Growth rate and mortality of Anthocoris minki Dohrn larvae reared on different prey at 74°F., range, 72-76°F.. Bracketed means not significant $P < 0.05$.

| Prey | No. of larvae | No. of adults | Mortality (%) | Days to maturity | Adult* weight | Growth Rate Index Range | Mean |
|---|---|---|---|---|---|---|---|
| Psyllopsis fraxinicola | 17 | 11 | 35.29 | 17.91 | 1.347 | 6.39 - 9.26 | 7.54 ) |
| Psylla mali | 22 | 12 | 45.45 | 19.08 | 1.376 | 5.82 - 8.72 | 7.24 ) |
| Acyrthosiphon pisum | 14 | 9 | 35.71 | 22.00 | 1.086 | 3.96 - 7.45 | 5.00 ) |
| Aulacorthum circumflexum | 21 | 12 | 42.86 | 22.17 | 1.064 | 3.77 - 5.55 | 4.83 ) |
| Aphis fabae | 7 | 0 | 100 | - | - | - | - |

* Male weights adjusted by 1.21 to be equivalent to female weights.

Analysis of Variance.

| Items | D.F. | S.S. | M.Sq. | V.R. |
|---|---|---|---|---|
| Prey | 3 | 68.4454 | 22.8151 | 31.04 |
| Residual | 40 | 29.3965 | 0.7349 | |
| Total | 43 | 97.8418 | | |

$P < 0.05$ when V.R. $> 3.46$

L.S.D. required for significance between means (Tukey test) @ N = 10, = 1.10

fed on aphids oviposited in 19 to 23 days, three died within the first week and the remainder entered reproductive diapause. Although this was a small sample the results suggest that A. minki will produce a second generation if the natural prey is available. There is a greater tendency to enter reproductive diapause when fed on other prey, even Psylla mali which gives the same growth rate index as P. fraxinicola.

No detailed fecundity experiments were carried out for A. minki fed on various prey but records were taken for 10 females from which eggs were obtained for larval rearing studies. Six overwintered females fed on A. circumflexum laid an average of 53.7 eggs (range, 23-106) in 28 days (range, 14-49) while four females fed on P. mali averaged 77.8 eggs (range, 47-100) in 30 days (range, 15-38). The difference in fecundity on the two diets is similar to that obtained for A. sarothamni when fed on psyllids as compared with aphids.

## 6. Other Factors Affecting Host Plant Preferences.

The food requirements of Anthocoris larvae, discussed in the previous section, may be considered a product of host plant specificity. However, the selection of the host plant is largely determined by the discrimination of the adults. Two aspects pertaining to the choice of host plants are briefly considered in the following section: olfactory attraction to plant stimuli, and oviposition preference.

### Olfactometer studies.

According to Dethier, 1947, "the ability to exercise a choice presupposes a means of recognition". He goes on to state that, in general, parasites are guided by host odours serving as attractants, while phytophagous insects are guided by plant odours. Studies were therefore attempted to determine whether Anthocoris were stimulated by plant odours in order to obtain information on the mechanism of host plant preference. A. nemorum aggregates on Salix in early spring; this species was available for experimental purposes in greater numbers than the other Anthocoris so olfactometer tests were concentrated on attraction by the scent of Salix catkins.

Extracts were prepared of male catkins in warm water, oil and ether. The latter two solvents were found to be repellant so the experiments were continued using only the water extract.

The olfactometer and experimental conditions are described on P. 13. A. nemorum females that had been artificially overwintered in a refrigerator were used in the initial experiments. Ten specimens were placed in the choice chamber and the number over the stimulus and over the charcoal were

recorded at thirty-second intervals. Each experiment lasted for 45 to 85 minutes.

It was found that the response of A. nemorum to the humidity gradient in the chamber varied between experiments; therefore it was necessary to run a simultaneous water control (i.e. water vs. charcoal, as well as extract vs. charcoal) in each test. The response attributed to the stimulus was then calculated as the difference between the numbers over the stimulus and the numbers over water. The results were analyzed by chi-squared tests.

Table 64 compares the numbers and per cent of A. nemorum over stimulus and over water in the first experiments. The results are for total counts in two 45-minute trials on April 14, 1960, using overwintered females taken from a refrigerator. The extract was of an unknown concentration. The table indicates: (a) a pronounced attraction to the stimulus as compared with charcoal, that decreased from 81 per cent at 10-15 minutes to 67 per cent at 40-45 minutes; and (b) a significantly greater attraction to the Salix extract than to water only for the first half of the total interval. These results are interpreted to mean that the concentration of extract was highly attractive to A. nemorum at 10-15 minutes but that the degree of attraction waned as the charcoal absorbed the odour and as the bugs became habituated. By 28-33 minutes the bugs were responding only to a humidity preference.

Further experiments were carried out in late April and May using an extract prepared from 10 gm. of catkins extracted in 100 ml. of water. Unfortunately, by this time artificially overwintered females were no longer available, so gravid overwintered females were collected from the field.

Table 65 compares the response of these females to the extract and to water. The results are the total counts in three tests. As with the previous experiment there was an attraction to the extract, but it was not so pronounced and it occurred in a different time interval. The differences between the two experiments are probably due to a combination of factors including differences in the concentration of the two extracts and changes in response by A. nemorum due to changes in the nutritional and physiological state. It is to be expected that the adults in the second series of experiments would show less attraction to Salix than the adults taken from hibernation. There is an aggregation on Salix at spring emergence but gravid females in late April and May are past the dispersive phase, and Salix is past the flowering period by that time.

TABLE 64. Numbers and per cent of Anthocoris nemorum (L.) hibernating females responding to male Salix extract (unknown concentration) in an olfactometer, compared with the numbers responding to water in a control series. April 14, 1960.

| | Time intervals (minutes) | | | | | |
|---|---|---|---|---|---|---|
| | 10-15.5 | 16-21.5 | 22-27.5 | 28-33.5 | 34-39.5 | 40-45 |
| Salix extract | | | | | | |
| Number | 97* | 89* | 92* | 80 | 77 | 80 |
| Per cent | 80.8 | 74.2 | 76.7 | 66.7 | 64.2 | 66.7 |
| Control (water) | | | | | | |
| Number | 66 | 63 | 67 | 88 | 86 | 85 |
| Per cent | 55.0 | 52.5 | 55.8 | 73.3 | 71.7 | 70.8 |

* Significantly greater attraction than control ($P < 0.05$).

TABLE 65. Numbers and per cent of Anthocoris nemorum (L.) field-collected females responding to male Salix extract (0.1 ml. of extract prepared from 10 gm. catkins in 100 ml. water) in an olfactometer, compared with the numbers responding to water in a control series. May 6-17, 1960.

| | Time intervals (minutes) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 5-15.5 | 15-24.5 | 25-34.5 | 35-44.5 | 45-54.5 | 55-64.5 | 65-74.5 | 75-84.5 |
| Salix extract | | | | | | | | |
| Number | 288 | 289 | 266 | 299 | 316 | 336* | 378* | 323 |
| Per cent | 48.0 | 48.2 | 44.3 | 49.8 | 52.7 | 56.0 | 63.0 | 53.8 |
| Control (water) | | | | | | | | |
| Number | 283 | 268 | 247 | 279 | 278 | 249 | 303 | 295 |
| Per cent | 47.2 | 44.7 | 41.2 | 46.5 | 46.3 | 41.5 | 50.5 | 49.2 |

* Significantly greater attraction than control ($P < 0.05$).

Oviposition preference.

The site of oviposition on the host plant varies according to the species of Anthocoris. A. nemorum and A. nemoralis generally insert their eggs into the leaf lamina. Sands, 1951, found that overwintered A. sarothamni females insert their eggs into stems, while in the summer eggs are also found in leaves and young seed pods. A. gallarum-ulmi oviposits in petioles or main veins of Ulmus leaves and sometimes in the lamina of galled leaves. A. confusus and A. minki eggs are inserted in petioles or the mid-rib of leaves.

Observations were made on the choice of oviposition site by females used in laboratory breeding experiments. The purpose of these experiments was to obtain eggs for rearing; information obtained on the choice of oviposition was therefore incidental to the major theme.

In the absence of plant material A. nemorum (and some of the other species) will oviposit in filter paper. A. nemorum eggs were also inserted in leaves, mid-ribs, Salix catkins, and even into thin bark. A large proportion of the eggs were not inserted except when tender leaves were available. The proportion of eggs inserted into plant tissue depends on three factors: inherent variation between species; age of the female; and conditioning. Some females inserted practically all eggs into plant tissue while others under identical conditions laid all loose eggs. The usual trend, however, was that the first eggs were loose, then insertion became common, and finally, just before death, loose eggs were again laid.

A. confusus females on bean leaves laid about half loose eggs and the remainder were inserted into the thickest available part of the mid-rib.

If a small piece of petiole from a deciduous leaf was placed in the cage, then practically all eggs were inserted in this in preference to the bean leaf. As with A. nemorum, an occasional female inserted all eggs even if only filter paper or leaf lamina were available.

A. gallarum-ulmi females deposited mostly loose eggs on both Ulmus or bean leaves in the rearing cages.

A high proportion of A. sarothamni eggs were inserted into the lamina of bean leaves. There was no apparent preference for Sarothamnus leaves when one of these was placed on the bean leaf. However, excised Sarothamnus leaves tend to wither rapidly which may account for their rejection.

A. minki preferred Fraxinus to bean leaves for oviposition; 34 of 36 (94 per cent) were inserted in Fraxinus, while only 45 of 82 ( 55 per cent) were inserted in bean leaves.

# DISCUSSION

## Food Consumption

Accurate estimation of food consumption by predacious insects is a difficult problem but it is basic to any studies of the role of predators in natural control. Although the present study is not directed towards assessing the importance of Anthocoris as predators, the information obtained on amount of food required for development and reproduction of A. nemorum should be useful basic data in this respect.

Previous workers (Peska, 1931; Collyer, 1953; Hill, 1957; and Smith, 1958) have given figures for the number of prey killed by A. nemorum; in all cases the number killed are based on feeding tests in which the predator was offered a number of prey confined in small cages. Fewkes, 1958, pointed out the failings of this method of assessing food consumption. The weight of food consumed by A. nemorum was obtained under conditions of ample biomass but with a limited number of prey available. This method in no way reproduces natural conditions but I suggest that it is a closer approximation of normal food consumption than that of previous studies.

The weight of food required by A. nemorum during a lifetime was estimated to be about 40 mg. of Acyrthosiphon pisum. In terms of the number of prey killed, the weight consumed depends on the size of the prey, the weight of meals, and the concentration of nutrients in the prey. The latter point is illustrated by a comparison of weight consumed by larvae fed on A. pisum larvae and those fed on Rhopalosiphum insertum eggs in Table 53; the amount required of the former was almost twice as high as of the latter. Johnson, 1937, reported that the weight of blood ingested by Cimex lectularius

from different hosts was positively correlated with the dry matter content of the blood.

The pattern of feeding by A. nemorum within an instar was found to be essentially the same as reported by Fewkes, 1958, for nabids. Food consumption is greatest within one to two days after a moult, then there is a period of decreased feeding during mid-instar and finally a non-feeding, pre-moulting period. Observations indicate that there is a short pre-feeding period after ecdysis and that feeding within each instar is cyclic, as demonstrated by Beck et al, 1958, for Oncopeltus fasciatus (Dallas), but as records were only taken at daily intervals, it is not possible to show the duration of these periods.

Adult feeding is greatest during the pre-oviposition period. Consumption decreases sharply once oviposition commences and then levels off to about one half of that in the pre-oviposition period. The data suggest that adult feeding is cyclic, with peaks between two and four days. The weight of food consumed by adults in reproductive diapause was not studied. Further work is necessary to determine the amount of food required to build up fat reserves in the pre-hibernation period. Field observations and laboratory experiments show that adults feed on a wider variety of prey during this period than they do as larvae.

The gross efficiency of food conversion by A. nemorum larvae was shown to vary on different prey. Efficiency was markedly lower than the figures given for nabids (Fewkes, 1960) or for Cimex lectularius (Johnson, 1960b), but is in the same range as the efficiency of Rhodnius prolixus, calculated from the data of Buxton, 1930. The variation between prey, and

between the different studies, can at least partially be explained by differences in water content of the prey. Further work on this subject is warranted to determine the gross efficiency on different prey compared on a dry weight basis. In theory, a predator with a low efficiency of food conversion would be more useful than one with a high efficiency because the former would require more food per unit of weight increase.

## Relative Value of Various Prey for *Anthocoris*.

Thompson, 1951, pointed out that contrary to popular belief, many predators are quite host specific. He showed that even though some coccinellids could be bred successfully on diaspine scales on conifers in sleeve cages, that they would not breed under the same conditions when the cages were removed even though no other suitable prey were available. The absence of *A. nemoralis* from *Sarothamnus* during the summer although it was successfully reared on this plant in sleeve cages is also probably due to prey preference. Thompson's, 1951, results illustrate a basic problem in the study of predator-prey relationships, namely, how can the preference of a predator be determined under experimental conditions ?

Hodek, 1958, has aptly pointed out that suitable prey for a predator cannot be based on a few observations of feeding. Mature coccinellids often feed on prey that are unsuitable for larval development. He concludes that a suitable (essential) food is one on which both larval development and oviposition can be successfully accomplished. The relative food value of potential prey can be assessed, on the basis of these criteria, by laboratory rearing. However, the ability to develop on a certain prey in no way proves that such will occur under natural conditions. Differential development on different prey only suggests that one is preferred to the other. The term "prey-preference" should therefore be used only when the results have been verified by detailed field studies.

Johnson, 1937, used the following criteria to compare the relative value of different hosts for *Cimex lectularius*: rate of larval development,

mortality, quantity of food ingested, fertility of females, longevity and weight loss during starvation, and fresh and dry weights of reared adults. Some combination of these criteria have been used by several other workers in assessing the feeding preferences of both predacious and phytophagous insects, for example; phytoseiid mites (Dosse, 1956; Chant, 1959), coccinellids (Hodek, 1957 and 1958), and cotton stainers (Geering and Coaker, 1960). The major factors used in the present study to assess the relative value of prey were: rate of larval development, weight of reared adults, and to some extent, fecundity of females.

The results of the larval rearing studies showed that some differences could be ascertained in the growth rate of Anthocoris larvae reared on different prey. Aphis fabae proved to be a poor quality diet for all species; it was acceptable for A. nemorum and A. gallarum-ulmi, but completely unsuitable for the other four species. A. fabae is apparently distasteful to Anthocoris because they do not ingest sufficient food for normal growth. Chant, 1959, found that the superiority of eriophyid mites over Panonychus ulmi as prey for Typhlodromus pyri Scheuten could be accounted for on the basis of the greater quantity of eriophyids consumed even if the quality of nutrients was equal. Hodek, 1957a, reported that Aphis sambuci L. was toxic to some coccinellids; A.fabae is not toxic to Anthocoris because larvae offered an alternative prey will survive even after they have attacked A. fabae.

Another important difference in the growth rate indices for larvae reared on aphids was that Aulacorthum circumflexum was inferior to Acyrthosiphon pisum as food for A. sarothamni. The former species is a

more suitable food for the anthocorids that normally feed on aphids. The fact that the reverse is the case for A. sarothamni suggests that it has become adapted to some extent to feed on Acyrthosiphon on Sarothamnus.

Psyllids proved to be a very suitable prey for the larvae of all Anthocoris. The growth rate indices for A. sarothamni, A. minki, and A. nemoralis were significantly higher when fed on psyllids than when fed on aphids; field studies indicated that these three species are partial to psyllids. A psyllid diet produced the heaviest adults for all six Anthocoris species. The growth rate indices for aphidophagous Anthocoris were slightly lower for specimens fed on psyllids as compared with specimens fed on the most suitable aphid because the larval development period was shorter for the latter. It is apparent from these results that the nutrient value of psyllids for larval development is definitely not a limiting factor preventing predation by A. gallarum-ulmi or A. confusus.

The rearing studies indicate that the food requirements of Anthocoris larvae could in some part explain the restricted range of some species. However, there are also other factors operating because all species can be successfully reared on other than their natural prey. The most striking example is A. gallarum-ulmi, a monophagous species that was successfully reared on three other aphids and one psyllid.

The feeding habits of adults are more important than those of the larvae from the standpoint of determining the host plant range of Anthocoris because the adults make the initial selection of the habitat. Some Anthocoris leave their breeding grounds on reaching maturity. In the species where dispersive flights were most marked (e.g. A. confusus from Fagus, and

A. nemoralis and A. sarothamni (in 1960) from Sarothamnus and A. gallarum-ulmi from Ulmus), the flights coincided with low densities of preferred prey in the original location. This evidence does not necessarily show a cause and effect relationship as pointed out by Johnson, 1960a. It does mean that the adults will not be feeding on the same prey as they did as larvae.

A. confusus was successfully reared through continuous generations. The prey, A. circumflexum, was not a species that A. confusus encounters in its natural habitat but it is apparently a very suitable substitute. Specimens fed on Psylla mali did not oviposit within three weeks (c.f. one week when fed on A. circumflexum). Natural prey, Eucallipterous tiliae, was then offered to these bugs, but the ovaries did not mature. I suggest that the females were forced into reproductive diapause because suitable prey was not available at the appropriate time.

The attempts to obtain oviposition from reared adults fed on various prey were inconclusive if each Anthocoris species is considered individually. However, most of the results can be explained if one postulates that the required condition for the production of a second generation is a preferred prey for the newly emerged adults. If a sub-standard food is available then the females enter reproductive diapause and lay down fat reserves for the coming season. Waloff, 1949, showed that Ephestia elutella Hübner could be induced to diapause by unfavourable nutrition and Lees, 1955, found that Panonychus ulmi produces diapausing eggs when its food supply becomes depleted. There was a greater tendency for A. minki to enter reproductive diapause when fed on aphids or P. mali

than when fed on its natural prey, Psyllopsis fraxinicola. A.sarothamni females reared on Arytaina genistae failed to oviposit when fed on aphids, even though this species has two generations in the field. A. gallarum-ulmi apparently has an obligatory diapause thus no females could be induced to oviposit regardless of the prey.

The above theory, applied to the field results, could explain the differences in the number and size of generations between species.

A. gallarum-ulmi has a single annual generation and obligatory diapause; its prey, Eriosoma ulmi,disperses from Ulmus in July and thus is not available to a second generation.

A. minki is also univoltine with the adults maturing at the same time as the adults of P. fraxinicola. A few larvae of an apparent second generation were found; this suggests that facultative diapause could be associated with the occurrence of suitable prey, which is in accord with the laboratory results.

A. confusus is predominantly univoltine but some of the earliest females to mature produce a small second generation. The explanation may be that these females occur when there is still a sufficient density of aphids on the primary host trees to stimulate ovarial maturation. It could be argued in this particular case that day-length is the operative factor in initiating reproductive diapause.

The first generation of A. nemoralis preys on psyllids. The second generation is produced only in the presence of a suitable type of aphid. Adults occur in large numbers on Acer, feeding on Drepanosiphum platanoides,

but no larvae are produced. On Tilia, with E. tiliae as prey, there is a second generation of A. nemoralis. Day-length is obviously not the factor initiating diapause in this case.

A. sarothamni produces two generations per year. There are also two generations of psyllids on Sarothamnus. The second generation of psyllids was very small in 1960; coincident with this, large numbers of A. sarothamni females were collected from adjacent trees. These females, unlike those that remained on Sarothamnus, diapaused without producing a second generation. Dempster, 1960, noted in his studies that the size of the second generation of A. sarothamni fluctuated considerably in different years. It may well be that this fluctuation was associated with differences in numbers of second-generation psyllids.

The sampling in the present study did not include enough herbaceous plants to determine whether the size of the second generation of A. nemorum varied in relation to the presence of suitable prey. It is probable that, as A. nemorum is polyphagous, the number of generations would be dependent on the length of the season and not on food requirements.

Although the presence or absence of a preferred prey appears to influence facultative diapause during the summer, preferred prey are not necessary for oviposition by overwintered females. Both A. minki and A. sarothamni reproduced successfully when fed on aphids during the spring. Also, A. confusus is widely dispersed during early spring; females do not aggregate on the primary breeding hosts until their ovaries are well developed. Therefore, the attraction to these plants (Fagus, Quercus, Tilia and Acer) is not a direct response to a preferred prey that is required for ovarial maturation.

## Interrelationship Between the Host Plant and *Anthocoris* spp.

Host plant specificity of *Anthocoris* cannot be entirely explained on the basis of the distribution of preferred prey. It is therefore necessary to consider the possible ways in which the plant itself could be attractive to a predator. Three ways in which *Anthocoris* could utilize specific host plants are: (a) as a oviposition site; (b) for food; and (c) as a token stimulus which brings the predator into the habitat of a suitable prey.

No tests were conducted in which females were given a choice of plants for oviposition, so little information is available on preference of oviposition sites. The usual plant material offered for oviposition was bean leaves. All species would insert eggs in this substrate, but the percentage inserted was extremely variable. *A. confusus* inserted eggs more readily if a petiole from a deciduous leaf was available. Only half as many eggs were inserted by *A. minki* in bean as compared with *Fraxinus* leaves. Sands, 1951, reported that *A. confusus* laid more readily in *Quercus* or *Ulmus* leaves than in *Salix* leaves. These limited data suggest that the type of leaf is important for oviposition, but further work is required to ascertain the relationship between the oviposition preference of *Anthocoris* and their host plant distribution.

Several authors have suggested that *Anthocoris* are partially phytophagous (see literature review). Carayon and Steffan, 1959, in the light of their discovery that *Orius pallidicornis* (Reut.) fed primarily on pollen, have suggested that other Anthocorinae may also feed on pollen

to some extent. They suggest that this feeding habit would explain why these "Flower Bugs" are more abundant on plants at the time of flowering and why they chiefly frequent male flowers.

The aggregation of A. nemorum and A. nemoralis on Salix in the early spring supports the idea that distribution of Anthocoris is sometimes associated with the occurrence of flowers. Also, A. minki first occurs on Fraxinus when the anthers are dehiscing. On the other hand, the appearance of A. sarothamni and A. gallarum-ulmi does not coincide with the flowering period of their host plants.

The olfactometer experiments showed that A. nemorum are attracted by the scent of male Salix catkins. However, pollen did not provide suitable nutriment for egg production or for increased longevity. Therefore, it is concluded that Anthocoris are not attracted to flowers to feed on pollen. A. nemoralis benefited from dilute sugar solution when no animal prey was available; longevity was increased although egg production was not. Thus, the bugs may derive some nourishment by sucking nectar from flowers but this could at most be considered a maintenance diet.

The present work has revealed that plant material, although sucked by all Anthocoris to some extent, cannot provide an alternate food to animal prey. The length of life of starved larvae or adults is not prolonged in the presence of plant material. The plant can provide a source of water for Anthocoris, and it was shown that the water requirements of these bugs are high. However, in the presence of adequate prey, the requirements could be easily met by the body fluids of the prey or by feeding on honeydew.

The most probable role of the host plant with respect to Anthocoris is that it provides a token stimulus which brings the predator into the habitat of suitable prey. In his review of insect nutrition, Trager, 1947, stated that food selection by phytophagous insects is often determined by characters of the food that are not connected with nutritional requirements. In a similar manner, it may be postulated that Anthocoris are attracted to a suitable habitat by olfactory stimuli from the plant, as has been demonstrated by the reaction of A. nemorum to Salix extracts.

The interrelations of Anthocoris and their host plants may be interpreted in terms of the general theories of host plant selection. Thompson, 1951, pointed out that there was a paucity of knowledge concerning predacious insects in this respect but there is no reason to believe that they would not be responding to the same stimuli as those that govern the activities of phytophagous and parasitic insects.

In general, the post-hibernation occurrence of Anthocoris is correlated with the bud-burst of plants, that is, with the appearance of either flowers or leaves. In terms of Nuorteva's, 1952, theory of host plant selection the attraction would be due to the overall colour pattern of the plant. Olfactory (or possibly gustatory) stimuli from either the flowers or leaves would act as the token stimuli for acceptance or rejection of the plant as a habitat. Then feeding on suitable prey would deter further dispersal and lead to maturation of the ovaries. The species which are restricted to breeding on a single host plant (A. minki, A. sarothamni and A. gallarum-ulmi) have apparently evolved more precise requirements than those species with less specialized habits.

A comparison of the behaviour of a restricted species, A. minki, with that of a semi-restricted species, A. confusus, illustrates possible differences in the reactions leading to selection of a breeding niche. In the case of A. minki it is appropriate to ascribe the source of the initial attraction to emanations from the host plant and not from the prey because P. fraxinicola larvae do not emerge until two to three weeks after A. minki first appears on Fraxinus. In contrast, A. confusus occurs on a number of trees in early spring and ovarial development is well advanced before aggregation occurs on the primary breeding trees. The attractive aspect of the latter is apparently the presence of preferred and abundant prey. The fact that there was a low population of overwintered adults of A. confusus and a low population of Pyllaphis fagi on Fagus in 1959 while in 1960 there was an epidemic of P. fagi and a correspondingly high population of A. confusus adults (p.64) indicates that the predators were responding to the numbers of prey. This does not necessarily indicate that the aphids attracted the predator, but only that they were responsible for retaining them.

Host plant specificity and the associated specialization in food preferences has obviously been important in evolutionary divergence within the genus Anthocoris. It is unwise to attempt to determine phylogenetic trends on the basis of British Anthocoris alone, but certain levels of specialization may be noted. Dethier, 1954, states that monophagy usually evolves from polyphagy. In this respect, A. nemorum is the most generalized species of British Anthocoris. A. nemoralis and A. confusus represent a second level of specialization; the former shows a preference for psyllids

on a range of plants and the latter breeds on several trees infested with callaphidid aphids. A. minki, A. sarothamni and A. gallarum-ulmi have proceeded a step further and have evolved an intimate host plant interrelationship.

## SUMMARY AND CONCLUSIONS.

1. The life-histories of six species of British *Anthocoris* have been studied for two years. Emphasis was placed on comparative studies, especially of arboreal species. Summaries of the life-histories are given on pp. 95-98.

2. Except in the case of the polyphagous *A. nemorum*, the life-cycle of each species is shown to be associated with the life-cycles of preferred prey.

3. The preferred prey and breeding sites are: *A. gallarum-ulmi*, *Eriosoma ulmi* in leaf galls, on *Ulmus*; *A. minki*, *Psyllopsis fraxinicola* on *Fraxinus*; *A. sarothamni*, psyllids on *Sarothamnus*; *A. nemoralis*, psyllids, especially on *Crataegus*, *Salix*, *Sarothamnus* and *Malus* (a small second generation occurs associated with aphids, especially on *Tilia*); and *A. confusus*, callaphidid aphids on *Fagus*, *Quercus*, *Tilia* and *Acer*.

4. All species have a reproductive diapause. Limited success was achieved in breaking diapause under constant illumination at 74°F. by starving specimens for a few weeks and then feeding them on suitable prey.

5. The mean length of the larval period at 74°F., when offered an excess of suitable prey is: *A. nemoralis* and *A. sarothamni*, 15 days; *A. gallarum-ulmi*, *A. confusus* and *A. minki*, 17-18 days, and *A. nemorum*, 24 days.

6. Anthocoris have a preference for small prey. However, in the small rearing cages larvae were able to develop normally on active insects many times their own size. Prey are killed by a slow paralysis.

7. It was demonstrated that plant juices and pollen have little or no nutritional value for A. nemorum. Honeydew increased the longevity of larvae of all species in the absence of animal prey. However, very few larvae moulted when fed on honeydew and none survived for two instars. Dilute sugar solution increased the length of life of starved A. nemoralis females but it was not adequate for normal egg production.

8. Under laboratory conditions, the number of prey killed is of little value in determining the amount of food required for larval development. A. nemorum, A. confusus and A. gallarum-ulmi were all reared to adult on one aphid (weighing 0.25 - 0.35 mg.) per day, although they will kill at least 10 aphids per day if they are available Development was slower than normal and the resultant adults were small when reared on a diet of one aphid of this size per day.

9. Normal growth of A. nemorum larvae and oviposition by overwintered females were obtained on a diet of one Acyrthosiphon pisum larva (weighing 1.00 - 1.50 mg.) per day.

10. The mean wet weight of A. pisum consumed during larval development was 7.9 mg. Overwintered adult females consumed an average of 0.63 mg. per day. It is estimated that the amount of food required by this species in a lifetime is about 40 mg. of A. pisum.

11. Gross efficiency of food conversion by A. nemorum larvae ranged between 12 and 30 per cent when fed on different prey. This large variation is probably due chiefly to differences in water content of the prey. Efficiency was highest in the third instar and lowest in the fifth instar.

12. The suitability of a series of prey insects, graded according to Growth Rate Indices $\left(\frac{\text{Adult weight}}{\text{days to maturity}}\right)$, differed for each species of Anthocoris. It was shown by this method that psyllids were significantly better prey than aphids for all Anthocoris that are associated with psyllids under natural conditions. All species could be successfully reared on insects other than their natural prey; for example, a diet of Psylla mali was suitable for all species although only A. nemorum and A. nemoralis breed on Malus. Thus, it is apparent that larval food requirements are not the only factor that limit the host plant range of some Anthocoris.

13. Some data are presented which indicate that the food requirements of newly-emerged adults are more critical than those of the larvae. The availability of preferred prey for the former may determine whether a second generation of larvae is produced during the summer.

14. The mechanism of host plant selection may be olfactory attraction to the plant and/or oviposition preference. Evidence that these factors are operative in Anthocoris was demonstrated by showing that A. nemorum responds to the scent of Salix catkins, and that A. minki and A. confusus exhibit preferences in the choice of oviposition sites.

## SUGGESTIONS FOR FUTURE WORK.

It is realised that some aspects of the life histories of Anthocoris in relation to feeding habits, food requirements, and host plant preference, have not been sufficiently investigated. Some of these studies are seasonal in nature, while others were too involved to be attempted at this time. In other instances the implications of the results were simply not realised in time to be investigated. The following subjects warrant further study to provide information on the interrelations between predators and prey, and between predators and their host plants.

1. Searching behaviour of Anthocoris. Information is required on the mode of perception of prey and factors influencing acceptance or rejection of prey under field conditions.

2. Olfactometer experiments. Chemoreception is probably a factor in the attraction of Anthocoris to preferred host plants. In order to investigate this aspect, experiments should be conducted when the bugs are in a dispersive phase. The most likely chance of determining a response would be to test overwintered adults when they are normally moving to the host plants.

3. Oviposition preference. The selection of a particular plant or part of a plant may have an important bearing on the choice of host plants by Anthocoris. In designing the experiments it would be necessary to exclude the possibility that females were responding to the presence of preferred prey. A suggested method would be to feed the females until they began ovipositing, then provide a choice of plants that were free of prey.

4. Pre-hibernation physiology. This would involve a study of the factors that initiate diapause and also the feeding behaviour and food consumption

of adults during late summer and autumn.

5. Factors affecting egg production by reared females. Before the nutritional requirements for oviposition can be ascertained it is necessary to understand other factors that influence oviposition. It is particularly important to establish: (a) whether larval feeding affects the potency of males; (b) how soon after emergence that mating can take place; (c) whether females of some species require a flight before mating.

6. Gross efficiency of food consumption. Further studies are required on the efficiency of different species of Anthocoris and the effects of different prey. The dry weight of food consumed should be determined so that comparisons between prey would have more meaning.

7. Feeding on honeydew. It has been shown that honeydew does not provide an adequate diet for growth. However, it would be interesting to determine whether under natural conditions it is a supplementary food to animal prey, and, if so, by how much does this reduce the requirements for animal prey.

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## APPENDIX 1.

Relative abundance of the major potential prey for *Anthocoris* on various host plants, 1959 and 1960.

*Urtica*, 1960. *Microlophium evansi* (Theobald) present in late March, abundant from April to mid-July; stunted the plants in May.

*Trioza urticae* (L.), present in small numbers all season.

*Ulmus*, 1959 and 1960, Jassids, (*Alebra*, *Ribauntiana*, and *Edwardsiana*) abundant from May to September.

*Eriosoma ulmi* (L.) very rare in 1959; common from mid-May to late June in 1960.

*Malus*, 1959 and 1960. *Psylla mali* Schmidt, abundant as larvae from early April to end of May; adults abundant until September.

*Rhopalosiphum insertum* (Walker), present from early April to end of May, and then from mid-September to end of season.

Jassids, (*Empoasca flaviscens* F.), red spider, *Panonychus ulmi* (Koch), and rosy apple aphid, *Dysaphis mali* (Buckt.) present but not common.

*Salix*, 1959 and 1960. Psyllids, *Psylla pulchra** and *Trioza albiventris* (Foerster), common as larvae from mid-March to early May; adults present in small numbers throughout the season.

Aphids, in general not common on the trees sampled. *Tranaphis capreae* Koch and *Cavariella archangelicae* (Scop.) were the most important aphid species.

Jassids (*Empoasca*, *Typhlocyba*, *Kybos*, *Edwardsiana* and *Idiocerus*) common throughout the autumn.

Thrips and lepidopterous larvae common when catkins were in flower.

* *P. pulchra* (Zett.) (= *nigrita* auctt. Brit.)

Fraxinus, 1960. Psyllopsis fraxinicola (Foerster) abundant as larvae from end of April to mid-June; adult present for the remainder of the season.

Sarothamnus, Psyllids, Psylla spartiophilus Foerster and Arytaina genistae Latr. abundant as larvae from late March to early June in both years. Second generation larvae of A. genistae prevalent in July and August, 1959, but less common in 1960. Acyrthosiphon spartii Koch very abundant from April to June, and declining in July of both years.

Crataegus, 1959 and 1960. Psyllids, (Psylla melanoneura (Foerster) and P. peregrina (Foerster) common as larvae from mid-April to early June; adults fairly common in late March and April and from June to end of season.

Aphids (chiefly Ovatus crataegarius (Walker) and Eriosoma lanigerum (Hausm.)) present, but not common from April to September.

Psocids and leafhoppers (Erythroneura, Edwardsiana, and Empoasca) common from June to end of season.

Tilia. Eucallipterus tiliae (L.) present in mid-April, abundant from June to mid-July, 1959, and present until October. In 1960, common in May and June but decreasing in July and remaining at low level until end of the season.

Psocids common, and leafhoppers (Pediopsis, Alebra and Edwardsiana ) present, from June to September in both years.

Acer, 1959 and 1960. Drephanosiphon platanoides (Schrk.) abundant from May to July and still numerous in late September. Periphyllus testudinatus (Thornton) present in smaller numbers.

Psocids, and jassids (Alebra, Neophilanus and Edwardsiana) common in August and September.

Fagus, Phyllaphis faqi (L.) present in early June and common from mid-June to late July in 1959. In 1960, present in mid-May, very abundant in June and early July and declining to rare by early August. Jassids, especially Typhlocyba cruenta H. & S., and psocids common from June to September in both years.

Quercus, 1959 and 1960. Tubercoloides annulatus (Hart.) present in mid-May and reaching a peak in early July. Common in both years but more numerous in 1960 than in 1959. Present in low numbers from August to October.

Jassids (Typhlocyba, Alebra, Eurhadina and Edwardsiana) common from June to September.

Psocids abundant, especially during August and September.

Betula, 1959. Euceraphis betulae (L.) abundant from April to September.

Jassids (Oncopsis and Kybos) common from April to September.